Received: 14 July 2021 | Revised: 26 October 2021 | Accepted: 17 November 2021

DOI: 10.1002/ecs2.4000

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Disease Ecology

Novel disease state model finds most juvenile green turtles develop and recover from fibropapillomatosis

Jake R. Kelley | **Kayla L. Kelley** | **Anna E. Savage** | **Kate L. Mansfield**

Department of Biology, University of Central Florida, Orlando, Florida, USA

Correspondence
Kate L. Mansfield
Email: kate.mansfield@ucf.edu

Funding information
Sea Turtle Grants Program; UCF College of Graduate Studies Open Access Publishing Fund

Handling Editor: Andrew Wargo

Abstract

Fibropapillomatosis (FP) is a sea turtle disease characterized by benign tumor development on the skin, eyes, and/or internal organs. It primarily affects juvenile green turtles (*Chelonia mydas*) in coastal foraging sites. The Indian River Lagoon (IRL), Florida, USA, is a coastal green turtle foraging site where the observed FP annual rate averaged 49% between 1983 and 2018. While FP is no longer considered a major cause of sea turtle mortality and most individuals fully recover, the overall dynamics of this disease are poorly understood because prior disease history is unknown for individuals without FP at capture time, and future disease outcome is unknown for individuals with FP at capture time. To better evaluate FP dynamics for green turtles in the IRL, we developed a hierarchical model for predicting disease state change. We used data from 4149 captures of 3700 individual green turtles captured in the IRL. The hierarchical disease state model contained two levels: Level 1 modeled whether an individual would develop FP, and Level 2 modeled disease state progression, including states for pre-FP affliction, active FP affliction, and full recovery from FP. From the hierarchical model, we estimated 99.8% (95% credibility intervals 99.1%–100%) of juvenile green turtles in the IRL developed FP, indicating that nearly every individual in the IRL is affected by this disease. The model also suggested that turtles quickly developed FP upon recruitment to the IRL and then recovered at different rates, with most completely recovering before emigrating from the IRL as they mature. This is the first analysis of long-term sea turtle data suggesting nearly every turtle in an aggregation both develops and recovers from FP.

KEYWORDS
Chelonia mydas, disease ecology, fibropapillomatosis, green sea turtle, hierarchical Bayesian modeling, Indian River Lagoon

INTRODUCTION

Fibropapillomatosis (FP) is a sea turtle disease found in every ocean basin and documented in all seven species in this group (Herbst, 1994, reviewed in K. Jones et al., 2016). FP affects juvenile green turtles (*Chelonia mydas*) in coastal habitats and is characterized by the proliferation of benign tumors on the skin, eyes, and/or

internal organs of afflicted individuals (see Figure 1) (Herbst, 1994; Lucké, 1938; Smith & Coates, 1938). Severe tumors may impair an individual by hindering locomotion, obstructing vision, and disrupting organ functions (Brooks et al., 1994; Chaloupka et al., 2008; Foley et al., 2005; Herbst, 1994). These and other complications from FP can be the cause of death for some turtles (Chaloupka et al., 2008; Flint et al., 2010; Work et al., 2004). However, FP does not appear to be a major cause of mortality in sea turtles overall (Borrowman, 2008; Patrício et al., 2011; Hargrove et al., 2016; reviewed in K. Jones et al., 2016). Full regression of FP tumors occurs naturally (Ehrhart, 1991; Hirama & Ehrhart, 2007; Machado Guimarães et al., 2013; Patrício et al., 2016), and most turtles afflicted with FP fully recover from the disease (Hargrove et al., 2016; Patrício et al., 2016). The causes of FP are unclear, but are likely a multifactorial etiology involving an infectious pathogen along with environmental and immunological factors (Aguirre, 1991; Herbst, 1994). Chelonid herpesvirus 5 (ChHV5) is significantly associated with FP tumors (Herbst et al., 1995; Quackenbush et al., 1998). Green turtles typically become infected with ChHV5 and develop FP while still immature and occupying coastal developmental foraging sites (Ene et al., 2005; Foley et al., 2005; Herbst, 1994; Hirama & Ehrhart, 2007; Patrício et al., 2016). Green turtles have several distinct life stages, spending the first couple years of their lives in offshore habitats, then shifting to coastal habitats as larger juveniles and eventually moving on to adult foraging sites near maturity (Lutz et al., 1997; Mansfield, Wyneken, & Luo, 2021). Fibropapillomatosis is common in the coastal juvenile life stage of green turtles and is absent or rare in other life stages (reviewed in K. Jones et al., 2016).

