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/Anse 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 (<2km) 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 disease, hosts and environmental factors.

1. 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; da Fonseca et al. 2020; Li and Chang 2020; Perrault et al. 2021). 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.

2. Material and methods

2.1. Study sites

[insert Figure 1 here]

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/Anse 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; Siegwalt et al., 2022; Lelong et al., 2024).

2.2. 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 (<1day) 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 (±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.

2.3. 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 (<0.5cm) 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. Maximum diameter and area were measured using Adobe Photoshop 2020©. Similar to Rossi et al. (2016), the total tumor area (TTA, cm²) was calculated for each afflicted turtle to assess FP severity.

2.4. Statistical analysis
2.4.1. 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 multi-event 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 ≥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 ≥70 cm, "4" = encountered with FP tumors and CCL ≥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).

[insert Figure 2 here]

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 pollution effect 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.

2.4.2. 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.

2.4.3. 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).

2.5. 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 [LAST AUTHOR'S NAME] (prefectural authorizations' owner) under strict compliance of the Police of Martinique's recommendations and French legal and ethical requirements to minimize animal disturbance.

3. Results

3.1. 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 cm² in ABAC and 0.029 − 133.964 cm² 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 provided in Table S2; Mann-Whitney test; p > 0.05).

[insert Figure 3 here]

3.2. Capture-Mark-Recapture analysis

3.2.1. Goodness-of-fit and model selection

GoF showed neither capture heterogeneity nor transience (χ^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, detailed in Table S4). ANODEV did not detect any effect of tested environmental covariates on FP development or recovery rates (Table S3).

3.2.2. 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 ≥ 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 (detailed 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.

3.3. Fibropapillomatosis probability

[insert Figure 4 here]

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 ~50 cm and 80 cm CCL, site-specific estimated confidence intervals did not overlap, with substantially lower FP probability in GA than in ABAC (Fig. 4b).

3.4. Fibropapillomatosis severity

[insert Figure 5 here]

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 cm² vs 0.74; CI$_{95\%}$: 0.37 – 1.48 cm², respectively; Fig. 5a). TTA peaked at 75 cm CCL in ABAC (~ 2.85 cm²; CI$_{95\%}$: 0.45 – 1.64 cm²) while TTA was not related to CCL in GA (Fig. 5b). In ABAC, four turtles were captured with TTA > 100cm² (maximum = 201.27 cm²), while in GA, only one turtle had TTA > 100 cm² (maximum = 133.96 cm²).

4. 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 lower 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 cm² 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 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.*, 85cm 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; Ψ_{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; Ψ_{Rec} = 0.17) was more similar to those reported in Hawaii (Ψ_{Rec} ~0.13-0.18; Chaloupka et al. 2009). The long duration required for FP progression in Martinique may explain the increasing prevalence up

to 85cm 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 50cm 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 despite the low connectivity between the two foraging grounds (Siegwalt et al., 2020; Lelong et al., 2024). These ecological parameters are thus not likely to explain observed differential FP rates, in contrast to the potential variations of several other cofactors between the bays.

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). Additionally, wastewater may contribute to enhance coastal eutrophication (Akinnawo, 2023). Main known pollution occurred inside ABAC, and resulting consequences on FP may be thus stronger in ABAC than in GA. Tourism pressure may also be variable between ABAC and GA, inducing geographic variation of pollution and human disturbance. Finally, ABAC and GA seems comparable in terms of topography (bathymetry, area, coastline), but there is potentially small-scale differences in physicochemical 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). Explaining differences in FP dynamics will thus urgently require measurements of site-specific environmental conditions and anthropogenic pressures undergoes by juvenile green turtles in ABAC and GA.

More generally, low habitat quality, chronic stress and co-infections may be linked to the presence of FP in Martinique 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).

5. 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 the 1) consequences of FP on demographic parameters (survival, emigration, somatic growth rate) in relation to the disease severity, 2) interactions between FP development and recovery rates, FP dynamics and developmental migration and 3) environmental cofactors, internal health status and genetics involved in FP dynamics with an emphasis on biotic and abiotic specificity of each foraging ground. Additionally, these efforts should extend beyond Martinique to assess 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.

6. Conflict of Interest

The authors declare that they have no conflict of interest.

7. References

Adnyana W, Ladds P, Blair D (1997) Observations of fibropapillomatosis in green turtles (*Chelonia mydas*) in Indonesia. *Australian Veterinary Journal* 75:737–742. https://doi.org/10.1111/j.1751-0813.1997.tb12258.x

Aguirre AA, Tabor GM (2008) Global factors driving emerging infectious diseases: impact on wildlife populations. *Annals of the New York Academy of Sciences* 1149:1–3. https://doi.org/10.1196/annals.1428.052

Akinnawo SO (2023) Eutrophication: Causes, consequences, physical, chemical and biological techniques for mitigation strategies. *Environmental Challenges* 12:100733. https://doi.org/10.1016/j.envc.2023.100733

Anderson DR, Burnham KP, White GC (1998) Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. *Journal of Applied Statistics* 25:263–282. https://doi.org/10.1080/02664769823250

Barroso P, Acevedo P, Vicente J (2021) The importance of long-term studies on wildlife diseases and their interfaces with humans and domestic animals: A review. *Transboundary and Emerging Diseases* 68:1895–1909. https://doi.org/10.1111/tbed.13916

Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. *Ecological Applications* 10:269–282. https://doi.org/10.1890/1051-0761(2000)010[0269:GTSGME]2.0.CO;2

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, Vedie F, Barnerias C, Laurent T, Bordes R, Guimera C, Aubert N, Bouaziz M, Pinson A, Frédéric F, Matthieu D, Benhalilou A, Céline M, Maillet 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, Habold 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). *Biology Open* 8:bio.048058. https://doi.org/10.1242/bio.048058

Bouchon C, Lemoine S, Dromard C, Bouchon-Navaro Y (2016) Level of contamination by metallic trace elements and organic molecules in the seagrass beds of Guadeloupe Island. *Environmental Science and Pollution Research* 23:61–72. https://doi.org/10.1007/s11356-015-5682-1

Brand CJ (2013) Wildlife Mortality Investigation and Disease Research: Contributions of the USGS National Wildlife Health Center to Endangered Species Management and Recovery. *EcoHealth* 10:446–454. https://doi.org/10.1007/s10393-013-0897-4

Brearley G, Rhodes J, Bradley A, Baxter G, Seabrook L, Lunney D, Liu Y, McAlpine C (2013) Wildlife disease prevalence in human-modified landscapes. *Biological Reviews* 88:427–442. https://doi.org/10.1111/brv.12009

Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M, Bolker B M (2017) glmmTMB balances speed and flexibility among

packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378. https://doi.org/10.32614/RJ-2017-066

Burac M (1996) Tourism and the environment in Guadeloupe and Martinique. In: Briguglio L, Butler R, Harrison D, Filho WL (eds) Sustainable tourism in islands and small states: case studies. Pinter, London, pp 63–74

Burnham KP, White GC, Anderson DR (1995) Model Selection Strategy in the Analysis of Capture-Recapture Data. *Biometrics* 51:888. https://doi.org/10.2307/2532990

