



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

Pierre Lelong^{a,b,*}, Aurélien Besnard^c, Marc Girondot^d, Caroline Habol^e, Fabienne Priam^f, Mathieu Giraudeau^g, Guillaume Le Loc'h^h, Aurélie Le Loc'hⁱ, Pascal Fournier^j, Christine Fournier-Chambrillon^j, Paco Bustamante^g, Sophie M. Dupont^{a,g}, Orsolya Vincze^g, Jean-Raphaël Gros-Desormeaux^k, Jordan Martin^a, Ouvéa Bourgeois^a, Muriel Lepori^a, Sidney Régis^a, Nicolas Lecerf^a, Fabien Lefebvre^l, Nathalie Aubert^l, Cédric Frouin^a, Frédéric Flora^a, Esteban Pimentel^a, Manon Pimentel^a, Flora Siegwalt^a, Lorène Jeantet^{m,n,o}, Philippine Chambault^{p,q}, Gaëlle Hielard^r, Alexandre Arqué^r, Mosiah Arthus^s, Laurent Louis-Jean^s, Aude Brador^t, Paul Giannasi^t, Denis Etienne^u, Nathaël Lecerf^a, Pascale Chevallier^v, Tao Chevallier^v, Stéphane Meslier^v, Anthony Landreau^v, Myriane Maceno^w, Eugène Larcher^x, Yvon Le Maho^{e,y}, Damien Chevallier^{a,*}

^a BOREA Research Unit, CNRS Borea, Laboratoire de Biologie des Organismes et des Ecosystèmes Aquatiques, MNHN, CNRS 8067, SU, IRD 207, UCN, UA, Campus Martinique, BP-7207, 97275 Schoelcher Cedex, Martinique FWI, France

^b Université des Antilles, Campus de Schoelcher, 97275 Schoelcher Cedex, Martinique, France

^c CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

^d Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique et Evolution, 91190, Gif-sur-Yvette, France

^e Université de Strasbourg, CNRS, IPHC UMR 7178, 23 rue Becquerel, 67000 Strasbourg, France

^f Groupe de Recherche BIOSPHERES, Université des Antilles, Campus de Schoelcher, 97275 Schoelcher Cedex, Martinique, France

^g Littoral, Environnement et Sociétés (LIENSs), UMR7266, CNRS Université de La Rochelle, 2 rue Olympe de Gouges, 17042 La Rochelle Cedex, France

^h IHAP, Université de Toulouse, INRAE, ENVT, Toulouse, France

ⁱ Laboratoire NAC&CO, 29 chemin de Bordeblanche, 31100 Toulouse, France

^j Groupe de Recherche et d'Etude pour la Gestion de l'Environnement, Route de Préchac, 33730 Villandraut, France

^k Laboratoire Caraïben de Sciences Sociales. UMR 8053, LC2S. Université des Antilles, 97275 Schoelcher Cedex, Martinique, France

^l Association ACWAA, rue grand fleur, quartier Epinay, 97228 Sainte-Luce, France

^m African Institute for Mathematical Sciences, 7 Melrose Rd, Muizenberg, Cape Town 7950, South Africa

ⁿ Department of Mathematical Sciences, Stellenbosch University, Victoria Street, 7602, South Africa

^o National Institute for Theoretical and Computational Science, South Africa

^p Greenland Institute of Natural Resources, Strandgade 91, 2, DK-1401 Copenhagen, Denmark

^q Department of Ecology and Evolutionary Biology, The University of California, Santa Cruz, CA, United States

^r Office de l'Eau Martinique, 7 avenue Condorcet, 97200 Fort-de-France, France

^s Parc naturel régional de la Martinique, Maison du Parc, Morne TARTENSON, BP 437, 97200 Fort-de-France, France

^t Office Français de la Biodiversité, Parc naturel marin de Martinique, Rue des Pionniers, 97200 Fort de France, France

^u DEAL Martinique, Pointe de Jaham, 97274 Schoelcher, France

^v ANSLO-S Association naturaliste de soutien logistique à la science, 7 Avenue Georges Clémenceau, 49280 La Tessoualle, France

^w Communauté d'Agglomération de l'Espace Sud, Lotissement des Frangipaniens, 97228 Sainte-Luce, France

^x Mairie des Anses d'Arlet, Boulevard des Arlésiens, 97217 Les Anses-d'Arlet, France

^y Centre Scientifique de Monaco. Principauté de Monaco

ARTICLE INFO

Keywords:
Demography
Capture-mark-recapture

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

* Corresponding author at: Laboratoire de Biologie des Organismes et des Ecosystèmes Aquatiques MNHN, CNRS 8067, SU, IRD 207, UCN, UA, Campus Martinique, BP-7207, 97275 Schoelcher Cedex, Martinique – FWI, France.

