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

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

Keywords: Demography; Capture-mark-recapture; Density-dependence; *Chelonia mydas*; Juveniles; Caribbean

1. Introduction

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

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

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

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

Juvenile green turtles recruiting in coastal waters of Martinique, French West Indies, originate from various Caribbean and Atlantic nesting sites (Chambault et al., 2018). There they spend several years, feeding on seagrass beds located in shallow sheltered bays. Once they reach a size close to sexual maturity, i.e. at around 80 cm curved carapace length (CCL), they embark on a major post-developmental migration, and they join Caribbean and Atlantic adult feeding grounds (Chambault et al., 2018). During their developmental phase in Martinique, juvenile green turtles show high fidelity to highly touristic areas (Siegwalt et al., 2020) making them vulnerable to local anthropic pressures such as bycatch and boat collision (Louis-Jean et al., 2008; Siegwalt et al., 2020). Moreover, coastal pollution might also enhance disease risk in green turtles, especially the development of fibropapillomatosis (Jones et al., 2016), a deadly neoplastic disease that has been observed in the green turtle population on the coast of Martinique (Bonola et al., 2019; Roost et al., 2022). Additionally, turtles face native seagrass meadows depletion by boat anchoring and exotic species invasion (Siegwalt et al., 2022). Green turtles primarily graze on seagrass beds composed of varying proportions of three marine phanerogams species: the turtle grass *Thalassia testudinum*, the manatee grass *Syringodium filiforme*, and the exotic *Halophila stipulacea* originating from the Red Sea. This last seagrass species was first documented in coastal waters of Martinique in 2006 (Maréchal et al., 2013)

and is currently the most widespread phanerogams in Martinique, but it has the lowest nutritional value (Siegwalt et al., 2022). Among listed anthropogenic factors, *H. stipulacea* invasion and native seagrasses loss may be the main candidates to affect demography of juvenile green turtles since they could both have an impact on their fitness (Siegwalt et al., 2022). Considering the important contribution of Martinique juvenile green turtle population to the Atlantic breeder stock (Chambault et al., 2018) and the numerous threats they face, it is necessary to assess their demographic parameters to ensure their conservation.

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

2. Material and Methods

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

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

Between 2013 and 2023, at the exception of 2014 and 2021, primary capture sessions have taken place yearly for one-week periods (Fig. A2). They occurred typically in the month of

October excepted for 2013 (September), 2015 (additional session in June), 2022 and 2023 (February). These yearly sessions were complemented by multiple irregular capture sessions of less than one day occurring throughout the year, with the exception of 2014, when no such short capture sessions took place (Fig. A2). During these capture sessions, immature green turtles were captured by free-divers at maximum depths of 25 m and lifted on a boat to carry out all the following protocols. Animals were identified by a Passive Integrated Transponder (ID-100, TROVAN). Capture and tagging procedures are described in Bonola et al. (2019). Carapace dimensions, including central curved carapace length (CCL), were measured using a flexible fiber glass tape at 0.1 cm precision (see Bonola et al., 2019 for details). Fibropapillomatosis tumors (if present) on the body of turtles were photographed next to a metal ruler. These photographs were later used to count and measure the tumors during animal data post-processing. Body condition of the animals was estimated visually with carapace and plastron concavity and carapace shape (Bonola et al., 2019). Flipper tissue, scale, claw and blood samplings were performed when animal (stress, health) and environmental (waves) conditions allowed them.

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

2.2. Data analysis

We considered a total of 412 marked individual green turtles captured between September 2013 to February 2023. The green turtle is a long-lived species with an expected high survival rate

and they experience little environmental seasonality in Martinique. Consequently, the data from primary and punctual capture sessions between June of year i and February of year $i+1$ were grouped on October of year i . For instance, February 2023 is grouped with October 2022 and analysis were then performed between 2013 and 2022. If an individual was captured multiple time among grouped capture sessions, only the first capture was retained for the analysis.

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

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

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

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

2.3. Structural parameter estimates

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

2.4. Abundance, density, recruitment and trends

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

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

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

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

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

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

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

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

3. Results

3.1. Site prospection and captured turtles

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

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

3.2. Goodness of Fit results and model selection

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

3.3. Structural parameter estimates

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

The modeled recapture probabilities p accounting for turbidity and sampling effort varied among years and sites. Specifically, p ranged from 0.32 (HPDI_{95%}: 0.24 – 0.39) to 0.56 (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 – 0.51) for ABAC.

3.4. Derived parameter estimates

In SC1, there were between 6.9 (HPDI_{95%}: 0.1 – 17.7) and 44.2 (HPDI_{95%}: 26.6 – 62.5) individuals that settled yearly in each bay. For SC2 and SC3, yearly number of new entrants 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) to 4.8 (HPDI_{95%}: 1.5 – 8.9) respectively (Fig.1, details in Table C1).