Chaloupka M, Balazs G (2005) Modelling the effect of fibropapilloma disease on the somatic growth dynamics of Hawaiian green sea turtles. *Marine Biology* 147:1251–1260. https://doi.org/10.1007/s00227-005-0026-1

Chaloupka M, Balazs GH, Work TM (2009) Rise and fall over 26 years of a marine epizootic in Hawaiian green sea turtles. *Journal of Wildlife Diseases* 45:1138–1142. https://doi.org/10.7589/0090-3558-45.4.1138

Chambault P, de Thoisy B, Huguin M, Martin J, Bonola M, Etienne D, Gresser J, Hiélard G, Mailles J, Védie F, Barnerias C, Sutter E, Guillemot B, Dumont-Dayot É, 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, Maillet 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. *Ecology and Evolution* 8:12790–12802. https://doi.org/10.1002/ece3.4708

Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R (2009a) 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

Choquet R, Rouan L, Pradel R (2009b) Program E-SURGE: A Software Application for Fitting Multievent Models. *Environmental and Ecological Statistics* 3:845–865

Costantini D (2022) A meta-analysis of impacts of immune response and infection on oxidative status in vertebrates. *Conservation Physiology* 10:coac018. https://doi.org/10.1093/conphys/coac018

Costantini D, Marasco V, Møller AP (2011) A meta-analysis of glucocorticoids as modulators of oxidative stress in vertebrates. J Comp Physiol B. https://doi.org/10.1007/s00360-011-0566-2

da Fonseca LA, Fagundes V, Girardi FM, Dornelas LRS (2020) Blood values of cortisol, glucose, and lactate in healthy green turtle (*Chelonia mydas*) and affected by fibropapillomatosis. *Comparative Clinical Pathology* 29:1099–1105. https://doi.org/10.1007/s00580-020-03148-2

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife-threats to biodiversity and human health. *Science, New Series* 287:443–449. https://doi.org/10.1126/science.287.5452.443

dos Santos R, Martins A, Torezani E, Baptistotte C, Farias J, Horta P, Work T, Balazs G (2010) Relationship between fibropapillomatosis and environmental quality: a case study with *Chelonia mydas* off Brazil. *Diseases of Aquatic Organisms* 89:87–95. https://doi.org/10.3354/dao02178

Dromard CR, Bodiguel X, Lemoine S, Bouchon-Navaro Y, Reynal L, Thouard E, Bouchon C (2016) Assessment of the contamination of marine fauna by chlordecone in Guadeloupe and Martinique (Lesser Antilles). *Environmental Science and Pollution Research* 23:73–80. https://doi.org/10.1007/s11356-015-4732-z

Dujon AM, Schofield G, Venegas RM, Thomas F, Ujvari B (2021) Sea Turtles in the Cancer Risk Landscape: A Global Meta-Analysis of Fibropapillomatosis Prevalence and Associated Risk Factors. *Pathogens* 10:1295. https://doi.org/10.3390/pathogens10101295

Dupont SM, Bustamante P, Duffy DJ, Fort J, Le Loc'h G, Lelong P, Chevallier D, Giraudeau M (2024) Future research avenues for the study of fibropapillomatosis in sea turtles. *Frontiers in Ecology and Evolution* 12:1372096. https://doi.org/10.3389/fevo.2024.1372096

Dyc C, Covaci A, Debier C, Leroy C, Delcroix E, Thomé J-P, Das K (2015) Pollutant exposure in green and hawksbill marine turtles from the Caribbean region. *Regional Studies in Marine Science* 2:158–170. https://doi.org/10.1016/j.rsma.2015.09.004

Espinoza J, Alfaro-Núñez A, Cedillo-Peláez C, Fernández-Sanz H, Mancini A, Zavala-Norzagaray AA, Ley-Quiñonez CP, López ES, Garcia-Bereguiain MA, Alonso Aguirre A, Reséndiz E (2024) Epidemiology of marine turtle fibropapillomatosis and tumour-associated chelonid alphaherpesvirus 5 (ChHV5; Scutavirus chelonidalpha5) in North-Western Mexico: a scoping review implementing the one health approach. Veterinary Research Communications. https://doi.org/10.1007/s11259-024-10429-6

Farrell JA, Yetsko K, Whitmore L, Whilde J, Eastman CB, Ramia DR, Thomas R, Linser P, Creer S, Burkhalter B, Schnitzler C, Duffy DJ (2021) Environmental DNA monitoring of oncogenic viral shedding and genomic profiling of sea turtle fibropapillomatosis reveals unusual viral dynamics. *Communications Biology* 4:565. https://doi.org/10.1038/s42003-021-02085-2

Fernandez A, Singh A, Jaffé R (2007) A literature review on trace metals and organic compounds of anthropogenic origin in the Wider Caribbean Region. *Marine Pollution Bulletin* 54:1681–1691. https://doi.org/10.1016/j.marpolbul.2007.08.007

Fuentes M, McMichael E, Kot C, Silver-Gorges I, Wallace B, Godley B, Brooks A, Ceriani S, Cortés-Gómez A, Dawson T, Dodge K, Flint M, Jensen M, Komoroske L, Kophamel S, Lettrich M, Long C, Nelms S, Patrício A, Robinson N, Seminoff J, Ware M, Whitman E, Chevallier D, Clyde-Brockway C, Korgaonkar S, Mancini A, Mello-Fonseca J, Monsinjon J, Neves-Ferreira I, Ortega A, Patel S, Pfaller J, Ramirez M, Raposo C, Smith C, Abreu-Grobois F, Hays G (2023) Key issues in assessing threats to sea turtles: knowledge gaps and future directions. *Endangered Species Research* 52:303–341. https://doi.org/10.3354/esr01278

Greenblatt RJ, Work TM, Balazs GH, Sutton CA, Casey RN, Casey JW (2004) The Ozobranchus leech is a candidate mechanical vector for the fibropapilloma-associated turtle herpesvirus found latently infecting skin tumors on Hawaiian green turtles (*Chelonia mydas*). *Virology* 321:101–110. https://doi.org/10.1016/j.virol.2003.12.026

Greenblatt RJ, Work TM, Dutton P, Sutton CA, Spraker TR, Casey RN, Diez CE, Parker D, St. Leger J, Balazs GH, Casey JW (2005) Geographic variation in marine turtle fibropapillomatosis. *Journal of Zoo and Wildlife Medicine* 36:527–530. https://doi.org/10.1638/04-051.1

Grosbois V, Gimenez O, Gaillard J -M., Pradel R, Barbraud C, Clobert J, Møller AP, Weimerskirch H (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* 83:357–399. https://doi.org/10.1111/j.1469-185X.2008.00047.x

Hargrove SA, Work TM, Brunson S, Foley AM, Balazs GH (2016) Proceedings of the 2015 international summit on fibropapillomatosis : global status, trends, and population impacts. https://doi.org/10.7289/V5/TM-PIFSC-54

Herbst L, Jacobson E, Moretti R, Brown T, Sundberg J, Klein P (1995) Experimental transmission of green turtle fibropapillomatosis using cell-free tumor extracts. *Diseases of Aquatic Organisms* 22:1–12. https://doi.org/10.3354/dao022001