E-mail addresses: lelongpierre53@gmail.com (P. Lelong), damiens.chevallier@cns.fr (D. Chevallier).

<https://doi.org/10.1016/j.biocon.2024.110471>

Received 7 November 2023; Received in revised form 17 January 2024; Accepted 20 January 2024

Available online 16 February 2024

0006-3207/© 2024 Elsevier Ltd. All rights reserved.

Density-dependence
Chelonia mydas
 Juveniles
 Caribbean

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.

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 are 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 (Bjorndal 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, 201,710-0005 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 h. 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 ($\text{pent}_{2013} + \text{pent}_{2014}$).

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(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 50,000 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 $N_{i,s}$ and the global annual abundance N_i .

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

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

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 \pm SD: 64.9 \pm 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 \pm SD: 66.0 \pm 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

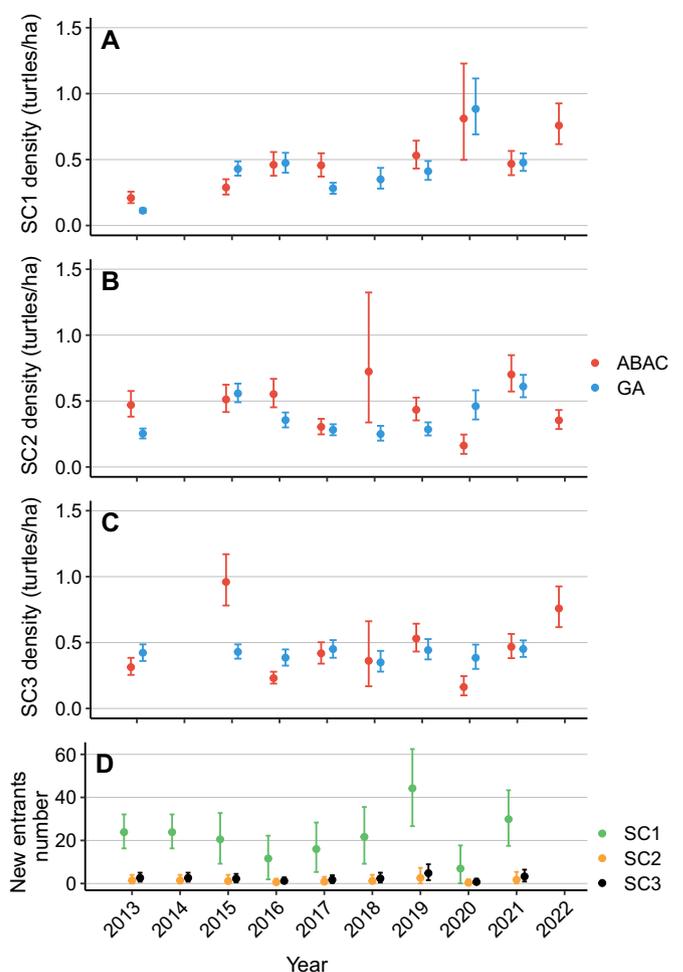


Fig. 1. Annual green turtle density in GA (blue dots) and ABAC (red dots) for (A) size-class 1, (B) size-class 2 and (C) size-class 3 and (D) size-class-specific number of new entrants with HPDI_{95%} from the best model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

($p = 0.092$) 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 to -0.61 , Fig. D1) than GA (-0.49 , HPDI_{95%}: -0.78 to -0.02 , Fig. D1). The relationship between E_i and D_i was only significant in GA (-0.39 , HPDI_{95%}: -0.66 to -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).

