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Original Contribution

Fibropapillomatosis Dynamics, Severity and Demographic Effect in Caribbean Green Turtles

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Abstract: Habitat degradation induced by human activities can exacerbate the spread of wildlife disease and could hinder the recovery of imperiled species. The endangered green turtle *Chelonia mydas* is impacted worldwide by fibropapillomatosis (FP), a neoplastic infectious disease likely triggered by the *Scutavirus chelonidalpha5* with coastal anthropogenic stressors acting as cofactors in disease development. Here, we studied fibropapillomatosis dynamics and its demographic consequences using an 11-year capture-mark-recapture dataset in Anse du Bourg d'Arlet/Chaudière (ABAC) and Grande Anse d'Arlet (GA), two juvenile green turtle foraging grounds in Martinique, French West Indies. Afflicted turtles had similar mortality and permanent emigration rates to the non-afflicted ones. Fibropapillomatosis was commonly observed in large individuals and disease recovery may take several years. Consequently, permanent emigration before full recovery from the disease is suspected and might affect the developmental migration success. Additionally, the results revealed that the FP had higher prevalence and severity, and progressed two times faster in ABAC than in GA despite the proximity (< 2 km) and the similarity of the two foraging grounds. The reasons for these differences remain unidentified. Locally, further studies should be focused on the determination of the external and internal cofactors related to the observed FP dynamics. Finally, the investigations should be extended at a global regional scale to determine potential deleterious effect of the FP on the adult life-stage. These perspectives improves upon our overall understanding on the interplay between wildlife diseases, hosts and environmental factors.

Keywords: wildlife disease, disease-state model, One Health, juvenile, French West Indies, Martinique

Introduction

The One Health approach considers the health of humans, animals and their environment as interconnected (Xie et al., 2017). Exotic species trade, intensive farming, habitat fragmentation and pollution increase the vulnerability of wildlife species to emerging diseases (Daszak et al., 2000; Aguirre and Tabor, 2008; Brearley et al., 2013; Pesavento et al., 2018), which represent a major threat to both human health and the conservation of biodiversity (Daszak et al., 2000). High mortality rates arising from wildlife diseases can limit the recovery of endangered species (Brand, 2013) as seen with Devil Facial Tumor Disease (Lachish et al., 2007) or *Chytridiomycosis* in amphibian populations (Scheele et al., 2019). In this context, long-term monitoring is therefore essential as it is a key tool for understanding disease dynamics and etiology in wild populations (Barroso et al., 2021).

Fibropapillomatosis (FP) is a disease that affects all seven sea turtle species globally (Jones et al., 2016). It has reached panzootic status in the green turtle (*Chelonia mydas*, Williams et al. 1994), classified as "Endangered" on the IUCN Red List (Seminoff, 2004). Characterized typically by external tumors, FP primarily impacts juvenile green turtles after they settle in coastal foraging grounds (Jones et al., 2016). In the most severe cases, internal tumors on the lungs, heart, kidneys, liver, or gastrointestinal tract have been reported (Herbst, 1994). FP tumors can notably impede movements and feeding activity and may lead to mortality (Herbst, 1994). Moreover, several studies have shown that FP-afflicted green turtles often have altered blood biochemistry (Work et al. 2001; Hirama et al. 2014; Perrault et al. 2017, 2021; da Fonseca et al. 2020; Li and Chang 2020). However, contrasting results have been found related to the effects of FP on growth (negative correlation: Chaloupka and Balazs, 2005; no relationship: Kubis et al., 2009; Patrício et al., 2014) and survival rates (Patrício et al., 2011; Hargrove et al., 2016).

The herpesvirus *Scutavirus chelonidalpha5* (ChHV5) is recognized as the primary etiological agent of FP (Herbst et al., 1995). It can spread through direct contact between individuals (Jones et al., 2020), viral shedding in the water column (Work et al., 2014; Page-Karjian et al., 2015; Page-Karjian et al., 2017; Farrell et al., 2021) or mechanical vectors (Lu et al., 2000; Greenblatt et al., 2004). Nonetheless, the development of

tumors also requires environmental and/or host factors (Jones, 2004; Page-Karjian et al., 2012; Zamana et al., 2021). Indeed, FP is often related to degraded seagrass beds, harmful algal blooms, high sea surface temperature, salinity fluctuations, eutrophication, and coastal water pollution (dos Santos et al. 2010; Van Houtan et al. 2010; Perrault et al. 2017; Jones et al. 2022; Manes et al. 2022; Roost et al. 2022; Oduor et al. 2024). Altered habitat quality may cause stress and immunomodulation in green turtles, which could in turn promote FP development (Sposato et al., 2021). FP prevalence and severity can differ drastically between sites that are separated by only few kilometers as reported in Martinique, French West Indies. Here, the role of local eutrophication and depleted seagrass beds is a suspected cofactor in FP tumor development (Roost et al., 2022; Siegwalt et al., 2022). Immatures green turtles in these areas show high fidelity to their foraging grounds, where they remain several years (Siegwalt et al., 2020). They aggregate in high densities on native seagrass patches (Roost et al., 2022; Siegwalt et al., 2022), and interact physically with conspecifics (Jeantet et al., 2020). High levels of tourism in Martinique may also contribute to pollution of local waters (Burac, 1996) and stress through tourism-based activities (Landry and Taggart, 2010). Environmental conditions and turtles' behavior reported in Martinique may lead turtles to chronic exposure to stressors and may create conditions favorable to the spread and development of FP (Jones et al., 2016; Dujon et al., 2021).

Considering the importance of the juvenile foraging grounds in Martinique for the viability of the Atlantic green turtle population (Chambault et al., 2018), investigating FP dynamics is critical to assess its drivers and its impact on the population demography (Fuentes et al., 2023). The aims of this study, based on a 11 years capture-mark-recapture (CMR) dataset of juvenile green turtles in Martinique, was to (i) assess current FP prevalence estimation, (ii) provide FP development and recovery rate estimations in relation to potential environmental cofactors, (iii) assess FP effects on survival and emigration rates, and (iv) characterize the severity of the disease as the total area covered by tumors on turtles' body.