Herbst LH (1994) Fibropapillomatosis of marine turtles. *Annual Review of Fish Diseases* 4:389–425. https://doi.org/10.1016/0959-8030(94)90037-X

Hirama S, Ehrhart L (2007) Description, prevalence and severity of green turtle fibropapillomatosis in three developmental habitats on the east coast of Florida. *Florida Scientist* 70:435–448

Hirama S, Ehrhart L, Rea L, Kiltie R (2014) Relating fibropapilloma tumor severity to blood parameters in green turtles *Chelonia mydas*. *Diseases of Aquatic Organisms* 111:61–68. https://doi.org/10.3354/dao02765

Jeantet L, Planas-Bielsa V, Benhamou S, Geiger S, Martin J, Siegwalt F, Lelong P, Gresser J, Etienne D, Hiélard G, Arque A, Regis S, Lecerf N, Frouin C, Benhalilou A, Murgale C, Maillet T, Andreani L, Campistron G, Delvaux H, Guyon C, Richard S, Lefebvre F, Aubert N, Habold 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. *Royal Society Open Science* 7:200139. https://doi.org/10.1098/rsos.200139

Jones AG (2004) Sea turtles: old viruses and new tricks. *Current Biology* 14:R842–R843. https://doi.org/10.1016/j.cub.2004.09.038

Jones K, Ariel E, Burgess G, Read M (2016) A review of fibropapillomatosis in Green turtles (*Chelonia mydas*). *The Veterinary Journal* 212:48–57. https://doi.org/10.1016/j.tvjl.2015.10.041

Jones K, Burgess G, Budd AM, Huerlimann R, Mashkour N, Ariel E (2020) Molecular evidence for horizontal transmission of chelonid alphaherpesvirus 5 at green turtle (*Chelonia mydas*) foraging grounds in Queensland, Australia. *PLOS ONE* 15:e0227268. https://doi.org/10.1371/journal.pone.0227268

Jones K, Limpus CJ, Brodie J, Jones R, Read M, Shum E, Bell IP, Ariel E (2022) Spatial distribution of fibropapillomatosis in green turtles along the Queensland coast and an investigation into the influence of water quality on prevalence. *Conservation Science and Practice* 4:e12755. https://doi.org/10.1111/csp2.12755

Kane RA, Christodoulides N, Jensen IM, Becker DJ, Mansfield KL, Savage AE (2021) Gene expression changes with tumor disease and leech parasitism in the juvenile green sea turtle skin transcriptome. *Gene* 800:145800. https://doi.org/10.1016/j.gene.2021.145800

Kelley JR, Kelley KL, Savage AE, Mansfield KL (2022) Novel disease state model finds most juvenile green turtles develop and recover from fibropapillomatosis. *Ecosphere* 13:e4000. https://doi.org/10.1002/ecs2.4000

Kubis S, Chaloupka M, Ehrhart L, Bresette M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. *Marine Ecology Progress Series* 389:257–269. https://doi.org/10.3354/meps08206

Labrada-Martagón V, Islas Madrid NL, Yáñez-Estrada L, Muñoz-Tenería FA, Solé M, Zenteno-Savín T (2024) Evidence of oxidative stress responses of green turtles (Chelonia mydas) to differential habitat conditions in the Mexican Caribbean. *Science of The Total Environment* 946:174151. https://doi.org/10.1016/j.scitotenv.2024.174151

Lachish S, Jones M, McCallum H (2007) The impact of disease on the survival and population growth rate of the tasmanian devil. *Journal of Animal Ecology* 76:926–936

Landry MS, Taggart CT (2010) "Turtle watching" conservation guidelines: green turtle (*Chelonia mydas*) tourism in nearshore coastal environments. *Biodiversity and Conservation* 19:305–312. https://doi.org/10.1007/s10531-009-9707-2

Lelong P, Besnard A, Girondot M, Habold C, Priam F, Giraudeau M, Le Loc'h G, Le Loc'h A, Fournier P, Fournier-Chambrillon C, Bustamante P, Dupont SM, Vincze O, Gros-Desormeaux J-R, Martin J, Bourgeois O, Lepori M, Régis S, Lecerf N, Lefebvre F, Aubert N, Frouin C, Flora F, Pimentel E, Pimentel M, Siegwalt F, Jeantet L, Chambault P, Hielard G, Arqué A, Arthus M, Louis-Jean L, Brador A, Giannasi P, Etienne D, Lecerf N, Chevallier P, Chevallier T, Meslier S, Landreau A, Maceno M, Larcher E, Le Maho Y, Chevallier D (2024) Demography of endangered juvenile green turtles in face of environmental changes: 10 years of capture-mark-recapture efforts in Martinique. *Biological Conservation* 291:110471. https://doi.org/10.1016/j.biocon.2024.110471

Li T-H, Chang C-C (2020) The impact of fibropapillomatosis on clinical characteristics, blood gas, plasma biochemistry, and hematological profiles in juvenile green turtles (*Chelonia mydas*). *Bulletin of Marine Science* 96:723–734. https://doi.org/10.5343/bms.2019.0120

Lu Y, Yu Q, Zamzow JP, Wang Y, Losey GS, Balazs GH, Nerurkar VR, Yanagihara R (2000) Detection of green turtle herpesviral sequence in saddleback wrasse *Thalassoma duperrey*: A possible mode of transmission of green turtle fibropapilloma. 12:58–63

Mahmoudabadi G, Milo R, Phillips R (2017) Energetic cost of building a virus. *Proceedings of the National Academy of Sciences* 114:E4324–E4333. https://doi.org/10.1073/pnas.1701670114

Manes C, Pinton D, Canestrelli A, Capua I (2022) Occurrence of fibropapillomatosis in green turtles (*chelonia mydas*) in relation to environmental changes in coastal ecosystems in Texas and Florida: a retrospective study. *Animals* 12:1236. https://doi.org/10.3390/ani12101236

Martin KR, Mansfield KL, Savage AE (2022) Adaptive evolution of major histocompatibility complex class I immune genes and disease associations in coastal juvenile sea turtles. *Royal Society Open Science* 9:211190. https://doi.org/10.1098/rsos.211190

Monteiro J, Duarte M, Amadou K, Barbosa C, El Bar N, Madeira FM, Regalla A, Duarte A, Tavares L, Patrício AR (2021) Fibropapillomatosis and the chelonid alphaherpesvirus 5 in green turtles from West Africa. *EcoHealth* 18:229–240. https://doi.org/10.1007/s10393-021-01526-y

Muñoz Tenería F, Labrada-Martagón V, Herrera-Pavón R, Work T, González-Ballesteros E, Negrete-Philippe A, Maldonado-Saldaña G (2022) Fibropapillomatosis dynamics in green sea turtles *Chelonia mydas* over 15 years of monitoring in Akumal Bay, Quintana Roo, Mexico. *Diseases of Aquatic Organisms* 149:133–143. https://doi.org/10.3354/dao03669

O'Connell D, Kehl CE, Taylor BK, Piacenza J, Piacenza S, Faller Ii KJ (2021) A computational framework for studying energetics and resource management in sea turtle migration and autonomous systems. *Journal of Theoretical Biology* 527:110815. https://doi.org/10.1016/j.jtbi.2021.110815