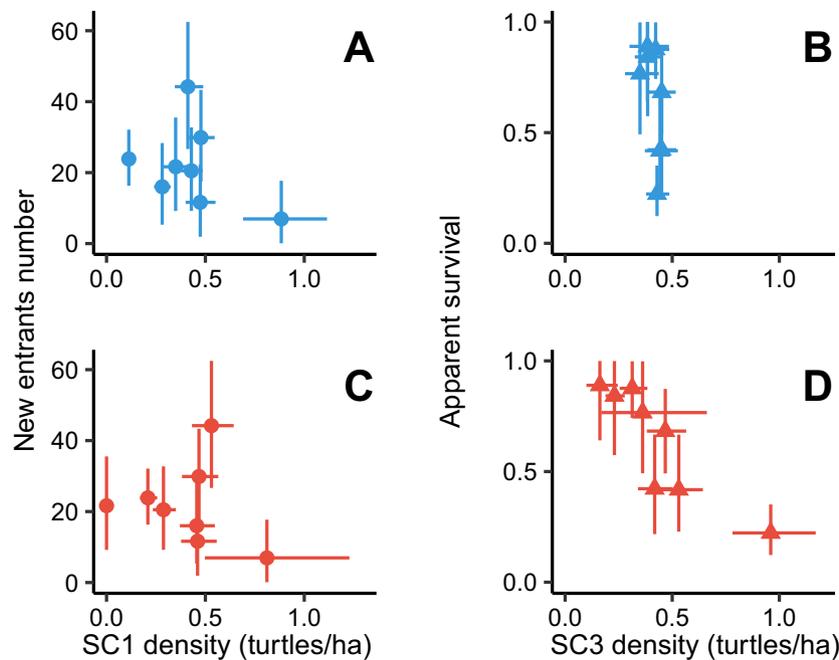


Fig. 2. (A, C) Yearly recruitment in SC1 as function of density of SC1 turtles (dots) and (B, D) apparent survival of SC3 as function of density of SC3 turtles (triangles) for (A, B) Grande Anse d'Arlet (blue) and (C, D) Anse du Bourg d'Arlet/Chaudière (red). Estimates of recruitment, apparent survival and density with HPDI_{95%} were obtained from the best model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 Patricio 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, 59 cm < CCL < 73 cm). These estimates align closely with apparent survival rates reported for similarly sized turtles in Puerto Rico (0.83, CI_{95%}: 0.79–0.87; Patricio 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; Patricio 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, Siegwalt et al., 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 ~60 cm straight or curved carapace length; Bjørndal 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 megaherbivores 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.

CRedit authorship contribution statement

Pierre Lelong: Investigation, Formal analysis, Writing- Original draft preparation, Writing- Reviewing and Editing, **Aurélien Besnard:** Formal analysis, Writing- Original draft preparation, Writing- Reviewing and Editing, **Marc Girondot:** Writing - Review & Editing, **Caroline Habol:** Investigation, Writing - Review & Editing, **Fabienne Priam:** Writing - Review & Editing, **Mathieu Giraudeau:** Writing - Review & Editing, **Guillaume Le Loc'h:** Investigation, Writing - Review & Editing, **Aurélien Le Loc'h:** Investigation, Writing - Review & Editing, **Pascal Fournier:** Investigation, Writing - Review & Editing, **Christine Fournier-Chambrillon:** Investigation, Writing - Review & Editing, **Paco Bustamante:** Investigation, Writing - Review & Editing, **Sophie M. Dupont:** Writing - Review & Editing, **Orsolya Vincze:** Writing - Review & Editing, **Jean-Raphaël Gros-Desormeaux:** Investigation, Writing - Review & Editing, **Jordan Martin:** Investigation, Writing - Review & Editing, **Ouvéa Bourgeois:** Investigation, Writing - Review & Editing, **Muriel Lepori:** Investigation, Writing - Review & Editing, **Sidney Régis:** Investigation, Writing - Review & Editing, **Nicolas Lecerf:** Investigation, Writing - Review & Editing, **Fabien Lefebvre:** Investigation, Writing - Review & Editing, **Nathalie Aubert:** Investigation, Writing - Review & Editing, **Cédric Frouin:** Investigation, Writing - Review & Editing, **Frédéric Flora:** Investigation, Writing - Review & Editing, **Esteban Pimentel:** Investigation, Writing - Review & Editing, **Manon Pimentel:** Investigation, Writing - Review & Editing, **Flora Siegwalt:** Investigation, Writing - Review & Editing, **Lorène Jeantet:** Investigation, Writing - Review & Editing, **Philippine Chambault:** Investigation, Writing - Review & Editing, **Gaëlle Hielard:** Investigation, Writing - Review & Editing, **Alexandre Arqué:** Investigation, Writing - Review & Editing, **Mosiah Arthus:** Investigation, Writing - Review & Editing, **Laurent Louis-Jean:** Investigation, Writing - Review & Editing, **Aude Brador:** Investigation, Writing - Review & Editing, **Paul Giannasi:** Investigation, Writing - Review & Editing, **Denis Etienne:** Investigation, Writing - Review & Editing, **Nathael Lecerf:** Investigation, Writing - Review & Editing, **Pascale Chevallier:** Investigation, Writing - Review & Editing, **Tao Chevallier:** Investigation, Writing - Review & Editing, **Stéphane Meslier:** Investigation, Writing - Review & Editing, **Anthony Landreau:** Investigation, Writing - Review & Editing, **Myriane Maceno:** Investigation, Writing - Review & Editing, **Eugène Larher:** Investigation, Writing - Review & Editing, **Yvon Le Maho:** Investigation, Writing - Review & Editing, **Damien Chevallier:** Conceptualization, Methodology, Data Curation, Project administration, Funding acquisition, Formal Analysis, Investigation, Supervision, Writing- Original draft preparation, Writing - Review & Editing.