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

3.5. Trends in annual abundance and annual recruitment

Trend analysis revealed that the green turtle population increased in GA at a rate of 9.99% per year ($p = 0.018$), largely driven by SC1 abundance growth (22.96% per year, $p = 0.01$, Table C3). At ABAC, green turtle abundance remained stable throughout the study ($p = 0.092$) despite an increase of SC1 turtle abundance of 14.08% per year ($p = 0.004$, Table C3). No significant

trend was detected for SC2 and SC3 abundance, nor for the yearly number of new entrants ($p > 0.05$, Table C3).

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

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

Most of the recruitment occurred in SC1 (Fig.1) while most of the emigration occurred in SC3. Thus, state-specific correlation tests were only performed on SC1 for recruitment E_i and on SC3 for apparent survival ϕ_i (Fig.2). Relationship between ϕ_i and D_i was stronger in ABAC (-0.84, HPDI_{95%}: -0.97 – -0.61, Fig. D1) than GA (-0.49, HPDI_{95%}: -0.78 – -0.02, Fig. D1). The relationship between E_i and D_i was only significant in GA (-0.39, HPDI_{95%}: -0.66 – -0.04, Fig. 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%}: 0.57 – 0.96, Fig. D1) and ABAC (0.61, HPDI_{95%}: 0.24 – 0.88, Fig. D1).

4. Discussion

Using wild-derived CMR data, this study provides key demographic results for a long-term investigation focusing on immature green turtle population dynamics in the Lesser Antilles. Importantly, we provide data on recruitment rates of juveniles at their foraging grounds, a key component of the population dynamics of this endangered reptile. Altogether, these findings will help to better understand the internal and external factors influencing the recruitment and emigration in and from the juvenile aggregations on the Martinique coasts, therefore providing a solid basis to support their conservation.

4.1. Dynamics of juvenile green turtle aggregations in Martinique

Apparent survival did not differ between Anse du Bourg d'Arlet/Chaudière (ABAC) and Grande Anse d'Arlet (GA) despite a higher prevalence of fibropapillomatosis in ABAC (Roost et al., 2022), suggesting that there is no effect of the disease on survival as observed in Patrício et al. (2011). Nonetheless, further studies should consider fibropapillomatosis severity in order to assess its impacts on green turtles. High apparent survival (ϕ) were estimated for SC1 (0.95, HPDI_{95%}: 0.90 – 0.99, 25 cm \leq CCL < 59 cm) and SC2 (0.84, HPDI_{95%}: 0.76 – 0.91, 59cm < CCL < 73cm). These estimates align closely with apparent survival rates reported for similarly sized turtles in Puerto Rico (0.83, CI_{95%} : 0.79 – 0.87; Patrício et al., 2011) and the southern Great Barrier Reef (0.88, CI_{95%} : 0.84 – 0.93; Chaloupka and Limpus, 2005). Moreover, true survival rates of the first 3 turtle cohort classes in the Bahamas (0.89; Bjorndal et al., 2003) were also similar. Conversely, ϕ estimates of ABAC and GA are higher than true survival estimated in Baja California (0.58, CI_{95%} : 0.36 – 0.78; Seminoff et al., 2003) where predation, and mostly poaching, are observed. This suggests low mortality rate and limited emigration of small turtles from ABAC and GA, probably due to the absence of poaching and natural predators (e.g. sharks). Considering that true survival increases with sea turtle age (Chaloupka and Limpus, 2005), difference in apparent survival observed between SC1/SC2 and SC3 could then be attributed to definitive emigration expected at large sizes. Indeed, the post-developmental migration of individuals over 78.5 cm CCL in the juvenile foraging ground of Martinique (Chambault et al., 2018) is thought to be the responsible for a lower apparent survival, as suggested by other CMR studies on immature green turtles (Bjorndal et al., 2003; Kameda et al., 2023; Patrício et al., 2011). Considering the structure of the model used in this study, apparent survival variations presented here seem therefore to be a proxy of emigration variations.

Settlement of new individuals predominantly took place in SC1. However, there were occasional instances of settlement of turtles belonging to SC3. These arrivals could originate from sites in Martinique not covered by this study or from feeding grounds on other islands. Earlier emigration of juvenile turtles at smaller sizes than expected has been observed under unfavorable environmental conditions, as reported in green turtles by Meylan et al. (2022) and Pillans et al. (2021). This behavior has been linked to turtles that exhibit slower growth rates in the Bahamas, potentially indicating an adaptive strategy to optimize their development by relocating to other feeding grounds offering more abundant or higher-quality resources (Bjorndal et al., 2019). Settlement of new large individuals, as well as the presence of resident turtles from 27 cm up to 100 cm CCL (Fig A4), demonstrate that the two sites studied are currently able to support the entire developmental stage of juvenile green turtles in the area.