Material and Methods

Study Sites

The study took place in Les Anses d'Arlet (14°30′9.64″N, 61°5′11.85″W, Martinique, French West Indies) in three sheltered bays: Grande Anse d'Arlet (GA), Anse du Bourg d'Arlet and Anse Chaudière (Fig. 1). Due to the absence of geographical barriers, the last two bays were considered here as a single entity, referred to as Anse du Bourg d'Arlet/Chaudière (ABAC). These bays are known as developmental poaching- and predator-free foraging grounds for immature green turtles affected by FP (Chambault et al., 2018; Siegwalt et al., 2020, 2022; Lelong et al., 2024).

Data Collection

From 2013 to 2024, one-week capture-recapture sessions were annually conducted in GA and ABAC, in combination with multiple short irregular sessions (< 1 day) in GA only (Fig. S1). Captured turtles were identified using Passive Integrated Transponder (PIT; ID-100, TROVAN). For each individual, minimum curved carapace length (CCL) was measured using flexible fiberglass tape ($\pm$ 0.1 cm). Complete capture, tagging and measurement procedures are described in Bonola et al. (2019). Biopsies of skin, tumor, blood, scale and claw were sampled.

A thorough external physical examination was performed to locate each external tumor. Internal tumors could not be detected, thus the present study concern only cutaneous form of FP. High-angle photos of each tumor or group of tumors were taken alongside a metal ruler, occasionally between 2015 and 2021 and routinely since 2022. To prevent disease transmission among successively manipulated individuals, latex gloves were changed between each turtle, and measurement tools and the boat floor were sanitized immediately after each release.

Fibropapillomatosis Status and Total Tumor Area

We classified the FP status of each turtle as a binary variable: "afflicted" when FP tumors were observed, or "non-afflicted" otherwise. Several small tumors (< 0.5 cm) were initially not considered as FP but were later identified based on their progression, using available pictures of the same animals over the years (*e.g.* Fig. S2). Subsequently, this expertise has helped to identify small tumors even if no other picture were available over the years. Consequently, 62 of the 455 turtles captured between 2013 and 2019, initially classified as "non-afflicted" in Roost et al. (2022), were reclassified as "afflicted" in the present study (25 in ABAC, 37 in GA).

We assigned a specific ID to each tumor and recorded its color, texture, shape, localization, and biopsies. Maxi-

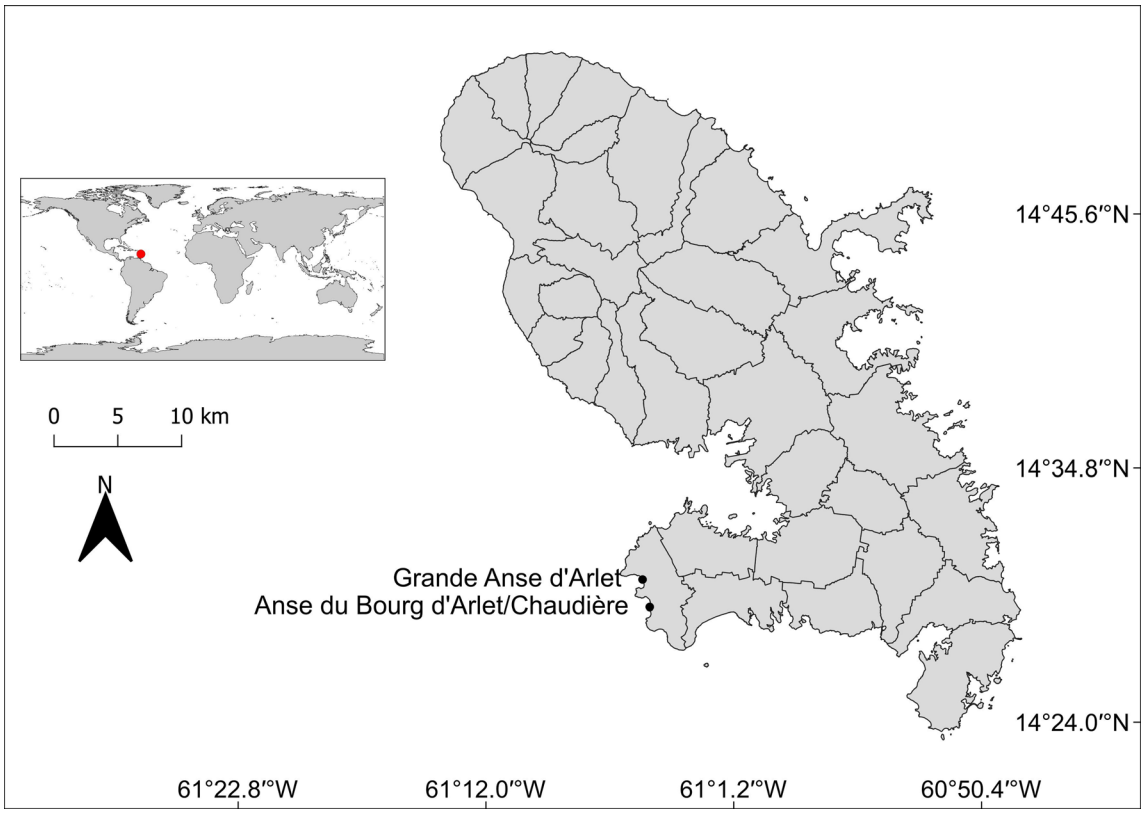

Figure 1. Location of Martinique on the world map (red dot) and the two sampling sites in Martinique, Grande Anse d'Arlet and Anse du Bourg d'Arlet/Chaudière (black dots) (Color figure online).

mum diameter and area were measured using Adobe Photoshop 2020©. Similar to Rossi et al. (2016), the total tumor area (TTA, cm^2) was calculated for each afflicted turtle to assess FP severity.

Statistical Analysis

Capture-Mark-Recapture Analysis

Similarly to Lelong et al. (2024), only captures that occurred from June of year i to February of year $i + 1$ were accounted and grouped in a yearly session for the year i, resulting in a dataset covering the years 2013 to 2023. Only the first capture of an individual was accounted in cases where multiple captures occurred within the same year.