Oduor NA, Munga CN, Imbayi LK, Botwe PK, Nyanjong EO, Muthama CM, Mise NA, Moosdorf N (2024) Anthropogenic nutrients and phytoplankton diversity in Kenya's coastal waters: An ecological quality assessment of sea turtle foraging sites. *Marine Pollution Bulletin* 199:115897. https://doi.org/10.1016/j.marpolbul.2023.115897

Page-Karjian A, Gottdenker NL, Whitfield J, Herbst L, Norton TM, Ritchie B (2017) Potential Noncutaneous Sites of Chelonid Herpesvirus 5 Persistence and Shedding in Green Sea Turtles *Chelonia mydas*. *Journal of Aquatic Animal Health* 29:136–142. https://doi.org/10.1080/08997659.2017.1321590

Page-Karjian A, Norton T, Ritchie B, Brown C, Mancia C, Jackwood M, Gottdenker N (2015) Quantifying chelonid herpesvirus 5 in symptomatic and asymptomatic rehabilitating green sea turtles. *Endangered Species Research* 28:135–146. https://doi.org/10.3354/esr00687

Page-Karjian A, Torres F, Zhang J, Rivera S, Diez C, Moore PA, Moore D, Brown C (2012) Presence of chelonid fibropapilloma-associated herpesvirus in tumored and non-tumored green turtles, as detected by polymerase chain reaction, in endemic and non-endemic aggregations, Puerto Rico. *SpringerPlus* 1:35. https://doi.org/10.1186/2193-1801-1-35

Patrício A, Diez C, van Dam R, Godley B (2016) Novel insights into the dynamics of green turtle fibropapillomatosis. *Marine Ecology Progress Series* 547:247–255. https://doi.org/10.3354/meps11644

Patrício AR, Velez-Zuazo X, Diez CE, Van Dam R, Sabat AM (2011) Survival probability of immature green turtles in two foraging grounds at Culebra, Puerto Rico. *Marine Ecology Progress Series* 440:217–227. https://doi.org/10.3354/meps09337

Patrício R, Diez C, van Dam R (2014) Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. *Endangered Species Research* 23:51–62. https://doi.org/10.3354/esr00554

Perrault JR, Levin M, Mott CR, Bovery CM, Bresette MJ, Chabot RM, Gregory CR, Guertin JR, Hirsch SE, Ritchie BW, Weege ST, Welsh RC, Witherington BE, Page-Karjian A (2021) Insights on immune function in free-ranging green sea turtles (*Chelonia mydas*) with and without fibropapillomatosis. *Animals* 11:861. https://doi.org/10.3390/ani11030861

Perrault JR, Stacy NI, Lehner AF, Mott CR, Hirsch S, Gorham JC, Buchweitz JP, Bresette MJ, Walsh CJ (2017) Potential effects of brevetoxins and toxic elements on various health variables in Kemp's ridley (*Lepidochelys kempii*) and green (*Chelonia mydas*) sea turtles after a red tide bloom event. *Science of The Total Environment* 605–606:967–979. https://doi.org/10.1016/j.scitotenv.2017.06.149

Pesavento PA, Agnew D, Keel MK, Woolard KD (2018) Cancer in wildlife: patterns of emergence. *Nature Reviews Cancer* 18:646–661. https://doi.org/10.1038/s41568-018-0045-0

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

Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949–954

Pradel R (2005) Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* 61:442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

R Core Team (2023) 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 N, Frouin C, Lefebvre F, Aubert N, Flora F, Pimentel E, Lafolle R, Thobor F, Arthus M, Etienne D, Lecerf N, Allenou J-P, Desigaux F, Larcher E, Larcher C, Curto AL, Befort J, Maceno-Panevel M, Lepori M, Chevallier P, Chevallier T, Meslier S, Landreau A, Habold 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

Rossi S, Sánchez-Sarmiento AM, Vanstreels RET, dos Santos RG, Prioste FES, Gattamorta MA, Grisi-Filho JHH, Matushima ER (2016) Challenges in evaluating the severity of fibropapillomatosis: a proposal for objective index and score system for green sea turtles (*Chelonia mydas*) in Brazil. *PLOS ONE* 11:e0167632. https://doi.org/10.1371/journal.pone.0167632

Schaub M, Pradel R, Jenni L, Lebreton J-D (2001) Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. *Ecology* 82:852. https://doi.org/10.2307/2680203

Scheele BC, Pasmans F, Skerratt LF, Berger L, Martel A, Beukema W, Acevedo AA, Burrowes PA, Carvalho T, Catenazzi A, De La Riva I, Fisher MC, Flechas SV, Foster CN, Frías-Álvarez P, Garner TWJ, Gratwicke B, Guayasamin JM, Hirschfeld M, Kolby JE, Kosch TA, La Marca E, Lindenmayer DB, Lips KR, Longo AV, Maneyro R, McDonald CA, Mendelson J, Palacios-Rodriguez P, Parra-Olea G, Richards-Zawacki CL, Rödel M-O, Rovito SM, Soto-Azat C, Toledo LF, Voyles J, Weldon C, Whitfield SM, Wilkinson M, Zamudio KR, Canessa S (2019) Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363:1459–1463. https://doi.org/10.1126/science.aav0379

Sebastiano M, Chastel O, De Thoisy B, Eens M, Costantini D (2016) Oxidative stress favours herpes virus infection in vertebrates: a meta-analysis. *Current Zoology* 62:325–332. https://doi.org/10.1093/cz/zow019

Seminoff JA (2004) *Chelonia mydas*: The IUCN Red List of Threatened Species

Siegwalt F, Benhamou S, Girondot M, Jeantet L, Martin J, Bonola M, Lelong P, Grand C, Chambault P, Benhalilou A, Murgale C, Maillet 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, Vedie 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, Chanteur B, Béranger C, Crillon J, Brador A, Habold 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. *Biological Conservation* 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, Habold 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*. *Global Ecology and Conservation* 37:e02169. https://doi.org/10.1016/j.gecco.2022.e02169

Sposato P, Keating P, Lutz PL, Milton SL (2021) Evaluation of immune function in two populations of green sea turtles (*Chelonia mydas*) in a degraded versus a nondegraded habitat. *Journal of Wildlife Diseases* 57:761–772. https://doi.org/10.7589/JWD-D-20-00204

Stringell TB, Clerveaux WV, Godley BJ, Phillips Q, Ranger S, Richardson PB, Sanghera A, Broderick AC (2015) Fisher choice may increase prevalence of green turtle fibropapillomatosis disease. *Frontiers in Marine Science* 2:57. https://doi.org/10.3389/fmars.2015.00057

Sugiura N (1978) Further analysis of the data by Akaike's information criterion and the finite corrections: Further analysis of the data by akaike' s. *Communications in Statistics - Theory and Methods* 7:13–26. https://doi.org/10.1080/03610927808827599

Tosic M, Martins F, Lonin S, Izquierdo A, Restrepo JD (2019) Hydrodynamic modelling of a polluted tropical bay: Assessment of anthropogenic impacts on freshwater runoff and estuarine water renewal. *Journal of Environmental Management* 236:695–714. https://doi.org/10.1016/j.jenvman.2019.01.104