Funding

The present study was co-financed by the FEDER Martinique and DEAL Martinique (European Union, Conventions 246239, 2012/DEAL/0010/4-4/31882, 2014/DEAL/0008/4-4/32947 & 2017/164894), ODE Martinique (Conventions 014-03-2015 and 180126), Collectivité Territoriale of Martinique (CTM, 258342) and Office Français de la Biodiversité/Parc Naturel Marin de Martinique (OFB-23-0563). Pierre Lelong's PhD scholarship was supported by the Collectivité Territoriale of Martinique (CTM).

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

Acknowledgements

This study was carried out within the framework of the Plan National d'Action Tortues Marines Antilles. We are grateful to Delphine Machy (DR02, CNRS) who managed the administrative part of the program, and to the numerous volunteers and free divers for their participation in the field operations. We thank the anonymous reviewers for their helpful comments. PB is an honorary member of the IUF (Institut Universitaire de France).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110471>.

References

- Amstrup, S.C., McDonald, T.L., Manly, B.F.J. (Eds.), 2005. *Handbook of Capture-Recapture Analysis*. Princeton University Press, Princeton, N.J.
- Bjorndal, K.A., 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar. Biol.* 56, 147–154. <https://doi.org/10.1007/BF00397131>.
- Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2003. Survival probability estimates for immature green turtles *Chelonia mydas* in the Bahamas. *Mar. Ecol. Prog. Ser.* 252, 273–281. <https://doi.org/10.3354/meps252273>.
- Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2005. Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the greater Caribbean. *Ecol. Appl.* 15, 304–314.
- Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2019. Green turtle somatic growth dynamics: distributional regression reveals effects of differential emigration. *Mar. Ecol. Prog. Ser.* 616, 185–195. <https://doi.org/10.3354/meps12946>.
- Bonola, M., Girondot, M., Robin, J.-P., Martin, J., Siegwalt, F., Jeantet, L., Lelong, P., Grand, C., Chambault, P., Etienne, D., Gresser, J., Hielard, G., Alexandre, A., Régis, S., Nicolas, L., Frouin, C., Lefebvre, F., Sutter, E., Védie, F., Barnerias, C., Laurent, T., Bordes, R., Guimera, C., Aubert, N., Bouaziz, M., Pinson, A., Frédéric, F., Matthieu, D., Benhalilou, A., Céline, M., Mailet, T., Andreani, L., Campistron, G., Sikora, M., Rateau, F., Francis, G., Joffrey, E., Woignier, T., Allenou, J.-P., Louis-Jean, L., Chanteur, B., Béranger, C., Crillon, J., Brador, A., Habol, C., Le Maho, Y., Chevallier, D., 2019. Fine scale geographic residence and annual primary production drive body condition of wild immature green turtles (*Chelonia mydas*) in Martinique Island (Lesser Antilles). *Biol. Open* 8, bio.048058. <https://doi.org/10.1242/bio.048058>.