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

4.2. Effect of density on juvenile green turtle population dynamics

Drivers of variations of demographic parameters could be multiple, especially those affecting emigration, as this parameter is highly sensitive to local environmental factors (Mollenhauer et

al., 2022; Pillans et al., 2021). Our analysis showed that the local density influenced negatively the apparent survival in large turtles (SC3, Fig.2). The most likely explanation is an effect of density on the probability of emigration, as discussed earlier, with a more pronounced effect observed in ABAC (Fig.2). Consequently, our results suggest that dispersal in older juveniles could be triggered by high densities, a phenomena commonly observed in population dynamics (Harman et al., 2020). In parallel, yearly recruited number of small turtles seems to have low density-dependence. This difference of sensitivity to density between small and large turtles suggests that the carrying capacity of the environment could be size-dependent. Indeed, green turtles exhibit size-specific diet and habitat use in juvenile foraging grounds (Bjørndal, 1980; Madeira et al., 2022). In Martinique, large turtles consume *T. testudinum* and *S. filiforme* (Siegwalt, 2021) which are less digestible resources (Siegwalt et al., 2022) while new recruits mainly consume highly digestible resources such as *H. stipulacea* and macroalgae (Siegwalt et al., 2021, 2022).

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

In contrast, it appears that the density of large turtles is approaching the maximum number that the environment can support. This maximum capacity is strongly linked to the health of the seagrass beds (Williams, 1988). In Martinique, native seagrass meadows face pressures from recreational boat anchoring and from eutrophication (Roost et al., 2022; Siegwalt et al., 2022). The rapid growth of *H. stipulacea* enables this species to colonize disturbed patches of sand (e.g. those cleared by anchors), and to outcompete native species such as *S. filiforme* and *T.*

testudinum (Smulders et al., 2017). Moreover, under eutrophic conditions, *H. stipulacea* tends to form dense meadows, thus preventing the development of native seagrass species (Van Tussenbroek et al., 2016). The decreasing availability of native seagrass meadows, which are preferred by large turtles, results in an increased density of turtles on these native patches (Siegwalt et al., 2022). Native seagrasses are consequently more likely to suffer from overgrazing, exacerbating the decline of their available biomass (Gangal et al., 2021) and associated density-dependent mechanisms. This reduction in the surface area and the scarcity of remaining native patches could lead to several interconnected consequences. Large turtles may need to expend more energy to locate suitable food sources (Meylan et al., 2022) and may be exposed to increased competition for food.

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

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

4.3. Conservation implications

High pressures observed on seagrass meadows may lead to anticipate negative impact on the structure of juvenile green turtle populations. Given the significant role played by the juvenile green turtle population of Martinique in supporting the Atlantic breeder population (Chambault et al., 2018), it is imperative to preserve favorable environmental conditions to ensure the viability of the entire Atlantic green turtle regional population. Conservation measures may need to focus on preventing native seagrass depletion and invasive seagrass expansion and on factors associated with these biotic changes. For instance, damages promoted by boat anchors and classic mooring could be avoided by the installation of sustainable mooring in foraging areas of green turtles (Luff et al., 2019). Moreover, sources of pollution should be identified and measures limiting pollutants emission in coastal waters should be implemented. The protection of the last areas of native seagrass is therefore a priority that must be implemented as quickly as possible, even if it is not enough to stop their disappearance (Siegwalt et al., 2022). Seagrass restoration may be a complementary long-term solution to consider, specifically in the Caribbean (Thorhaug et al. 2020). Complementary monitoring studies will be essential to understand seagrass bed dynamics under anthropic pressures and to assess the effectiveness of restoration measures in improving the demography of green turtles and the overall health of these critical ecosystems. Foraging habitat health is critical for the demography of megaherbivore in general and pastures conservation measures have been similarly proposed for land herbivores, since their abundance is affected by grassland and savannah degradation (Lima et al., 2018).

5. Conclusion and perspectives

We provided results supporting the hypothesis that seagrass beds changes could 1) alter the structure of juvenile green turtle aggregations and 2) hinder the capacity of Martinique foraging

grounds to support the entire juvenile life-stage. Considering the worldwide decline of seagrass beds, results and conservation measures outlined in this study could prove highly valuable in the management of other green turtle developmental grounds. Moreover, these measures could benefit other species, also threatened by seagrass bed depletion (e.g. manatees, fishes, birds).