A multievent capture-recapture model (Pradel, 2005) was set up based on seven states merging two size-classes (Small/Medium juveniles CCL $<$ 70 cm, SMJ; Large juveniles CCL $\geq$ 70 cm, LJ) and four health status (non-afflicted, afflicted, recovered, dead; Fig. 2). Non-afflicted corresponds to individuals that were initially captured with no tumors, while recovered corresponds to complete remission of tumors after earlier encounters, where the turtle had FP tumors. Estimated parameters were the transition probabilities between states: Ψ the health transition (Ψ_{Dev} the FP development rate and Ψ_{Rec} the FP recovery rate), Φ the apparent survival (*i.e.*, probability of surviving and staying in the study area) conditional on Ψ, and δ the size-class transition rate of turtles, conditional on Ψ and Φ. It is important to note that Φ is a proxy of survival for SMJ, since they are not expected to emigrate at this life-stage class (Lelong et al., 2024). Moreover, Ψ and δ are one-way transitions (Fig. 2). The following five possible events were defined: "0" = not encountered, "1" = encountered without FP tumors and CCL $<$ 70 cm, "2" = encountered with FP tumors and CCL $<$ 70 cm, "3" = encountered without FP tumors and CCL $\geq$ 70 cm, "4" = encountered with FP tumors and CCL $\geq$ 70 cm. Events where no external tumors were recorded could correspond to non-afflicted or recovered states, dealing with uncertainty in state assignment (Pradel, 2005). The probability of being recaptured conditional to the state of the individuals is noted p. Models were run using E-Surge v2.2.3 (Choquet et al., 2009b).

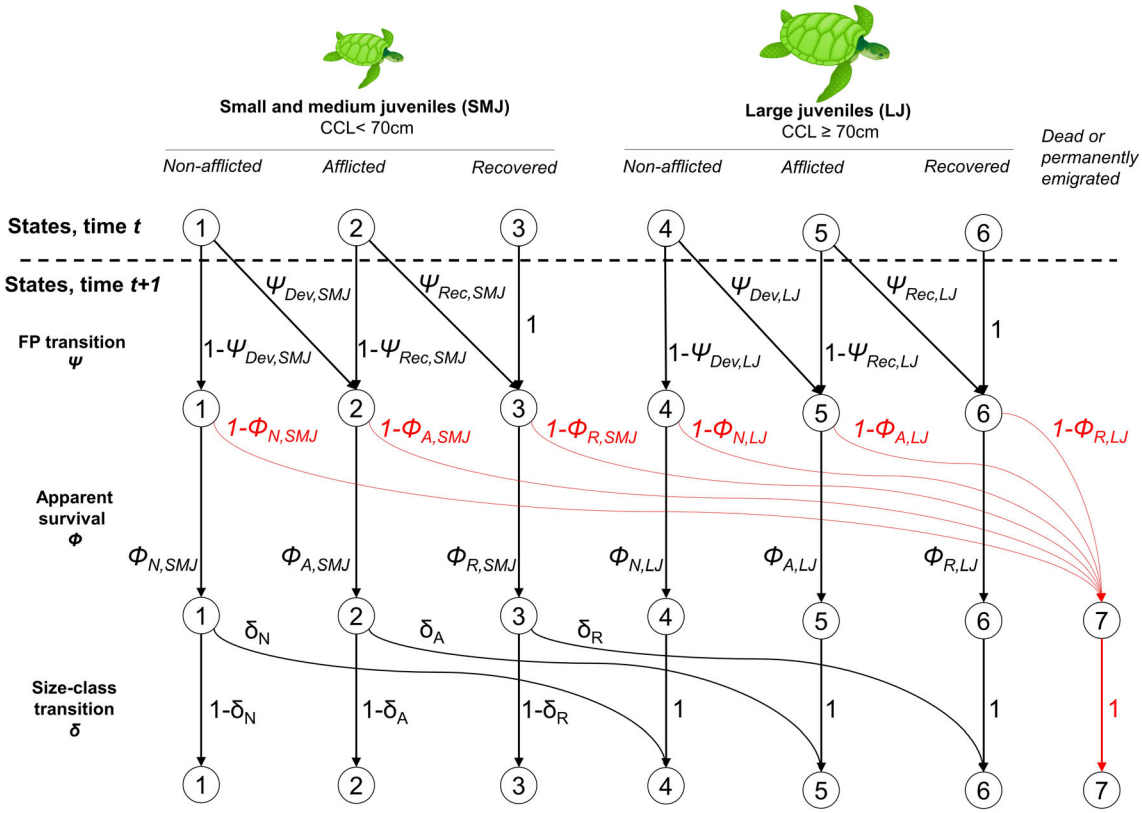

Figure 2. Transition probability structure between the seven states of green sea turtles (*Chelonia mydas*) of the multi-event model set up on the Martinique capture-mark-recapture dataset. Transitions to death or permanent emigration states are represented in red. Abbreviations: CCL, minimum curved carapace length; FP, Fibropapillomatosis; *Dev*, FP development; *Rec*, FP recovery; *N*, Non-afflicted; *A*, Afflicted; *R*, Recovered (Color figure online).

Capture effort, expressed as the log-transformed half-days of capture (logCE), years with high turbidity in coastal water (2018 and 2020) and site differences are parameters that affect recapture rates (Lelong et al., 2024) and were included systematically in the models.

The effect of FP status on each transition probability was tested through model selection procedure (see below). Additionally, non-afflicted and recovered turtles were grouped to create the variable FP2, used to control for post-recovery effect of the disease on Φ and δ transition probabilities. Moreover, a third FP-related effect, called FP3, was tested on Φ_{LJ} and δ_{SMJ} excluding recovered individuals. Indeed, recovery from FP may take several years and is more prone to concern larger individuals (Patrício et al., 2016; Kelley et al., 2022), with potential confounding effect on emigration and size-class transition rates (Bjorndal et al., 2000; Lelong et al., 2024).