- Chaloupka, M.Y., Limpus, C., 2001. Trends in the abundance of sea turtles resident in southern great barrier reef waters. *Biol. Conserv.* 102, 235–249. [https://doi.org/10.1016/S0006-3207\(01\)00106-9](https://doi.org/10.1016/S0006-3207(01)00106-9).
- Chaloupka, M.Y., Limpus, C.J., 2005. Estimates of sex- and age-class-specific survival probabilities for a southern great barrier reef green sea turtle population. *Mar. Biol.* 146, 1251–1261. <https://doi.org/10.1007/s00227-004-1512-6>.
- Chambault, P., de Thoisy, B., Huguin, M., Martin, J., Bonola, M., Etienne, D., Gresser, J., Hielard, G., Mailles, J., Védie, F., Barnerias, C., Sutter, E., Guillemot, B., Dumont-Dayot, E., Régis, S., Lecerf, N., Lefebvre, F., Frouin, C., Aubert, N., Guimera, C., Bordes, R., Thieulle, L., Duru, M., Bouaziz, M., Pinson, A., Flora, F., Queneherve, P., Woignier, T., Allenou, J., Cimiterra, N., Benhalilou, A., Murgale, C., Mailet, T., Rangon, L., Chanteux, N., Chanteur, B., Béranger, C., Le Maho, Y., Petit, O., Chevallier, D., 2018. Connecting paths between juvenile and adult habitats in the Atlantic green turtle using genetics and satellite tracking. *Ecol. Evol.* 8, 12790–12802. <https://doi.org/10.1002/ece3.4708>.
- Chevallier, D., Girondot, M., Berzins, R., Chevalier, J., De Thoisy, B., Fretey, J., Kelle, L., Lebreton, J., 2020. Survival and breeding interval of an endangered marine vertebrate, the leatherback turtle *Dermochelys coriacea*, in French Guiana. *Endang. Species. Res.* 41, 153–165. <https://doi.org/10.3354/esr01013>.
- Choquet, R., Lebreton, J.-D., Gimenez, O., Reuboulet, A.-M., Pradel, R., 2009. U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* 32, 1071–1074. <https://doi.org/10.1111/j.1600-0587.2009.05968.x>.
- Colman, L.P., Patrício, A.R.C., McGowan, A., Santos, A.J.B., Marcovaldi, M.Á., Bellini, C., Godley, B.J., 2015. Long-term growth and survival dynamics of green turtles (*Chelonia mydas*) at an isolated tropical archipelago in Brazil. *Mar. Biol.* 162, 111–122. <https://doi.org/10.1007/s00227-014-2585-5>.
- Crowder, L.B., Crouse, D.T., Heppell, S.S., Martin, T.H., 1994. Predicting the impact of turtle excluder devices on Loggerhead Sea turtle populations. *Ecol. Appl.* 4, 437–445. <https://doi.org/10.2307/1941948>.
- Domiciano, I.G., Domit, C., Bracarense, A.P.F.R.L., 2017. The green turtle *Chelonia mydas* as a marine and coastal environmental sentinels: anthropogenic activities and diseases. *SCA* 38, 3417–3434. <https://doi.org/10.5433/1679-0359.2017v38n5p3417>.
- Dupuis, J.A., Schwarz, C.J., 2007. A Bayesian approach to the multistate jolly-Seber capture-recapture model. *Biometrics* 63, 1015–1022. <https://doi.org/10.1111/j.1541-0420.2007.00815.x>.
- Fujiwara, M., Caswell, H., 2001. Demography of the endangered North Atlantic right whale. *Nature* 414, 537–541. <https://doi.org/10.1038/35107054>.