Estimating both recruitment, abundance, survival and emigration of juvenile sea turtle aggregations represents a critical step to fill the knowledge gaps regarding this crucial life-stage (Wildermann et al., 2018). This is paramount given the vast geographical range of sea turtle life cycles and their vulnerability to anthropogenic threats in each of their life-stages, underscoring the necessity for conservation measures that transcend regions and life-stages. To further advance our knowledge and conservation efforts, future studies should consider the following objectives: (1) Quantify the presence of pollutant in the coastal environment and their effect on seagrass bed depletion. (2) Extend the knowledge about juvenile demography by exploring somatic growth rate in function of habitat/food quality and turtles diet; this could be useful to determine time of residency of turtles in the foraging grounds and to investigate potential density-dependent effects on growth rates. (3) Pursue the juvenile green turtle demography monitoring with yearly CMR sessions in Martinique, mainly focused on ABAC and GA, to enable the detection of decline in abundance or survival rates, and facilitate the assessment of the effectiveness of local conservation measures. (4) Extend the investigations to related nesting rookeries (e.g. French Guiana) to establish connections between the demography of the different life-stages and develop efficient regional conservation measures that encompass the entire range of sea turtle habitats.

7. Conflict of interest

The authors declare no conflict of interest.

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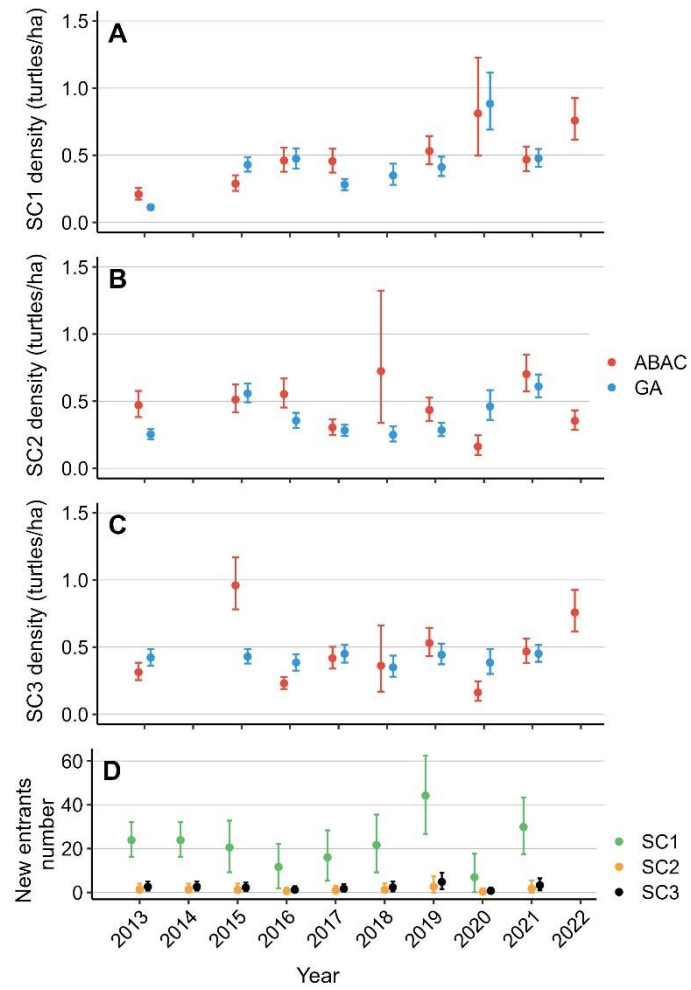


Fig.1: Annual green turtle density in GA (blue dots) and ABAC (red dots) for (A) size-class 1, (B) size-class 2 and (C) size-class 3 and (D) size-class-specific number of new entrants with HPDI_{95%} from the best model.

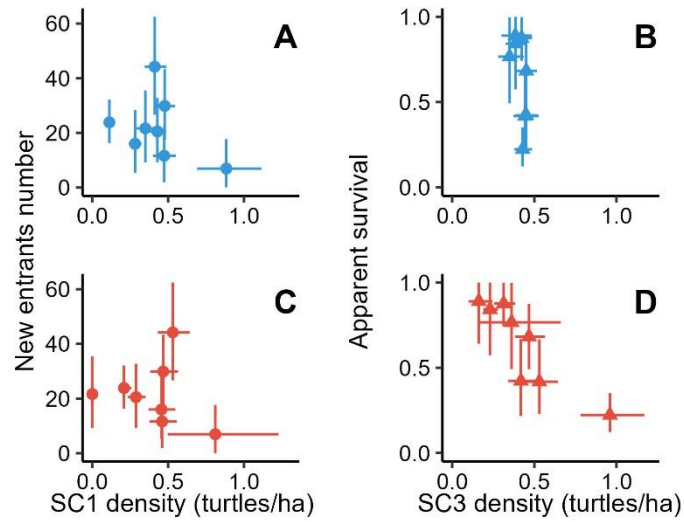


Fig.2: (A, C) Yearly recruitment in SC1 as function of density of SC1 turtles (dots) and (B, D) apparent survival of SC3 as function of density of SC3 turtles (triangles) for (A, B) Grande Anse d'Arlet (blue) and (C, D) Anse du Bourg d'Arlet/Chaudière (red). Estimates of recruitment, apparent survival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