Van Houtan KS, Hargrove SK, Balazs GH (2010) Land use, macroalgae, and a tumor-forming disease in marine turtles. *PLoS ONE* 5:e12900. https://doi.org/10.1371/journal.pone.0012900

Williams EH, Bunkley-Williams L, Peters EC, Pinto-Rodriguez B, Matos-Morales R, Mignucci-Giannoni AA, Hall KV, Rueda-Almonacid JV, Sybesma J, De Calventi IB, Boulon RH (1994) An Epizootic of Cutaneous Fibropapillomas in Green *Turtles Chelonia* mydas of the Caribbean: Part of a Panzootic? *Journal of Aquatic Animal Health* 6:70–78. https://doi.org/10.1577/1548-8667(1994)006<0070:AEOCFI>2.3.CO;2

Work TM, Ackermann M, Casey JW, Chaloupka M, Herbst L, Lynch JM, Stacy BA (2014) The story of invasive algae, arginine, and turtle tumors does not make sense

Work TM, Balazs GH (1999) Relating tumor score to hematology in green turtles with fibropapillomatosis in Hawaii. *Journal of Wildlife Diseases* 35:804–807. https://doi.org/10.7589/0090-3558-35.4.804

Work TM, Dagenais J, Willimann A, Balazs G, Mansfield K, Ackermann M (2020) Differences in antibody responses against chelonid alphaherpesvirus 5 (ChHV5) suggest differences in virus biology in ChHV5-seropositive green turtles from Hawaii and ChHV5-seropositive green turtles from Florida. *Journal of Virology* 94:15. https://doi.org/10.1128/ JVI.01658-19

Work TM, Rameyer RA, Balazs GH, Cray C, Chang SP (2001) Immune status of free-ranging green turtles with fibropapillomatosis from Hawaii. *Journal of Wildlife Diseases* 37:574–581. https://doi.org/10.7589/0090-3558-37.3.574

Xie T, Liu W, Anderson BD, Liu X, Gray GC (2017) A system dynamics approach to understanding the One Health concept. *PLOS ONE* 12:e0184430. https://doi.org/10.1371/journal.pone.0184430

Yetsko K, Farrell JA, Blackburn NB, Whitmore L, Stammnitz MR, Whilde J, Eastman CB, Ramia DR, Thomas R, Krstic A, Linser P, Creer S, Carvalho G, Devlin MA, Nahvi N, Leandro AC, deMaar TW, Burkhalter B, Murchison EP, Schnitzler C, Duffy DJ (2021) Molecular characterization of a marine turtle tumor epizootic, profiling external, internal and postsurgical regrowth tumors. *Communications Biology* 4:152. https://doi.org/10.1038/s42003-021-01656-7

Zamana RR, Gattamorta MA, Cruz Ochoa PF, Navas-Suárez PE, Sacristán C, Rossi S, Grisi-Filho JHH, Silva IS, Matushima ER (2021) High occurrence of chelonid alphaherpesvirus 5 (ChHV5) in green sea turtles *Chelonia mydas* with and without fibropapillomatosis in feeding areas of the São Paulo coast, Brazil. *Journal of Aquatic Animal Health* 33:252–263. https://doi.org/10.1002/aah.10142

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*). The best model for each step is in bold and the best model of the overall procedure is in bold red.

Step	N°	Model	N Par.	Deviance	QAICc	ΔQAICc
	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
p	**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
	6	Φ(SizexFP2)Ψ(FPxt+Site)δ(FP)p(Site+logEC+Turb)	36	2924.4745	3000,2161	20,786
Φ	**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
	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
Ψ	**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
	16	Φ(SMJ. LJxFP3)Ψ(Dev.+Recxt+Site)δ(FP2)p(Site+logEC+Turb)	26	2931.2026	2985.1472	5.7171
δ	**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

Abbreviations: "**.**", 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*). Best models are highlighted in bold.

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**

Abbreviations: CCL, minimum curved carapace length; N par., Number of parameters.

Table 3: Model selection among Linear Mixed Models applied to log(Total Tumor Area). Best model is highlighted in bold.

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

Abbreviations: CCL, minimum curved carapace length; NPP, net primary production; poly(CCL, 2), quadratic polynomial of CCL; SSTa, sea surface temperature anomaly; TTA, total tumor area

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).

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.

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.

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.

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.

Supplementary materials

Fibropapillomatosis dynamics, severity and demographic effect in Caribbean green turtles

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Supplementary materials

GEPAT matrix in E-SURGE v2.2.3

Initial state

$$\begin{bmatrix} 1 & 2 & 3 & 4 & 5 & 6 \\ \pi_1 & \pi_2 & \pi_3 & \pi_4 & \pi_5 & * \end{bmatrix}$$

FP transition rate Ψ :

$$\begin{array}{c} \\ 1 \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \\ \dagger \end{array} \begin{bmatrix} 1 & 2 & 3 & 4 & 5 & 6 & \dagger \\ * & \Psi_{12} & - & - & - & - & - \\ - & * & \Psi_{23} & - & - & - & - \\ - & - & * & - & - & - & - \\ - & - & - & * & \Psi_{45} & - & - \\ - & - & - & - & * & \Psi_{56} & - \\ - & - & - & - & - & * & - \\ - & - & - & - & - & - & * \end{bmatrix}$$

Apparent survival Φ :

$$\begin{array}{c} \\ 1 \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \\ \dagger \end{array} \begin{bmatrix} A1 & A2 & A3 & A4 & A5 & A6 & \dagger \\ \varphi_1 & - & - & - & - & - & * \\ - & \varphi_2 & - & - & - & - & * \\ - & - & \varphi_3 & - & - & - & * \\ - & - & - & \varphi_4 & - & - & * \\ - & - & - & - & \varphi_5 & - & * \\ - & - & - & - & - & \varphi_6 & * \\ - & - & - & - & - & - & * \end{bmatrix}$$

Size development rate δ :

$$\begin{array}{c} \\ A1 \\ A2 \\ A3 \\ A4 \\ A5 \\ A6 \\ \dagger \end{array} \begin{bmatrix} 1 & 2 & 3 & 4 & 5 & 6 & \dagger \\ * & - & - & \delta_{14} & - & - & - \\ - & * & - & - & \delta_{25} & - & - \\ - & - & * & - & - & \delta_{36} & - \\ - & - & - & * & - & - & - \\ - & - & - & - & * & - & - \\ - & - & - & - & - & * & - \\ - & - & - & - & - & - & * \end{bmatrix}$$

Recapture rate p:

$$\begin{array}{c} \\ 1 \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \\ \dagger \end{array} \begin{bmatrix} 0 & 1 & 2 & 3 & 4 \\ * & p_1 & - & - & - \\ * & - & p_2 & - & - \\ * & p_3 & - & - & - \\ * & - & - & p_4 & - \\ * & - & - & - & p_5 \\ * & - & - & p_6 & - \\ * & - & - & - & - \end{bmatrix}$$

$\dagger$: Dead, Ai : alive in state i.