- Gangal, M., Gafoor, A.-B., D'Souza, E., Kelkar, N., Karkarey, R., Marbà, N., Arthur, R., Alcoverro, T., 2021. Sequential overgrazing by green turtles causes archipelago-wide functional extinctions of seagrass meadows. *Biol. Conserv.* 260, 109195 <https://doi.org/10.1016/j.biocon.2021.109195>.
- Girondot, M., Mourrain, B., Chevallier, D., Godfrey, M.H., 2021. Maturity of a giant: age and size reaction norm for sexual maturity for Atlantic leatherback turtles. *Mar. Ecol.* 42 <https://doi.org/10.1111/maec.12631>.
- Harman, R.R., Goddard, J., Shivaji, R., Cronin, J.T., 2020. Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration. *Am. Nat.* 195, 851–867. <https://doi.org/10.1086/708156>.
- Heppell, S.S., Crowder, L.B., Menzel, T.R., 1999. Life Table Analysis of Long-Lived Marine Species with Implications for Conservation and Management, in: Musick, J.A. (Ed.), *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals: Proceedings of the Symposium Conservation of Long-Lived Marine Animals Held at Monterey, California, USA 24 August 1997*. American Fisheries Society Symposium, pp. 137–148.
- Jeantet, L., Planas-Bielsa, V., Benhamou, S., Geiger, S., Martin, J., Siegwalt, F., Lelong, P., Gresser, J., Etienne, D., Hielard, G., Arque, A., Régis, S., Lecerf, N., Frouin, C., Benhalilou, A., Murgale, C., Mailliet, T., Andreani, L., Campistron, G., Delvaux, H., Guyon, C., Richard, S., Lefebvre, F., Aubert, N., Hahold, C., le Maho, Y., Chevallier, D., 2020. Behavioural inference from signal processing using animal-borne multi-sensor loggers: a novel solution to extend the knowledge of sea turtle ecology. *R. Soc. Open Sci.* 7, 200139 <https://doi.org/10.1098/rsos.200139>.
- Jones, K., Ariel, E., Burgess, G., Read, M., 2016. A review of fibropapillomatosis in green turtles (*Chelonia mydas*). *Vet. J.* 212, 48–57. <https://doi.org/10.1016/j.tvjl.2015.10.041>.
- Kameda, K., Wakatsuki, M., Takase, M., Nakanishi, Y., Kamezaki, N., 2023. Apparent survival probability and abundance of juvenile green turtles in the foraging ground at Kuroshima Island, Ryukyu archipelago. *Endang. Species. Res.* 50, 209–215. <https://doi.org/10.3354/esr01228>.
- Lasala, J.A., Macksey, M.C., Mazzarella, K.T., Main, K.L., Foote, J.J., Tucker, A.D., 2023. Forty years of monitoring increasing sea turtle relative abundance in the Gulf of Mexico. *Sci. Rep.* 13, 17213. <https://doi.org/10.1038/s41598-023-43651-4>.
- Lima, D.O.D., Lorini, M.L., Vieira, M.V., 2018. Conservation of grasslands and savannas: a meta-analysis on mammalian responses to anthropogenic disturbance. *J. Nat. Conserv.* 45, 72–78. <https://doi.org/10.1016/j.jnc.2018.08.008>.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science, New Series* 312, 1806–1809. <https://doi.org/10.1126/science.112803>.
- Louis-Jean, L., Lenfant, P., Galzin, R., Marechal, J.-P., 2008. Crossing Fishery Statistics with Marine Turtle Bycatch Data and Habitat Mapping in Martinique, FWI. Presented at the Proceedings of the 61st Gulf and Caribbean Fisheries Institute. Gosier, Guadeloupe, French West Indies, pp. 375–379.
- Luff, A.L., Sheehan, E.V., Parry, M., Higgs, N.D., 2019. A simple mooring modification reduces impacts on seagrass meadows. *Sci. Rep.* 9, 20062. <https://doi.org/10.1038/s41598-019-55425-y>.
- Lutz, P.L., Musick, J.A., Wyneken, J. (Eds.), 2003. *The Biology of Sea Turtles, Marine Science Series*. CRC Press, Boca Raton, Fla.
- Madeira, F.M., Rebelo, R., Catry, P., Neiva, J., Barbosa, C., Regalla, A., Patrício, A.R., 2022. Fine-scale foraging segregation in a green turtle (*Chelonia mydas*) feeding ground in the Bijagós archipelago. *Guinea Bissau. Front. Mar. Sci.* 9, 984219 <https://doi.org/10.3389/fmars.2022.984219>.
- Maréchal, J.-P., Meesters, E.H., Védie, F., Helliou, C., 2013. Occurrence of the alien seagrass *Halophila stipulacea* in Martinique (French West Indies). *Mar. Biodivers. Rec.* 6, e127 <https://doi.org/10.1017/S1755267213000961>.