Supplementary materials

Appendix A: Study sites and dataset characteristics

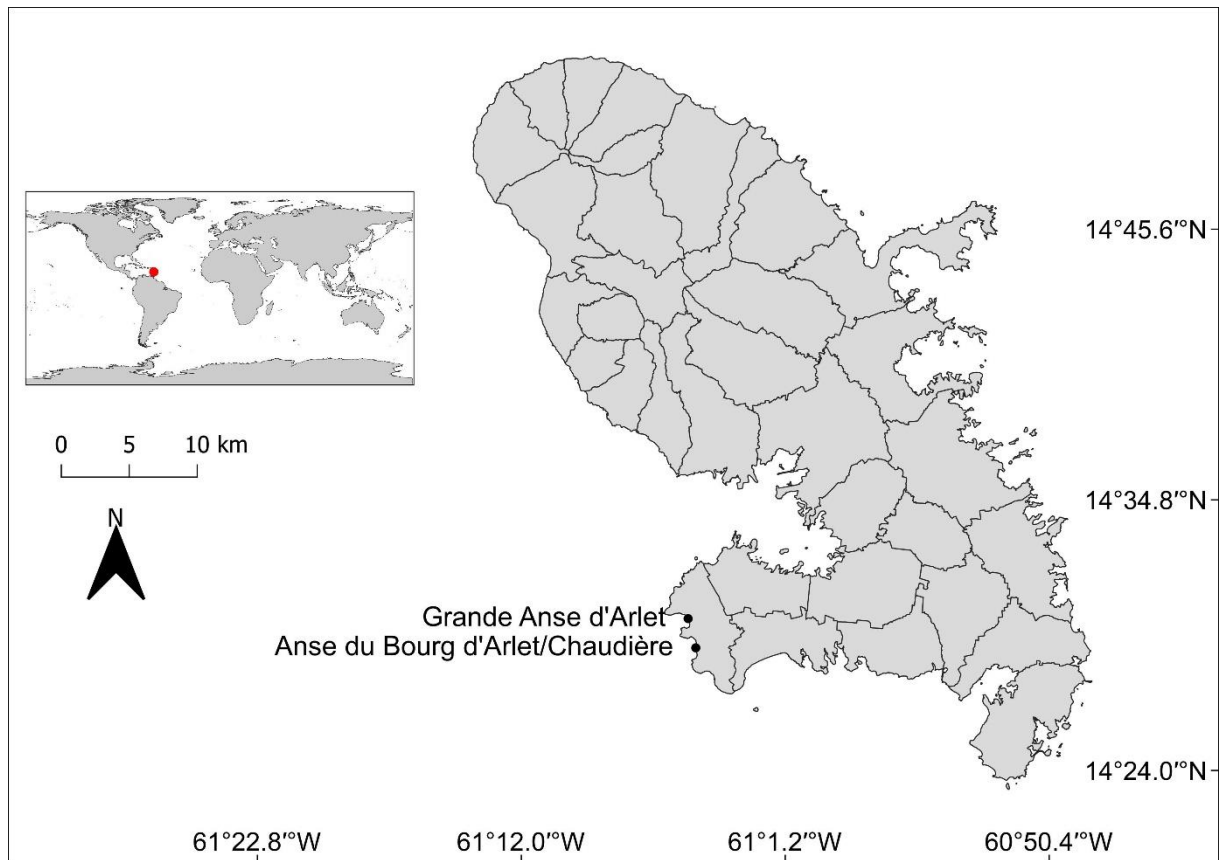


Figure A1: Location of Martinique Island in the world map (red dot) and location of the two sampled sites in Martinique, Grande Anse d'Arlet and Anse du Bourg d'Arlet/Chaudière (black dots).