Supplementary materials
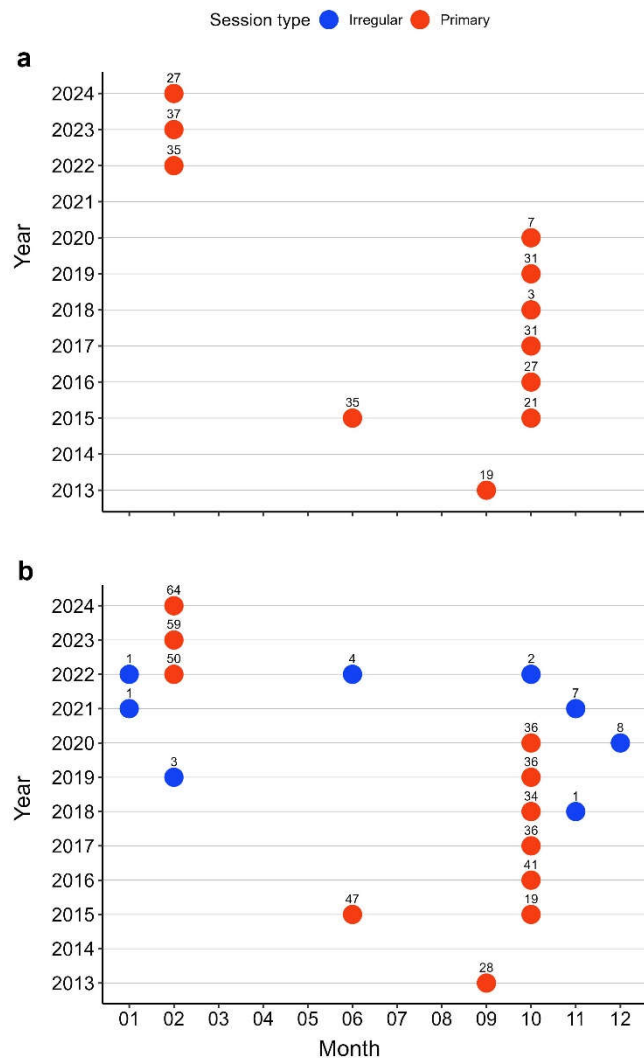
Figures

Figure S1 : Calendar of capture occasions of green sea turtles (*Chelonia mydas*) in (a)

Grande Anse d'Arlet and (b) Anse du Bourg d'Arlet/Chaudière between 2013 and 2024.

Primary and irregular capture occasions are represented by red and blue dots respectively.

The number of turtles captured per session is indicated above each point.

Supplementary materials
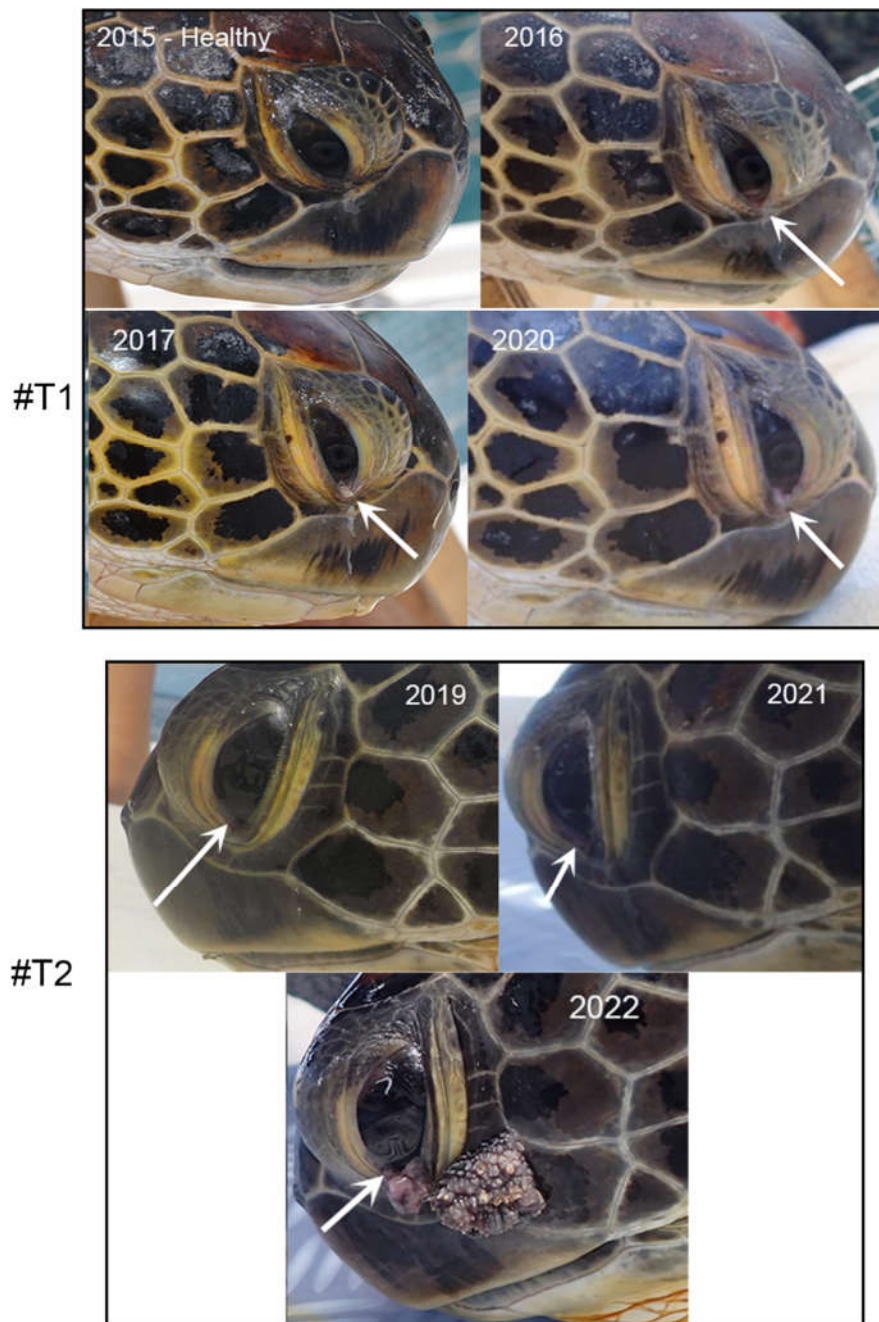
Figure S2: Example of inconspicuous tumors detected in green sea turtles (*Chelonia mydas*) using photographic monitoring. Eye tumor of turtle #1 (#T1) was confirmed in 2016 using the 2017 and 2020 pictures where the same tumor was more developed. For comparison, we provided #T1 eye picture in 2015 without tumor. For turtle #2 (#T2), tumor was slightly visible behind the anterior eyelid in 2019 and 2021 and could be confounded with the third eyelid.The neoplastic nature of the object was confirmed by photography of the same animal in 2022.