- Mazaris, A.D., Schofield, G., Gkazinou, C., Alpanidou, V., Hays, G.C., 2017. Global sea turtle conservation successes. *Sci. Adv.* 3, e1600730 <https://doi.org/10.1126/sciadv.1600730>.
- Meylan, P.A., Hardy, R.F., Gray, J.A., Meylan, A.B., 2022. A half-century of demographic changes in a green turtle (*Chelonia mydas*) foraging aggregation during an era of seagrass decline. *Mar. Biol.* 169, 74. <https://doi.org/10.1007/s00227-022-04056-5>.
- Mollenhauer, R., Lamont, M.M., Foley, A., 2022. Long-term apparent survival of a cold-stunned subpopulation of juvenile green turtles. *Ecosphere* 13. <https://doi.org/10.1002/ecs2.4221>.
- Monadjem, A., Wolter, K., Neser, W., Kane, A., 2014. Effect of rehabilitation on survival rates of endangered cape vultures: effect of rehabilitation on survival of cape vultures. *Anim. Conserv.* 17, 52–60. <https://doi.org/10.1111/acv.12054>.
- Patrício, A.R., Velez-Zuazo, X., Diez, C.E., Van Dam, R., Sabat, A.M., 2011. Survival probability of immature green turtles in two foraging grounds at Culebra, Puerto Rico. *Mar. Ecol. Prog. Ser.* 440, 217–227. <https://doi.org/10.3354/meps09337>.
- Pillars, R.D., Fry, G.C., Haywood, M.D.E., Rochester, W., Limpus, C.J., Patterson, T., Babcock, R.C., 2021. Residency, home range and tidal habitat use of green turtles (*Chelonia mydas*) in port Curtis. *Australia. Mar. Biol.* 168, 88. <https://doi.org/10.1007/s00227-021-03898-9>.
- Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J.S., Albouy, C., Rasher, D.B., Davis, M., Svenning, J.-C., Griffin, J.N., 2020. Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* 6, eaay7650 <https://doi.org/10.1126/sciadv.aay7650>.
- Pinheiro, J., Bates, D., R Core Team, 2022. *Nlme: linear and nonlinear mixed effects models*. R package version 3, 1–158. <https://CRAN.R-project.org/package=nlme>.
- Plummer, M., Best, N., Cowles, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. *R News* 6, 7–11.
- Pradel, R., Wintbert, C.M.A., Gimenez, O., 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* 59, 43–53. <https://doi.org/10.1111/1541-0420.00006>.
- R Core Team, 2022. R: A language and environment for statistical computing.
- Roost, T., Schies, J.-A., Girondot, M., Robin, J.-P., Lelong, P., Martin, J., Siegwalt, F., Jeantet, L., Giraudeau, M., Le Loch, G., Bejarano, M., Bonola, M., Benhalilou, A., Murgale, C., Andreani, L., Jacaria, F., Campistron, G., Lathière, A., Martial, F., Hielard, G., Arqué, A., Régis, S., Lecerf, Nicolas, Frouin, C., Lefebvre, F., Aubert, N., Flora, F., Pimentel, E., Lafolle, R., Thobor, F., Arthus, M., Etienne, D., Lecerf, Nathaël, Allenou, J.-P., Desigaux, F., Larcher, E., Larcher, C., Curto, A.L., Befort, J., Maceno-Panevel, M., Lepori, M., Chevallier, P., Chevallier, T., Meslier, S., Landreau, A., Hahold, C., Le Maho, Y., Chevallier, D., 2022. Fibropapillomatosis prevalence and distribution in immature green turtles (*Chelonia mydas*) in Martinique Island (Lesser Antilles). *EcoHealth* 19, 190–202. <https://doi.org/10.1007/s10393-022-01601-y>.
- Seber, G.A.F., 1982. *The Estimation of Animal Abundance and Related Parameters*, 2nd ed. Griffin, London.
- Seminoff, J.A., 2004. *Chelonia mydas*: The IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T4615A247654386.en>.
- Seminoff, J.A., Jones, T.T., Resendiz, A., Nichols, W.J., Chaloupka, M.Y., 2003. Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices to describe population status. *J. Mar. Biol. Ass.* 83, 1355–1362. <https://doi.org/10.1017/S0025315403008816>.
- Siegwalt, F., 2021. Ecologie trophique de la tortue verte *Chelonia mydas* dans les herbiers marins des Antilles françaises : Rôles et conséquences dans la dynamique des écosystèmes dans un contexte de colonisation par *Halophila stipulacea*. Université de Strasbourg 303p. <https://doi.org/10.13140/RG.2.2.27216.69120>.