Considering their potential promoting effect on FP disease (Manes et al., 2022; Roost et al., 2022), annual mean values for Sea Surface Temperature Anomaly (SSTa, °C), Net Primary Production (NPP, $mgC.m^{-2}$) and salinity ($g.L^{-1}$) were extracted from NOAA ERDAPP database (https://coastwatch.pfeg.noaa.gov/erddap, accessed 18/06/2024) and included in the model. Wastewater discharged from a damaged outfall in ABAC between 2014 and 2019 was accounted as a binary variable at both sites, as it may also have contaminated GA given the northward marine currents in the area (Fig. S5). The possibility that the wastewater leak did not affect GA was also tested in a second model including this effect of pollution only in ABAC. The role of these environmental covariates on FP development and recovery rates were investigated using Analysis of DEViance (ANODEV, Grosbois et al. 2008).

The most general model included FP status in addition to site, logCE and turbidity effect on recapture rate, state-specific apparent survival, time variation and site effect on both FP development and recovery rates, and FP status on size-class transition rate. From this general model, we used a backward stepwise model selection procedure. Effects were removed in the following order when present: time

variation, FP status and size-class. FP status was first reduced to FP2 then to FP3. Model selection was based on QAICc (Burnham et al. 1995; Anderson et al. 1998). When ΔQAICc $>$ 2, the model with the lowest QAICc was kept. Otherwise, the model with the lowest number of parameters was retained. Goodness-of-Fit (GoF) was assessed on the most general model using the Jolly-Movement (JMV) test implemented in U-CARE v3.3 (Choquet et al., 2009a).

Following CMR model selection, the mean time spent on the foraging grounds after settlement before the first FP clinical signs, and the mean time required to recover from FP were estimated according to Schaub et al. (2001) using mean FP development and recovery rates over the study duration from the best model. Associated standard errors were calculated using the delta-method (Powell, 2007). Additionally, the mean size at first capture in the different FP status was compared between sites using a Mann–Whitney U test.

Fibropapillomatosis Probability

Effect of site, year and CCL, including year*site and year*CCL interactions on FP probability were tested using a Binomial Generalized Linear Mixed Model with logit link function using the package *glmmTMB* (Brooks et al., 2017) in R v4.3.0 (R Core Team, 2023). Moreover, FP probability may have a non-linear relationship on logit scale with years and CCL (Patrício et al. 2016; Kelley et al. 2022; Muñoz Tenería et al. 2022; Roost et al. 2022). Thus, it was modeled as a quadratic polynomial function of year and CCL effects. Turtle ID was included as a random effect to deal with repeated measurements. Model selection was performed using AICc (Sugiura, 1978). Several models had a ΔAICc $<$ 2 (see results) and were thus averaged to obtain FP probability estimates.

Fibropapillomatosis Severity

TTA was analyzed using a Linear Mixed Model (LMM) with Gaussian distribution. A log-transformation was applied on TTA to approach normality of the residuals. CCL and capture site in interaction, year, SSTa, NPP and salinity were tested as fixed effects. Moreover, TTA variations could be non-linear across size-classes (dos Santos et al., 2010), thus a quadratic function was applied on CCL. Turtle ID was implemented as a random effect. Model selection was performed using AICc (Sugiura 1978). LMMs were fitted using packages *nlme* (Pinheiro et al., 2022).

Ethical Approval

The capture 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 was carried out under the certification of Damien Chevallier (prefectural authorizations' owner) under strict compliance of the Police of Martinique's recommendations and French legal and ethical requirements to minimize animal disturbance.

Results

Data Description

Among the 750 total capture events occurring within the study duration, 211 involved FP-afflicted turtles (Table S1) and 19 were known recovered turtles. A total of 450 individuals were identified, including 151 turtles captured at least once with FP clinical signs. Total FP captures resulted in 135 TTA measurement on 104 individuals (Table S1). TTA ranged 0.022−201.278 cm^2 in ABAC and 0.029–133.964 cm^2 in GA.

Juvenile green turtles were captured between one and five times during the study period (Fig. S3, mean ± SD in ABAC = 1.40 ± 0.64 captures/turtle and in GA = 1.79 ± 1.15 captures/turtle). There was no significant geographic variation in terms of CCL at first non-afflicted capture, first afflicted capture and first recovered capture (Fig. 3; values shown in Table S2; Mann–Whitney test; $p > 0.05$).

Capture-Mark-Recapture Analysis

Goodness-of-Fit and Model Selection

GoF showed neither capture heterogeneity nor transience ($\chi^2 = 54.737$, $df = 83$, $p = 0.993$). The best model indicated an effect of turtle size and FP3 categories on apparent survival, a site effect on constant FP development rate and time-varying recovery rate, and size-class transition rate depending of FP3 categories (Table 1). FP status had no effect on recapture probability (Table 1, shown in Table S4). ANODEV did not detect any effect of tested environmental covariates on FP development or recovery rates (Table S3).