Supplementary materials

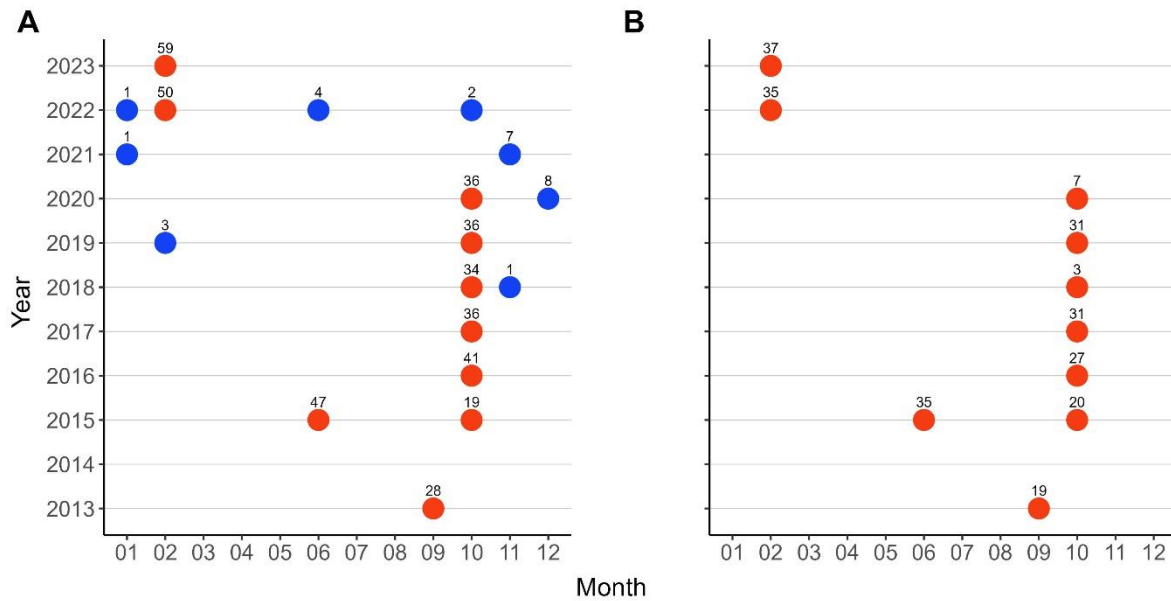


Figure A2: Calendar of capture occasions in (A) Grande Anse d'Arlet and (B) Anse du Bourg d'Arlet/Chaudière between 2013 and 2023. Number of capture per session are indicated above each dot. Primary and irregular sessions are symbolized by red and blue dots respectively.

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

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

Supplementary materials

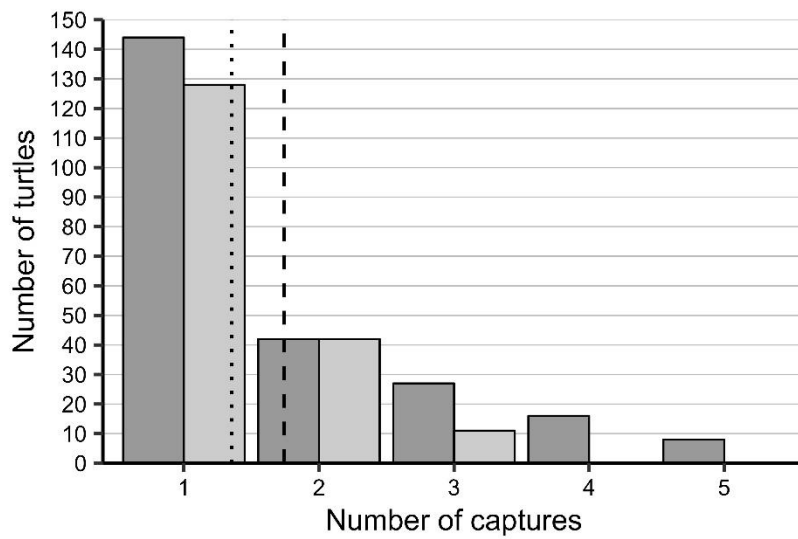


Figure A3: Frequency of individual-specific number of captures on Grande Anse d'Arlet (dark grey) and on Anse du Bourg d'Arlet/Chaudière (light grey). Mean numbers of captures per turtle were represented for Grande Anse d'Arlet (dashed vertical line, 1.74 ± 1.11 captures) and Anse du Bourg d'Arlet/Chaudière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