- Siegwalt, F., Benhamou, S., Girondot, M., Jeantet, L., Martin, J., Bonola, M., Lelong, P., Grand, C., Chambault, P., Benhalilou, A., Murgale, C., Mailliet, T., Andreani, L., Campistron, G., Jacaria, F., Hielard, G., Arqué, A., Etienne, D., Gresser, J., Régis, S., Lecerf, N., Frouin, C., Lefebvre, F., Aubert, N., Védie, F., Barnerias, C., Thieulle, L., Guimera, C., Bouaziz, M., Pinson, A., Flora, F., George, F., Eggenspieler, J., Woignier, T., Allenou, J.-P., Louis-Jean, L., Chantaur, B., Béranger, C., Crillon, J., Brador, A., Hahold, C., Le Maho, Y., Robin, J.-P., Chevallier, D., 2020. High fidelity of sea turtles to their foraging grounds revealed by satellite tracking and capture-mark-recapture: new insights for the establishment of key marine conservation areas. *Biol. Conserv.* 250, 108742 <https://doi.org/10.1016/j.biocon.2020.108742>.
- Siegwalt, F., Jeantet, L., Lelong, P., Martin, J., Girondot, M., Bustamante, P., Benhalilou, A., Murgale, C., Andreani, L., Jacaria, F., Campistron, G., Lathière, A., Barotin, C., Buret-Rochas, G., Barre, P., Hielard, G., Arqué, A., Régis, S., Lecerf, N., Frouin, C., Lefebvre, F., Aubert, N., Arthus, M., Etienne, D., Allenou, J.-P., Delnatte, C., Lafolle, R., Thobor, F., Chevallier, P., Chevallier, T., Lepori, M., Assio, C., Grand, C., Bonola, M., Tursi, Y., Varkala, P.-W., Meslier, S., Landreau, A., Le Maho, Y., Hahold, C., Robin, J.-P., Chevallier, D., 2022. Food selection and habitat use patterns of immature green turtles (*Chelonia mydas*) on Caribbean seagrass beds dominated by the alien species *Halophila stipulacea*. *Glob. Ecol. Conserv.* 37, e02169 <https://doi.org/10.1016/j.gecco.2022.e02169>.
- Smulders, F.O.H., Vonk, J.A., Engel, M.S., Christianen, M.J.A., 2017. Expansion and fragment settlement of the non-native seagrass *Halophila stipulacea* in a Caribbean bay. *Mar. Biol. Res.* 13, 967–974. <https://doi.org/10.1080/17451000.2017.1333620>.
- Thorhaug, A., Belaire, C., Verduin, J.J., Schwarz, A., Kiswara, W., Prathep, A., Gallagher, J.B., Huang, X.P., Berlyn, G., Yap, T.-K., Dorward, S., 2020. Longevity and sustainability of tropical and subtropical restored seagrass beds among Atlantic, Pacific, and Indian oceans. *Mar. Pollut. Bull.* 160, 111544 <https://doi.org/10.1016/j.marpolbul.2020.111544>.
- Van Tussenbroek, B.I., Van Katwijk, M.M., Bouma, T.J., Van Der Heide, T., Govers, L.L., Leuven, R.S.E.W., 2016. Non-native seagrass *Halophila stipulacea* forms dense mats under eutrophic conditions in the Caribbean. *J. Sea Res.* 115, 1–5. <https://doi.org/10.1016/j.seares.2016.05.005>.
- Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Mortimer, J.A., Seminoff, J.A., Amorcho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Brisenno Duenas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabrino, A., Finkbeiner, E.M., Girard, A., Girondot, M., Hamann, M., Hurley, B.J., López-Mendilaharsu, M., Marcovaldi, M.A., Musick, J.A., Nel, R., Pilcher, N.J., Tröng, S., Witherington, B., Mast, R.B., 2011. Global conservation priorities for marine turtles. *PloS One* 6, e24510. <https://doi.org/10.1371/journal.pone.0024510>.
- Warret Rodrigues, C., Angin, B., Besnard, A., 2021. Favoring recruitment as a conservation strategy to improve the resilience of long-lived reptile populations: insights from a population viability analysis. *Ecol. Evol.* 11, 13068–13080. <https://doi.org/10.1002/ece3.8021>.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139. <https://doi.org/10.1080/00063659909472239>.
- Wildermann, N., Gredzens, C., Avens, L., Barrios-Garrido, H., Bell, I., Blumenthal, J., Bolten, A., Braun McNeill, J., Casale, P., Di Domenico, M., Domit, C., Epperly, S., Godfrey, M., Godley, B., González-Carman, V., Hamann, M., Hart, K., Ishihara, T., Mansfield, K., Metz, T., Miller, J., Pilcher, N., Read, M., Sasso, C., Seminoff, J., Seney, E., Willard, A., Tomás, J., Vélez-Rubio, G., Ware, M., Williams, J., Wyneken, J., Fuentes, M., 2018. Informing research priorities for immature sea turtles through expert elicitation. *Endang. Species. Res.* 37, 55–76. <https://doi.org/10.1038/esr00916>.
- Williams, S.L., 1988. *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Mar. Biol.* 98, 447–455. <https://doi.org/10.1007/BF00391121>.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Academic Press, San Diego.