Supplementary materials
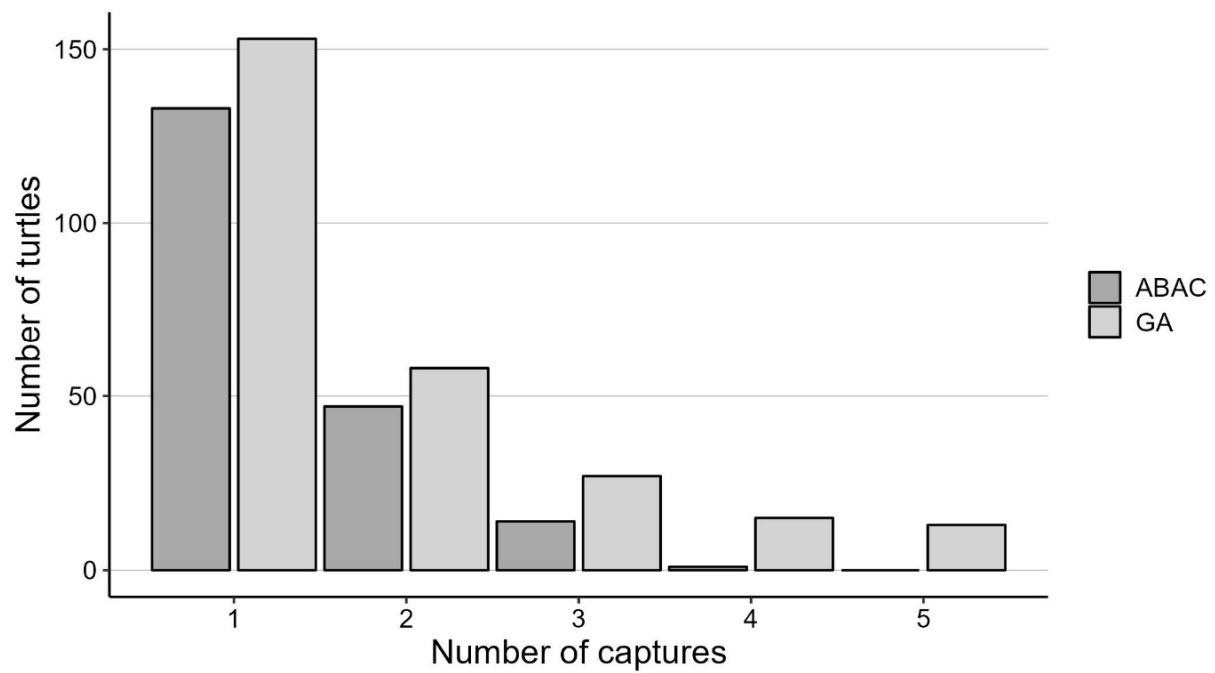
Figure S3: Individual specific-number of captures of green sea turtles (*Chelonia mydas*) in the dataset used for capture-mark-recapture analysis. Abbreviations : ABAC, Anse du Bourg d'Arlet/Chaudière; GA, Grande Anse d'Arlet

Supplementary materials
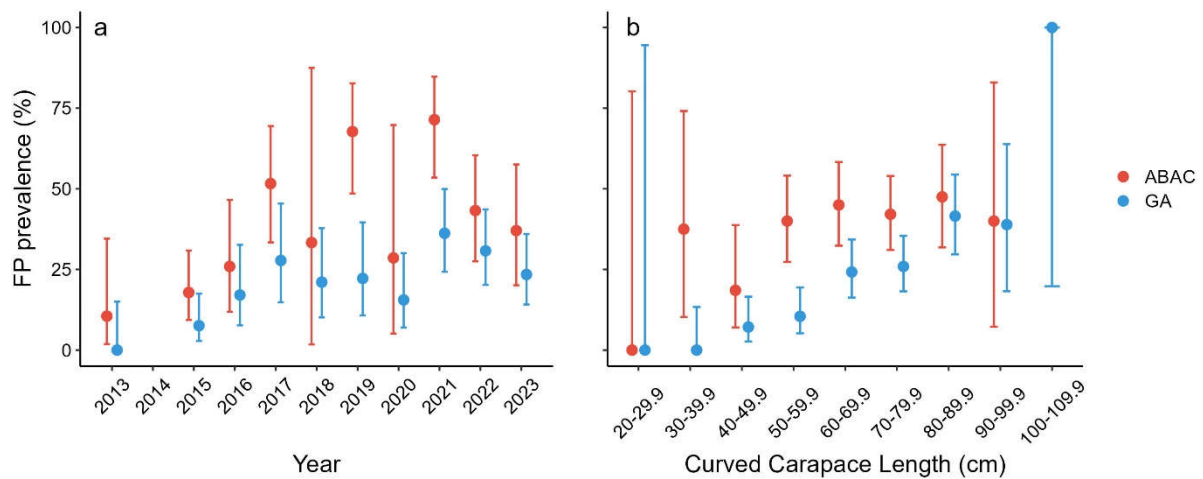
Figure S4: Observed fibropapillomatosis (FP) prevalence with Wilson 95% binomial confidence intervals (Wilson 1927) in Anse du Bourg d'Arlet/Chaudière (ABAC, red) and Grande Anse d'Arlet (GA, blue) by (a) year (2013–2023) and (b) 10 cm minimum curved carapace length (CCL, cm) classes.

Supplementary materials
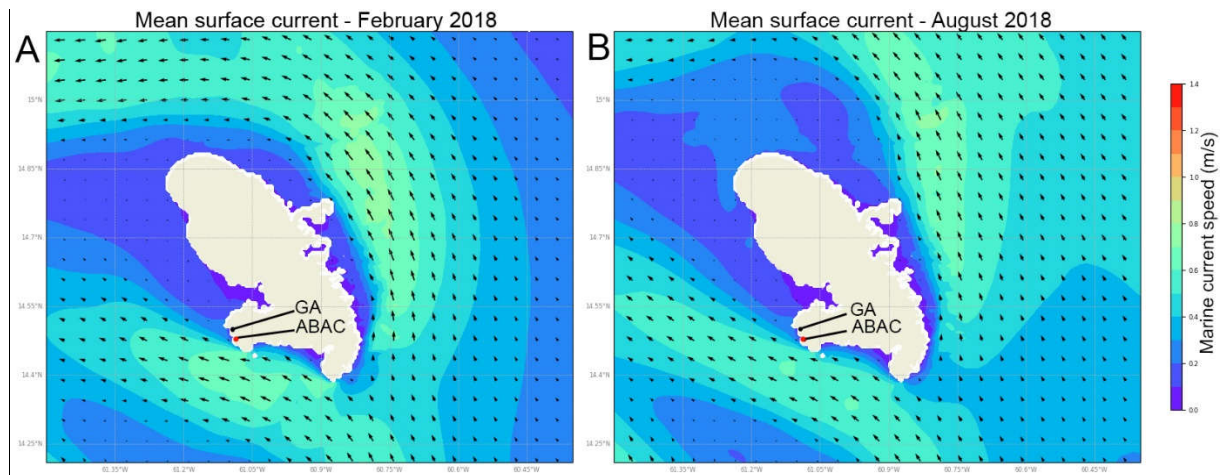
Figure S5: Mean surface current direction and speed around Martinique island in (A) February 2018 and (B) August 2018. Marine current direction is indicated by dark arrows and speed is provided by color range. Anse du Bourg d'Arlet/Chaudière (ABAC), where pollution event occurred (red point) and Grande Anse d'Arlet (GA) are indicated. Maps are extracted from IFREMER - ACTIMAR report (2020).