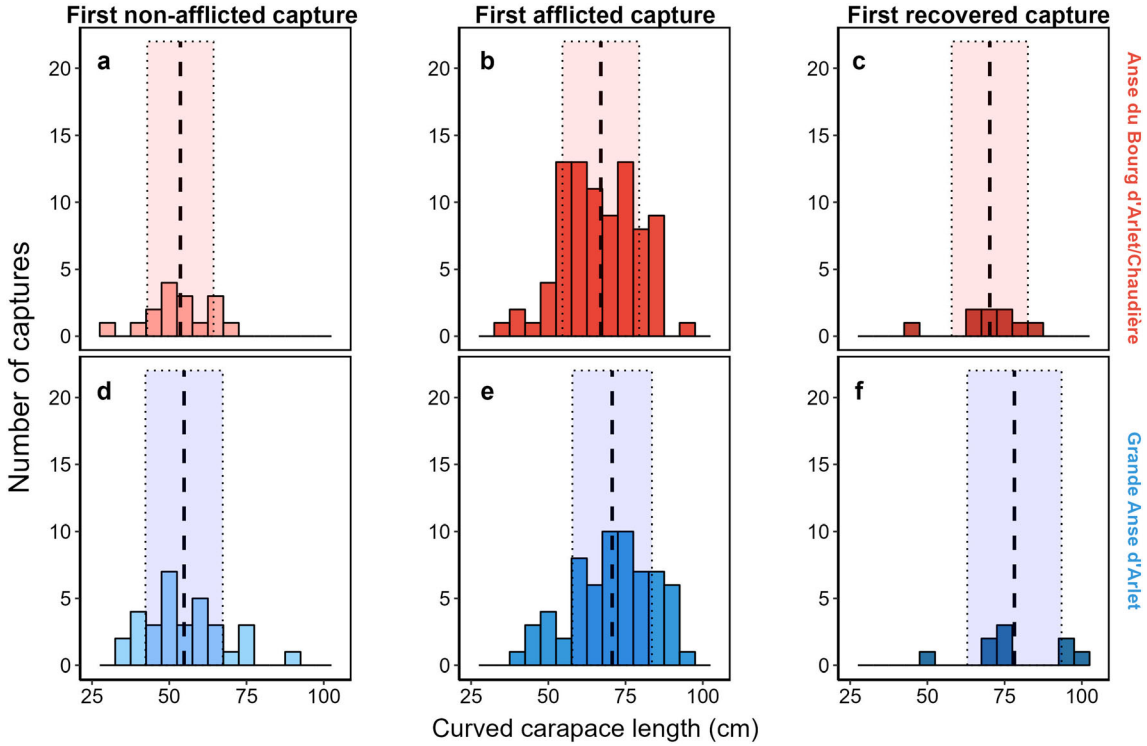

Figure 3. Curved carapace length (CCL, cm) distribution of green sea turtle (*Chelonia mydas*) at first non-afflicted capture, first afflicted capture and first recovered capture at Anse du Bourg d'Arlet/Chaudière (**a**, **b**, **c**) and Grande Anse d'Arlet (**d**, **e**, **f**) for turtles that were captured at least one time with fibropapillomatosis. Mean minimum curved carapace length is indicated by the vertical dashed line with associated ± standard deviation in the shaded rectangles (Color figure online).

Demographic Parameter Estimates

Apparent survival (Φ) differed between size-classes. It was estimated at 0.90 ($CI_{95\%}$: 0.82–0.94) for SMJ turtles (CCL $<$ 70 cm) regardless of their health status. For LJ turtles (CCL $\geq$ 70 cm), there was no difference in apparent survival between non-afflicted and afflicted turtles (both equal to 0.71; $CI_{95\%}$: 0.61–0.80). However, recovered LJ showed a low apparent survival (0.37; $CI_{95\%}$: 0.24–0.52).

FP development rates (Ψ_{Dev}) were higher at ABAC (0.28; $CI_{95\%}$: 0.17–0.42) than in GA (0.14; $CI_{95\%}$: 0.10–0.20). Time-dependent FP values of recovery rates (Ψ_{Rec}) were poorly estimated by the model with a wide confidence interval (shown in Table S4). Consequently, Ψ_{Rec} estimates were averaged across the study duration and revealed higher values in ABAC (0.31; $CI_{95\%}$: 0.21–0.44) than in GA (0.17; $CI_{95\%}$: 0.10–0.27). Turtles developed the first clinical signs of the disease within 3.2 ($CI_{95\%}$: 1.6–4.8) years after settlement in foraging grounds and recovered completely from FP 2.7 ($CI_{95\%}$: 1.4–3.9) years after first FP clinical signs in ABAC. In GA, the disease emerged within 6.5 ($CI_{95\%}$: 4.1–8.9) years and recovered completely after 5.4 ($CI_{95\%}$: 2.3–8.4) years.

Fibropapillomatosis Probability

Models n°6 to n°9 presented the lowest values of AICc, and similar values of AICc Weights (Table 2). All models included site and quadratic polynomials of CCL and years. They were averaged to obtain the estimates of FP probabilities (Fig. 4). The largest difference in FP probability between the sites was in 2020 (0.73; $CI_{95\%}$: 0.51–0.88 in ABAC *vs* 0.15; $CI_{95\%}$: 0.06–0.35 in GA; Fig. 4a). Moreover, FP probability estimates increased with size in both sites, with a maximum around 80 cm CCL in ABAC (0.82; $CI_{95\%}$: 0.52–0.95) and at 100 cm CCL in GA (0.40; $CI_{95\%}$: 0.08 – 0.83). Between $\sim$ 50 and 80 cm CCL, site-specific estimated confidence intervals did not overlap, with substantially lower FP probability in GA than in ABAC (Fig. 4b).

Table 1. Capture-Mark-Recapture model selection procedure in E-SURGE v2.2.3 on recapture rate (p), apparent survival (Φ), health transitions (Ψ) and size-class transition rate (δ) of green sea turtles (*Chelonia mydas*).

Step	N°	Model	N Par	Deviance	QAICc	ΔQAICc
p	1	Φ(St)Ψ(FPxt + Site)δ(FP)p(FP + Site + logEC + Turb)	40	2919.9108	3004.5436	25.1135
	2	Φ(St)Ψ(FPxt + Site)δ(FP)p(FP2 + Site + logEC + Turb)	39	2915.7283	2998.1289	18.6988
	3	**Φ(St)Ψ(FPxt + Site)δ(FP)p(Site + logEC + Turb)**	**38**	**2916.2942**	**2996.4689**	**17.0388**
	4	Φ(St)Ψ(FPxt + Site)δ(FP)p(Site)	35	2954.6402	3028.1746	48.7445
	5	Φ(St)Ψ(FPxt + Site)δ(FP)p(.)	34	2970.9429	3042.2762	62.8461
Φ	6	Φ(SizexFP2)Ψ(FPxt + Site)δ(FP)p(Site + logEC + Turb)	36	2924.4745	3000,2161	20,786
	7	**Φ(SMJ. LJxFP3)Ψ(FPxt + Site)δ(FP)p(Site + logEC + Turb)**	**35**	**2918.0542**	**2991,5886**	**12,1585**
	8	Φ(Size)Ψ(FPxt + Site)δ(FP)p(Site + logEC + Turb)	34	2927.2498	2998,5831	19,153
	9	Φ(.)Ψ(FPxt + Site)δ(FP)p(Site + logEC + Turb)	33	2982.3661	3051,5045	72,0744
Ψ	10	Φ(SMJ. LJxFP3)Ψ(FP + t + Site)δ(FP)p(Site + logEC + Turb)	27	2939.3865	2995.4836	16.0535
	11	Φ(SMJ. LJxFP3)Ψ(FP + Site)δ(FP)p(Site + logEC + Turb)	19	2945.3522	2984.3947	4.9646
	12	**Φ(SMJ. LJxFP3)Ψ(Dev. + Recxt + Site)δ(FP)p(Site + logEC + Turb)**	**27**	**2923.5793**	**2979.6763**	**0.2462**
	13	Φ(SMJ. LJxFP3)Ψ(Devxt + Rec. + Site)δ(FP)p(Site + logEC + Turb)	27	2938.4787	2994.5758	15.1457
	14	Φ(SMJ. LJxFP3)Ψ(Dev. + Recxt)δ(FP)p(Site + logEC + Turb)	26	2929.2648	2983.2094	3.7793
	15	Φ(SMJ. LJxFP3)Ψ(.)δ(FP)p(Site + logEC + Turb)	17	2953.411	2988.2482	8.8181
δ	16	Φ(SMJ. LJxFP3)Ψ(Dev. + Recxt + Site)δ(FP2)p(Site + logEC + Turb)	26	2931.2026	2985.1472	5.7171
	17	*Φ(SMJ. LJxFP3)Ψ(Dev. + Recxt + Site)δ(FP3)p(Site + logEC + Turb)*	*26*	*2925.4855*	*2979.4301*	*0*
	18	Φ(SMJ. LJxFP3)Ψ(Dev. + Recxt + Site)δ(.)p(Site + logEC + Turb)	25	2932.0166	2983.8147	4.3846