Supplementary materials

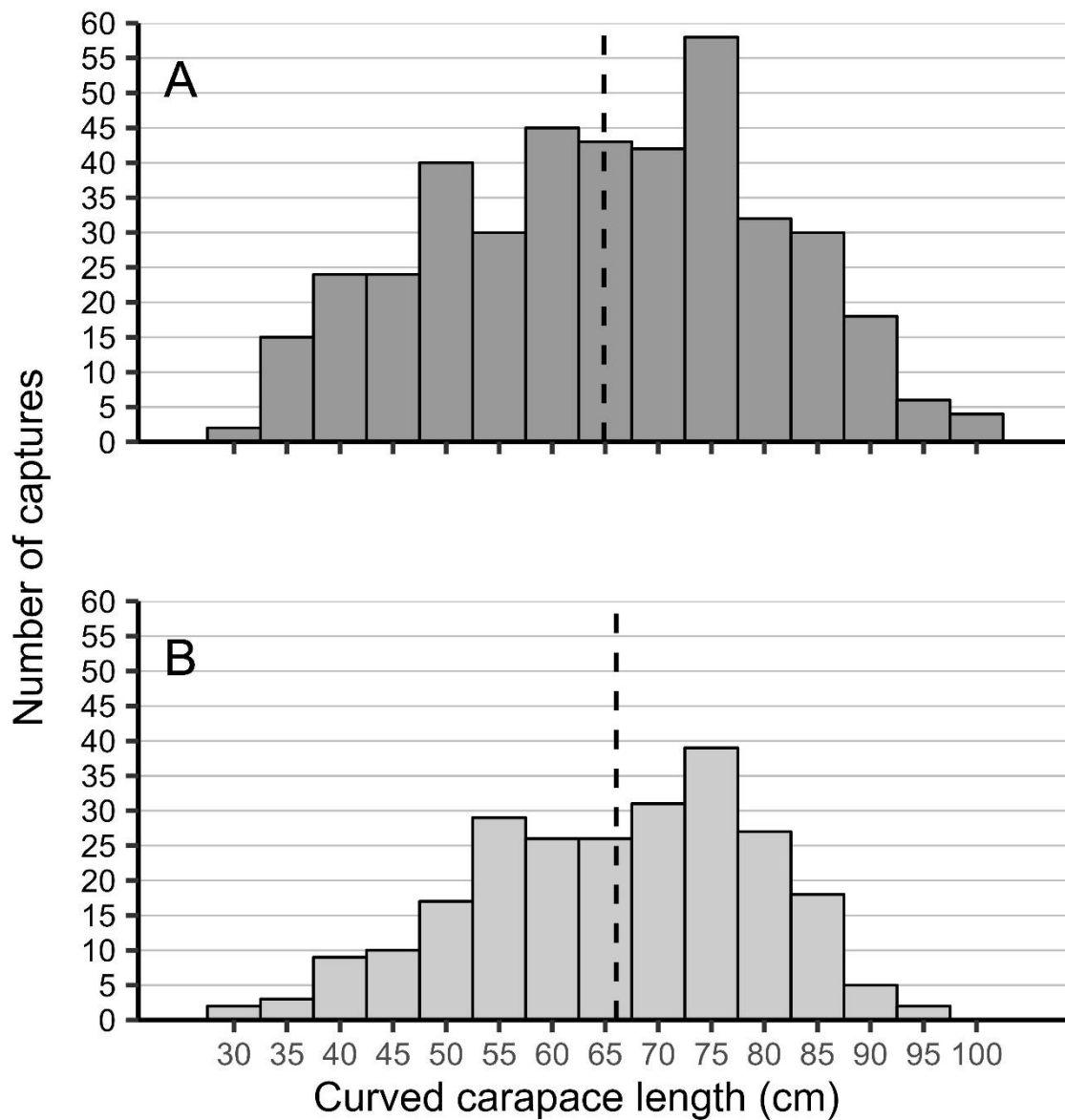


Figure A4: Central curved carapace length (CCL, cm) distribution in Grande Anse d'Arlet (A, dark grey, n=413) and Anse du Bourg d'Arlet/Chaudière (B, light grey, n=245) of captures used by the MSJS model with mean CCL represented by dashed line for each site.