Supplementary materials

Tables

Table S1 : Capture number of green sea turtles (*Chelonia mydas*) *per* year (total and with fibropapillomatosis [FP]) and number of total tumor area (TTA) measurements for the dataset used in capture-mark-recapture analysis. Abbreviations : ABAC, Anse du Bourg d'Arlet/Chaudière; GA, Grande Anse d'Arlet

| Site	Year	Total captures	Total captures with FP	Number of TTA measurements
ABAC	2013	19	2	0
	2014	0	0	0
	2015	56	10	0
	2016	27	7	2
	2017	31	16	7
	2018	3	1	1
	2019	31	21	12
	2020	7	2	2
	2021	35	25	24
	2022	37	16	16
	2023	27	10	10
Subtotal ABAC		273	110	74
GA	2013	28	0	0
	2014	0	0	0
	2015	66	5	0
	2016	41	7	0
	2017	36	10	1
	2018	38	8	0
	2019	36	8	4
	2020	45	7	2
	2021	58	21	20
	2022	65	20	19
	2023	64	15	15
Subtotal GA		477	101	61
Total		**750**	**211**	**135**

Supplementary materials

Table S2: Site-specific mean minimum curved carapace length (cm) of green sea turtles (*Chelonia mydas*) at first capture in the different fibropapillomatosis statuses and associated standard deviation (SD).

Health status	Site	Size at first capture (cm)	
		Mean	*SD*
Non-afflicted	Anse du Bourg/Chaudière	53.6	10.7
Afflicted	Anse du Bourg/Chaudière	67.0	12.4
Recovered	Anse du Bourg/Chaudière	70.2	12.3
Non-afflicted	Grande Anse	54.8	12.5
Afflicted	Grande Anse	70.7	12.9
Recovered	Grande Anse	78.2	15.3

Supplementary materials

Table S3: Summary of the ANODEV tests for fibropapillomatosis development and recovery rate parameters for sea surface temperature anomaly (SSTa), net primary production (NPP), salinity and pollution.

Parameter	Model	Deviance	N par	F-stat	df1	df2	p-value
	Constant	2945.35	19				
	Time	2923.58	27				
	SSTa	2943.13	20	3.34	1	7	0.11
Development	NPP	2944.75	20	0.68	1	7	0.44
	Salinity	2945.09	20	0.28	1	7	0.61
	Pollution	2945.19	20	0.17	1	7	0.69
	Pollution (ABAC only)	2944.27	20	1.31	1	7	0.29
	Constant	2945.35	19				
	Time	2923.58	27				
	SSTa	2939.73	20	2.44	1	7	0.16
Recovery	NPP	2942.57	20	1.02	1	7	0.35
	Salinity	2944.79	20	0.19	1	7	0.68
	Pollution	2943.52	20	0.64	1	7	0.45
	Pollution (ABAC only)	2943.75	20	0.55	1	7	0.48

N par = number of parameters, *df1* = (number of parameter Covariate – number of parameter Constant), *df2* = (number of parameter Time – number of parameter Covariate)

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Table S4: Summary of the best CMR model output : **(SizexFP3)Psi(Dev.+Recxt+Site)d(FP3)p(Site+logEC+Turb)**. Estimated probabilities are provided for initial state at first capture, FP development rates (Ψ_1), FP recovery rates (Ψ_2), apparent survival (Φ), size development rate (δ) and recapture rate (p). Param. = Parameters, CI-/CI+ = Respectively lower and upper confidence intervals (95%), SE = Standard error. "-" means that the effect is constant. Abbreviations: ABAC, Anse du Bourg d'Arlet/Chaudière; GA, Grande Anse d'Arlet

Param.	Site	Size-class	FP status	Year	Estimate	CI-	CI+	SE
Initial state	-	SMJ	Non-afflicted	-	0.56	0.51	0.60	0.02
	-	SMJ	Afflicted	-	0.12	0.10	0.16	0.02
	-	SMJ	Recovered	-	0	0	0	0
	-	LJ	Non-afflicted	-	0.07	0.03	0.16	0.03
	-	LJ	Afflicted	-	0.10	0.08	0.13	0.01
Ψ_1	ABAC	-	-	-	0.28	0.17	0.42	0.07
	GA	-	-	-	0.14	0.10	0.20	0.02
Ψ_2	ABAC	-	-	2013/2014	0.88	0.04	1.00	0.28
	ABAC	-	-	2015	0.57	0.16	0.91	0.25
	ABAC	-	-	2016	0	0	0	0
	ABAC	-	-	2017	0.26	0.05	0.71	0.19
	ABAC	-	-	2018	0.14	0.02	0.54	0.12
	ABAC	-	-	2019	0	0	0	0
	ABAC	-	-	2020	0	0	0	0
	ABAC	-	-	2021	0.49	0.28	0.71	0.12
	ABAC	-	-	2022	0.47	0.24	0.72	0.14
	GA	-	-	2013/2014	0.76	0.02	1.00	0.48
	GA	-	-	2015	0.37	0.07	0.81	0.24
	GA	-	-	2016	0	0	0	0
	GA	-	-	2017	0.13	0.02	0.53	0.12
	GA	-	-	2018	0.06	0.01	0.35	0.06
	GA	-	-	2019	0	0	0	0
	GA	-	-	2020	0	0	0	0
	GA	-	-	2021	0.30	0.14	0.51	0.10
	GA	-	-	2022	0.28	0.12	0.53	0.11
Φ	-	SMJ	-	-	0.9	0.82	0.94	0.03
	-	LJ	Non-afflicted+Afflicted	-	0.71	0.61	0.8	0.05
	-	LJ	Recovered	-	0.37	0.24	0.52	0.07
δ	-	SMJ	Non-afflicted+Afflicted	-	0.29	0.23	0.35	0.03
	-	SMJ	Recovered	-	0.61	0.37	0.81	0.12
p	ABAC	-	-	2015	0.67	0.48	0.82	0.09
	ABAC	-	-	2016	0.24	0.18	0.31	0.03
	ABAC	-	-	2017	0.35	0.27	0.44	0.04
	ABAC	-	-	2018	0.15	0.09	0.24	0.04
	ABAC	-	-	2019	0.19	0.13	0.27	0.03
	ABAC	-	-	2020	0.15	0.09	0.24	0.04
	ABAC	-	-	2021	0.30	0.23	0.37	0.04
	ABAC	-	-	2022	0.29	0.22	0.37	0.04
	ABAC	-	-	2023	0.26	0.20	0.33	0.03
	GA	-	-	2015	0.82	0.67	0.91	0.06
	GA	-	-	2016	0.41	0.34	0.48	0.04

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GA	-	-	2017	0.54	0.46	0.62	0.04
GA	-	-	2018	0.29	0.19	0.40	0.05
GA	-	-	2019	0.34	0.27	0.43	0.04
GA	-	-	2020	0.29	0.20	0.40	0.05
GA	-	-	2021	0.48	0.41	0.55	0.03
GA	-	-	2022	0.48	0.41	0.55	0.04
GA	-	-	2023	0.44	0.37	0.50	0.03

Supplementary materials

References

IFREMER - ACTIMAR (2020) Final Report - Projet CARIB-COAST- Modélisation de la circulation 3D des masses d'eau, 72p

Wilson EB (1927) Probable inference, the law of succession, and statistical inference. Journal of the American Statistical Association 22:209–212. https://doi.org/10.1080/01621459.1927.10502953