The best model for each step is in bold and the best model of the overall procedure is in italics.
"." Constant, *Dev* FP development, *FP* fibropapillomatosis status, *FP2* FP group [afflicted vs non-afflicted + recovered], *FP3* FP group [non-afflicted + afflicted vs recovered], *logEC* log-transformed capture effort, *Rec* FP recovery., *St* state, *t* time-dependent, *Turb* turbidity, *N. Par* number of parameters.

Table 2. Summary of model selection among Generalized Linear Mixed Model with binomial distribution to FP probability of green sea turtle (*Chelonia mydas*).

N°	Model	N par	Deviance	AICc	ΔAICc	Akaike weight
1	Null	1	844.65	848.66	149.18	0.00
2	Site	2	815.33	821.37	121.88	0.00
3	Site + CCL	3	755.99	764.05	64.56	0.00
4	Site + poly(CCL,2)	4	755.08	765.16	65.68	0.00
5	Site + poly(CCL,2) + Year	5	712.48	724.60	25.11	0.00
6	**Site + poly(CCL,2) + poly(Year,2)**	**6**	**685.70**	**699.85**	**0.37**	**0.24**
7	**Site*poly(CCL,2) + poly(Year,2)**	**8**	**681.24**	**699.48**	**0.00**	**0.29**
8	**poly(CCL,2) + Site*poly(Year,2)**	**8**	**681.32**	**699.56**	**0.08**	**0.27**
9	**Site*poly(CCL,2) + Site*poly(Year,2)**	**10**	**677.80**	**700.16**	**0.67**	**0.20**

Best models are highlighted in bold.
CCL Minimum curved carapace length, *N par.* Number of parameters.

Fibropapillomatosis Severity

LMM selection suggested an effect of capture site and quadratic polynomial CCL on TTA, with no effect of year or environmental covariates (Table 3). Turtles captured in ABAC exhibited higher mean TTA than those in GA (2.79; $CI_{95\%}$: 1.55–5.03 cm^2 vs 0.74; $CI_{95\%}$: 0.37–1.48 cm^2, respectively; Fig. 5a). TTA peaked at 75 cm CCL in ABAC ($\sim$ 2.85 cm^2; $CI_{95\%}$: 0.45–1.64 cm^2), while TTA was not related to CCL in GA (Fig. 5b). In ABAC, four turtles were

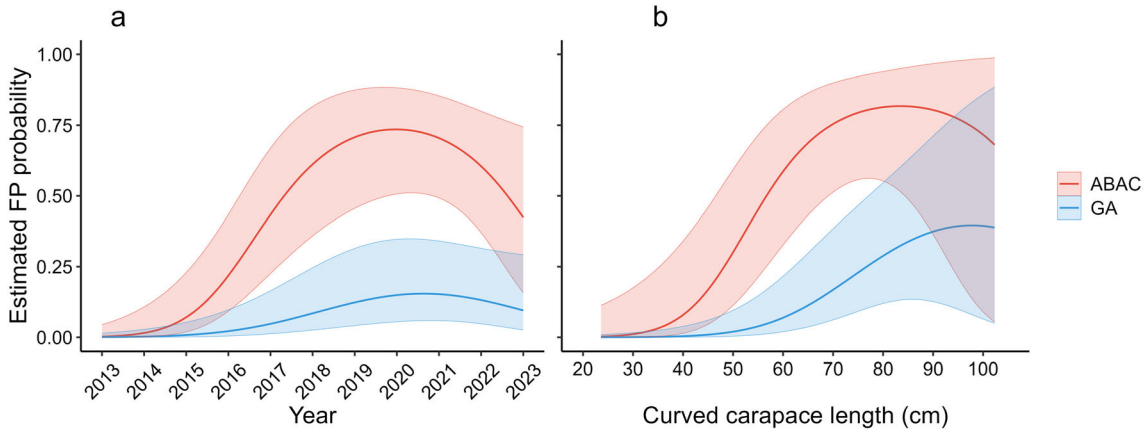

Figure 4. Estimated FP probabilities (solid lines) with associated 95% confidence interval (shaded areas) in green sea turtles (*Chelonia mydas*) extracted from the averaging of the four best model in Anse du Bourg d'Arlet/Chaudière and Grande Anse d'Arlet (blue) by (**a**) year from 2013 to 2023 and (**b**) minimum curved carapace length (Color figure online).

Table 3. Model selection among Linear Mixed Models applied to log(Total Tumor Area).