Supplementary materials

Appendix B: Model structure and selection

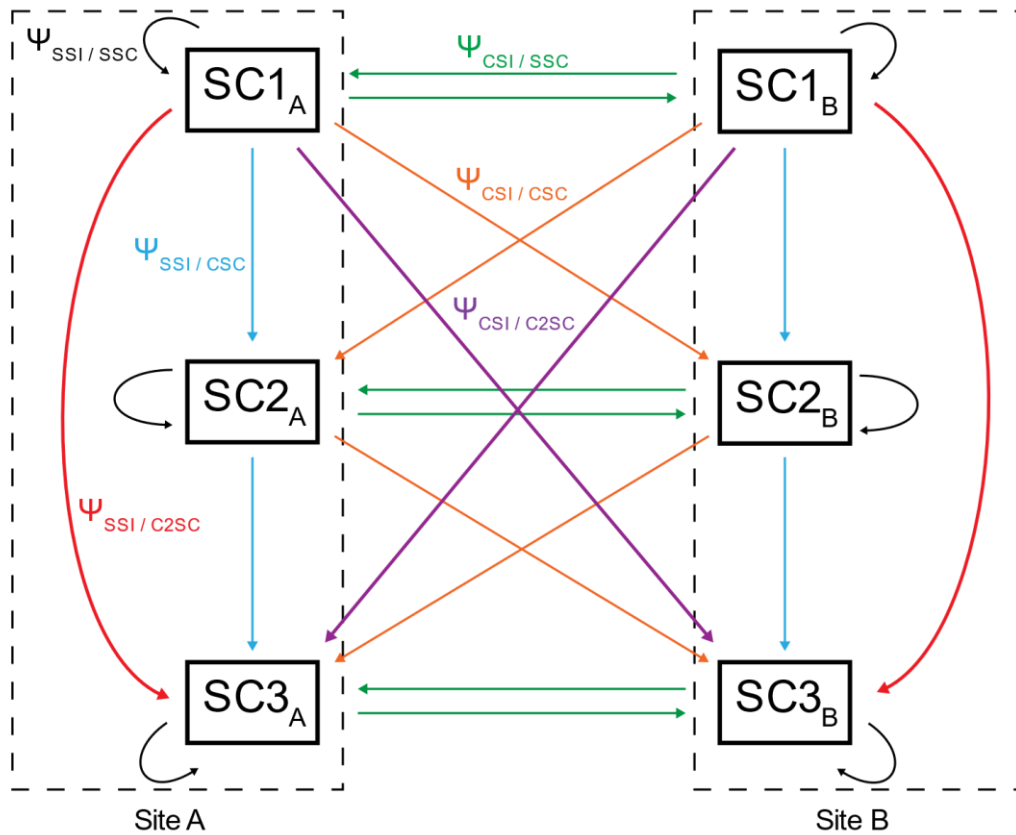


Figure B1: Transitions between three size classes (from the smaller to the larger : SC1, SC2 and SC3) on two sites (Site A and Site B) and associate probabilities Ψ . *SSI/SSC* = Same site/same size class (black), *SSI/CSC* = same site/change size class (blue), *CSI/SSC* = change site/same size class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

Supplementary materials

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
	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
P	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
	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
Φ	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
	16	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St) \pi(St)$	4592.7805	7.3192	31	707.95
$pent$	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

Supplementary materials

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

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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

Supplementary materials

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

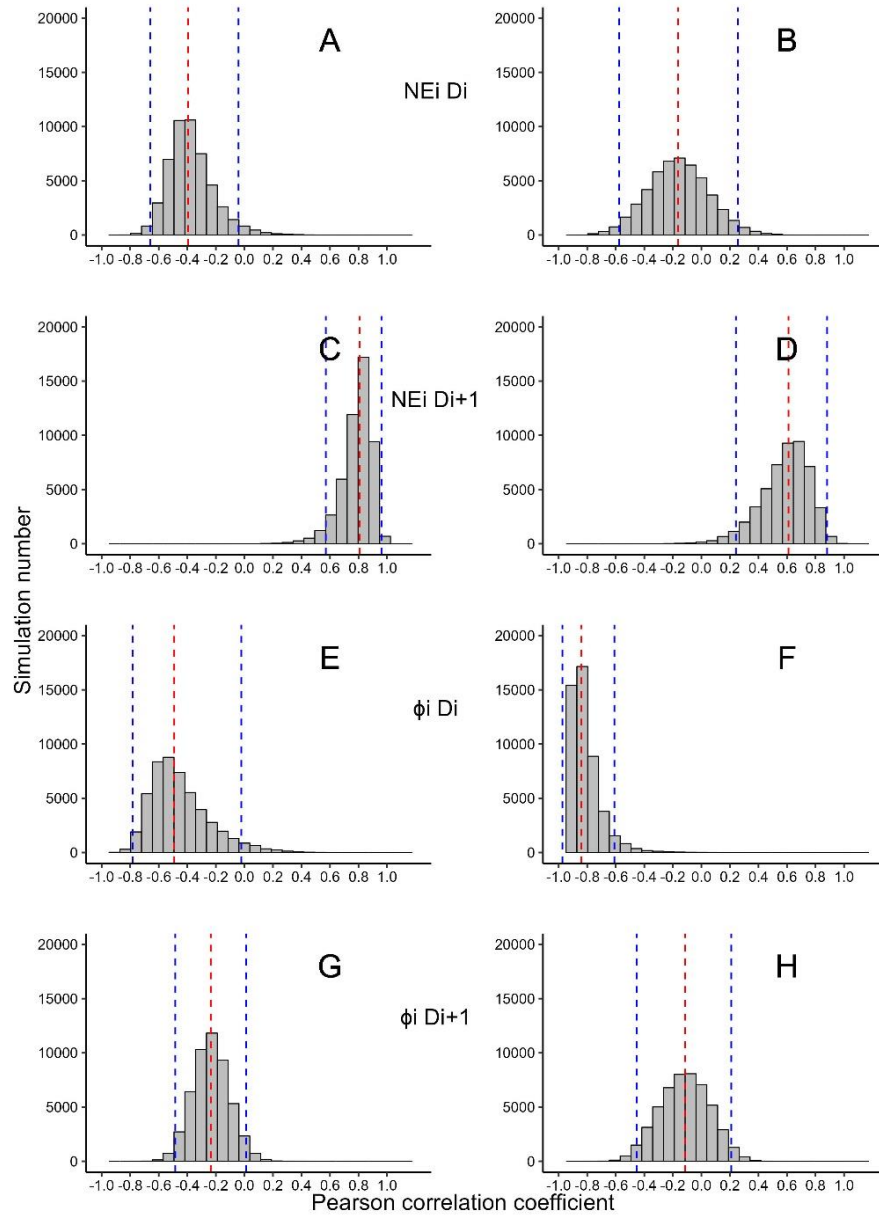


Figure D.1: Posterior distribution with median (dashed red line) and 95% highest posterior distribution interval (dashed blue lines) of Pearson correlation coefficients between : number of new recruit between year i and $i+1$ and density at year i ($NE_i D_i$); number of new recruit between year i and $i+1$ 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.