N	Model	N par	Deviance	AICc	ΔAICc	Akaike weight
1	Null	1	571.39	577.58	16.80	0.00
2	Site	2	564.89	573.20	12.43	0.00
3	Site + CCL	3	570.36	580.84	20.06	0.00
4	Site + poly(CCL,2)	4	554.88	567.56	6.79	0.02
5	**Site*poly(CCL,2)**	**6**	**543.58**	**560.78**	**0.00**	**0.54**
6	Site*poly(CCL,2) + Year	7	544.44	563.96	3.19	0.11
7	Site*(poly(CCL,2) + Year)	8	542.11	564.00	3.23	0.11
8	Site*poly(CCL,2) + SSTa	7	544.18	563.71	2.93	0.12
9	Site*poly(CCL,2) + SSTa + NPP	8	542.96	564.86	4.09	0.07
10	Site*poly(CCL,2) + SSTa + NPP + Salinity	9	542.20	566.52	5.74	0.03

Best model is highlighted in bold.
CCL Minimum curved carapace length, *NPP* Net primary production, *poly*(*CCL, 2*) Quadratic polynomial of CCL, *SSTa* Sea surface temperature anomaly, *and TTA* Total tumor area.

captured with TTA > 100cm^2 (maximum = 201.27 cm^2), while in GA, only one turtle had TTA > 100 cm^2 (maximum = 133.96 cm^2).

Discussion

This study presents critical insights on the FP dynamics and demographic consequences in juvenile green turtles. FP-affliction did not affect apparent survival rates but the FP prevalence, severity, and progression rates were higher in ABAC than in GA. The recapture probability was similar between afflicted and non-afflicted turtles, consistent with other studies (Chaloupka et al., 2009; Patrício et al., 2011). The lower number of turtles captured in ABAC (Table S1) was mainly due to lower capture effort (ABAC = 23 half-days; GA = 43 half-days) and more fearful turtles than in GA (authors pers. obs.), leading to a lower overall capture probability in ABAC (Lelong et al., 2024). While FP prevalence observed in ABAC or GA (∼ 70% and ∼ 35% respectively, Fig. S4 are among the highest reported in Caribbean juvenile green turtle foraging grounds (Hirama and Ehrhart, 2007; Stringell et al., 2015; Patrício et al., 2016; Kelley et al., 2022; Muñoz Tenería et al., 2022), FP severity was locally limited compared to Brazil (5 turtles with TTA > 100 cm^2 among 135 TTA measurements *vs* 49 among 216 in Brazil; Rossi et al. 2016).

High apparent survival of SMJ (proxy of survival rate) independently of their FP status indicates no FP effect on

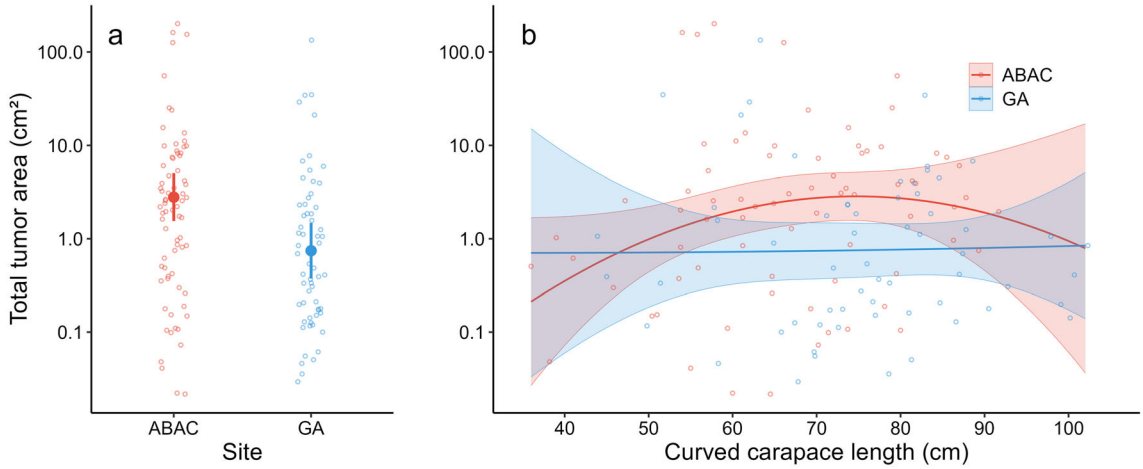

Figure 5. (**a**) Mean estimated total tumor area (TTA) per individual green sea turtle (*Chelonia mydas*) in Anse du Bourg d'Arlet/Chaudière (ABAC) and Grande Anse d'Arlet (GA) with associated 95% confidence interval and (**b**) site-specific estimated TTA per individual function of minimum curved carapace length with associated 95% confidence interval (half-shaded ribbon) from selected Linear Mixed Model. On both panels, each red or blue dot corresponds to the raw data. Y-axis is on a logarithmic-scale (Color figure online).

survival rate. These results are similar to those in green turtles from Puerto Rico (Patrício et al., 2011). Moreover, apparent survival were similar between non-afflicted and afflicted LJ turtles indicating no FP effect on emigration rate. CCL of recovered LJ turtles is close to the mean size at emigration for this species, *i.e.*, 85 cm CCL (Fig. 3c, f; Chambault et al., 2018), and their lower apparent survival was thus more likely due to a higher emigration rate than mortality as a result of FP infection. Consistently with other studies, green turtles appeared to mostly survive and recover from FP (Chaloupka et al., 2009; Kelley et al., 2022). The low cutaneous FP severity in Martinique may mitigate its impact on survival and emigration rates (Patrício et al., 2011) as the most important consequences are typically seen in severely afflicted individuals (Work and Balazs, 1999; Chaloupka and Balazs, 2005; Rossi et al., 2016). Nonetheless, FP may affect other key life history traits, such as growth rate (Chaloupka and Balazs, 2005), potentially delaying maturity and negatively impacting the breeding population. Although the recent routine measurement of tumors prevented us from including TTA in the CMR analysis, we strongly recommend incorporating disease severity in future assessments of the impact of FP.

Estimated time to develop FP in ABAC (3.2 years) and GA (6.5 years) were substantially higher than those reported in Puerto Rico (1.8 years; Patrício et al. 2016). FP recovery in ABAC (2.7 years; $\Psi_{Rec} = 0.31$) was identical to that described in Puerto Rico (2.7 years; Patrício et al. 2016). Conversely, FP recovery in GA (5.4 years; $\Psi_{Rec} = 0.17$) was more similar to those reported in Hawaii ($\Psi_{Rec} \sim 0.13$–0.18; Chaloupka et al. 2009). The long duration required for FP progression in Martinique may explain the increasing prevalence up to 85 cm CCL, similarly to Indonesia and Mexico (Adnyana et al. 1997; Muñoz Tenería et al. 2022). Conversely, FP occurrence decreased above 50–60 cm straight carapace length (SCL) or CCL in the Caribbean and West Africa (Hirama and Ehrhart 2007; Patrício et al. 2016; Monteiro et al. 2021; Perrault et al. 2021; Kelley et al. 2022). ChHV5 or host genetic may affect FP expression (Greenblatt et al. 2005; Hirama and Ehrhart 2007; Jones et al. 2016; Work et al. 2020; Kane et al. 2021; Yetsko et al. 2021; Martin et al. 2022; Dupont et al. 2024) potentially contributing to the diversity in FP dynamics and expression documented worldwide. In Florida, larger juveniles typically achieve complete recovery before leaving foraging grounds (Kelley et al., 2022). In Martinique, the high FP prevalence at large size, the lack of FP's effect on apparent survival and the limited number of known recovered turtles (n = 19) suggests that definitive emigration without complete recovery likely occurred. The presence of residual tumors could have negative effects on migration, such as increased energy expenditure due to the drag of tumors (O'Connell et al., 2021) and the defense against infection (Mahmoudabadi et al., 2017), potentially impacting demographic parameters of the breeding life-stage.

FP development and recovery rates estimations indicated a faster progression of the disease in ABAC than in

GA. Consequently, FP tumors developed at 50 cm CCL on turtles that settled in ABAC (Fig. 4b) and TTA reached then its maximum at 70 cm CCL in ABAC (Fig. 5b). Temporal prevalence in ABAC followed an epizootic curve (Fig. 4a) as reported in Australia (Jones et al., 2022), Hawaii (Chaloupka et al., 2009), Mexico (Muñoz Tenería et al., 2022) and Puerto Rico (Patrício et al., 2016). Conversely, FP prevalence and severity in GA showed no peaks during the study period (Fig. 4a), similar to prevalence pattern observed in Australia (Jones et al., 2022). Unlike Chaloupka et al. (2009), CMR analysis indicated a constant FP development rate though the recovery rate appeared to fluctuate over time. Given the differences in FP prevalence curves between the two sites, it is possible that temporal variations in recovery rate also vary between ABAC and GA. Yet, FP recovery estimates had low precision (Table S3). Additionally, there was no available site-specific measurements of the tested environmental cofactors and only large-scale variables were implemented in the models. As a result, the specific role of the disease recovery rate in the site-specific FP dynamics and its potential fine-scale external drivers in our study area therefore remain unknown.

Seagrass beds' structure, its alteration by boat anchorage and the presence of the invasive phanerogam *Halophila stipulacea* are known to be equivalent between the two studied sites (Siegwalt et al., 2022). Moreover, high density of conspecifics and the recruitment of new susceptible individuals have been suggested as potential drivers of FP dynamics (Patrício et al., 2016; Roost et al., 2022). Nonetheless, the demography and size structure of the green turtle population were identical on ABAC and GA (Siegwalt et al., 2020; Lelong et al., 2024). These ecological parameters are therefore unlikely to explain the differential FP rates observed, unlike the potential variations of several other cofactors between the bays.

Genetic profile could affect the resistance of individuals to infectious disease (Uller et al., 2003). In ABAC and GA combined, the genetic origin of juvenile green turtles is known to be highly diverse (Chambault et al., 2018). Considering there is a poor connectivity between these two foraging grounds (Siegwalt et al., 2020; Lelong et al., 2024), site-specific genetic composition of juvenile green turtle population could vary and should be thus explored as it may modify FP dynamics.

Persistent organic pollutants and trace elements are present in the French West Indies marine ecosystem and in sea turtles (Dyc et al., 2015; Bouchon et al., 2016; Dromard et al., 2016), partially originating from sewage (Fernandez et al., 2007). Main known pollution occurred inside ABAC, and resulting consequences on FP may be thus stronger in ABAC than in GA. Tourism pressure can also vary between ABAC and GA, leading to a geographic variation of pollution and human disturbance. Finally, there is potentially small-scale differences between ABAC and GA in physico-chemical parameters (*e.g.* hydrodynamics, salinity, temperature) that could affect both FP (Manes et al., 2022) and/or coastal water quality through water renewal (Tosic et al., 2019). To explain the differences in FP dynamics between bays, there is an urgent need to measure the site-specific environmental conditions and anthropogenic pressures experienced by juvenile green turtles.

More generally, the presence of FP in Martinique may be linked to low habitat quality, chronic stress and co-infections through oxidative stress (Costantini et al., 2011; Costantini, 2022; Labrada-Martagón et al., 2024), which is known to alter immunity and facilitate herpesvirus infection in vertebrates (Sebastiano et al., 2016). Considering the potential role of anthropogenic stressors in FP, the comprehension of this disease and its dynamics requires further cross-disciplinary investigations in a One Health framework with the aim of improving the health of green turtles, of their environment and of humans exploiting the coastal resources (Xie et al., 2017; Espinoza et al., 2024).

Conclusion and Perspectives

This study reveal substantial differences in the occurrence and severity of FP between two geographically close sites, but the underlying environmental and internal cofactors that drive the disease remain unknown. Further research should focus on 1) the consequences of FP on demographic parameters (survival, emigration, somatic growth rate) in relation to the disease severity, 2) the interactions between FP development and recovery rates, FP dynamics and developmental migration and 3) the environmental cofactors, internal health status and genetics involved in the FP dynamics with an emphasis on the biotic and abiotic specificity of each foraging ground. Additionally, these efforts should be extended beyond Martinique to assess the consequences of FP on the demography of Atlantic green turtle populations. A better understanding of FP dynamics and its possible drivers will enable useful measures for sea turtle conservation (Fuentes et al., 2023), given that FP affects all seven species of sea turtles worldwide. More

generally, FP serves as a key case for understanding the relationships between wildlife diseases, hosts and potential external stressors.

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Declarations

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

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