The Indian River Lagoon (IRL) is a mixed-stock juvenile green turtle foraging site on the east central coast of Florida, USA (Bagley, 2003) in the western North Atlantic. It is also the location of a long-term (1982–present) sea turtle mark–recapture program conducted by the University of Central Florida Marine Turtle Research Group (UCFMTRG). Over the course of this IRL study, over 3000 green turtles were captured and the prevalence of FP among these turtles averaged 49% (Hirama & Ehrhart, 2007). The duration of this study, number of captures, and high FP prevalence make this dataset one of the largest and most complete FP datasets for green turtles at a single site. Despite these extensive data, assessing the dynamics of FP remains difficult because of multiple unknowns related to sampling. Recapture rates in the IRL are just 10% for green turtles, thus long-term FP histories across multiple captures are relatively limited. If a turtle is captured without FP, no straightforward method exists to determine whether the turtle did or did not previously have FP and subsequently recover. Testing for ChHV5, the putative pathogen of FP, is not reliable for nontumor tissues (Lawrance et al., 2018; Page-Karjian et al., 2015; Quackenbush et al., 2001) further limiting insight for turtles without visible external FP tumors at the time of sampling. More information on probable

FIGURE 1 Images of juvenile green turtles afflicted with fibropapillomatosis. Photograph credit: Jake Kelley; UCFMTRG (permits NMFS #19508 and Florida MTP-231)

disease state for each turtle capture (healthy, afflicted with FP, recovered from FP) would allow for advancements in our understanding of FP dynamics including questions about why some turtles get FP but not others, timing of FP progression, and what factors affect the severity and length of time of individual FP affliction. Here, we developed a hierarchical model for disease state that provides insights into FP dynamics in the IRL. This model can be extended to further assessments of FP on a global scale.

METHODS

Study site and long-term data collection

The UCFMTRG conducted netting sessions for sea turtle sampling in the IRL (approximately 27.8312 N, −80.4395 W; Figure 2) starting in 1982 (Ehrhart et al., 2007). These sampling sessions typically occurred twice a month; 961 sessions occurred from 1982 through 2018. During each sampling event, UCFMTRG captured turtles using a 455-m-long large-mesh entanglement net that had a soak time of up to 3 h per session (Ehrhart et al., 2007). All captured turtles were tagged (flipper tags and/or PIT tags) using standardized protocols (Balazs, 1999) to keep track of individuals during any subsequent captures. Data we collected from each turtle and each capture event included straight carapace length (SCL, a standard size measurement for turtles; Bolten, 1999), FP status (presence/absence of external FP tumors), and capture date. We used data from 4149 captures of 3700 individuals from 1983 to 2018 in our analyses. We verified there were no major and obvious errors (besides small measurement error) in recorded SCL values and excluded any capture data with missing SCL values. Because transient adult green turtles were occasionally captured, we also excluded turtles greater than 79.9 cm SCL from our dataset to minimize mixing animals at contrasting developmental stages.

Data summarization and initial statistical analyses

We summarized the data and conducted all statistical analyses using the program R version 3.5.2 (R Core Development Team, 2018). This included creating histograms and plots of FP status variation by size (SCL), season, and year. We defined northern hemisphere seasons by monthly groupings, where March–May were grouped as spring, June–August were grouped as summer, September–November were grouped as fall, and December–February were grouped as winter.

We used logistic regression models to investigate the interactive effects of size (SCL) and season on probability of FP occurrence. Because of the nonlinear shape of their relationship, we evaluated FP status as a quadratic polynomial function of logarithm-transformed SCL considering variation among seasons. We compared four models: one with interactive effects of SCL and season, one with additive effects of SCL and season, one with just SCL, and one with just season.

We ran the models in a Bayesian framework using the program OpenBUGS version 3.2.3 via the R package R2OpenBUGS (Lunn et al., 2000; Sturtz et al., 2005). We used uninformed priors and set the MCMC settings to three chains of 3000 iterations with a 1000-iteration burn-in and chains thinned by two. We verified convergence of the model by inspecting trace plots and verifying Rhat values were less than 1.1 for all parameters. We evaluated goodness of fit by inspecting graphical plots of posterior predictive checks. We used deviance information criterion (DIC) values to compare the models and evaluated the results for the model with the lowest DIC.

Hierarchical modeling of FP state

Recapture rates in the IRL are relatively low, with most individuals only captured one or two times. Low recapture rates limit direct insight on disease status and progression over time for each turtle in the IRL because each capture represents a narrow snapshot of an individual's time in the IRL. Thus, to allow for inference on FP state with limited recapture data, we developed a Bayesian hierarchical model to predict FP state of green turtle captures based on SCL. By using SCL as an explanatory variable, we assumed that size-specific capture probabilities did not vary between FP and non-FP turtles (see "Discussion" for more detail on how this could affect results). To establish our FP states of interest, we defined State 0 as having not yet developed FP, State 1 as having FP, and State 2 as having fully cleared FP (see Figure 3). Because data were not available for disease state at every capture, we developed a dataset for FP state based on available information, where each turtle capture was assigned a binomial value for each FP state (0 for not belonging to that state, 1 for belonging to that state, and NA if not enough information to assign a value for that state). Every turtle captured with FP was assigned to State 1, and those without FP were assigned as not belonging to State 1. However, for turtles captured without FP, it is impossible to tell if that capture is State 0 or State 2 without appropriate recapture data. If a turtle captured without FP had a subsequent capture with FP, the capture was assigned to State 0. Likewise, if a turtle captured without FP had a preceding capture with FP, that

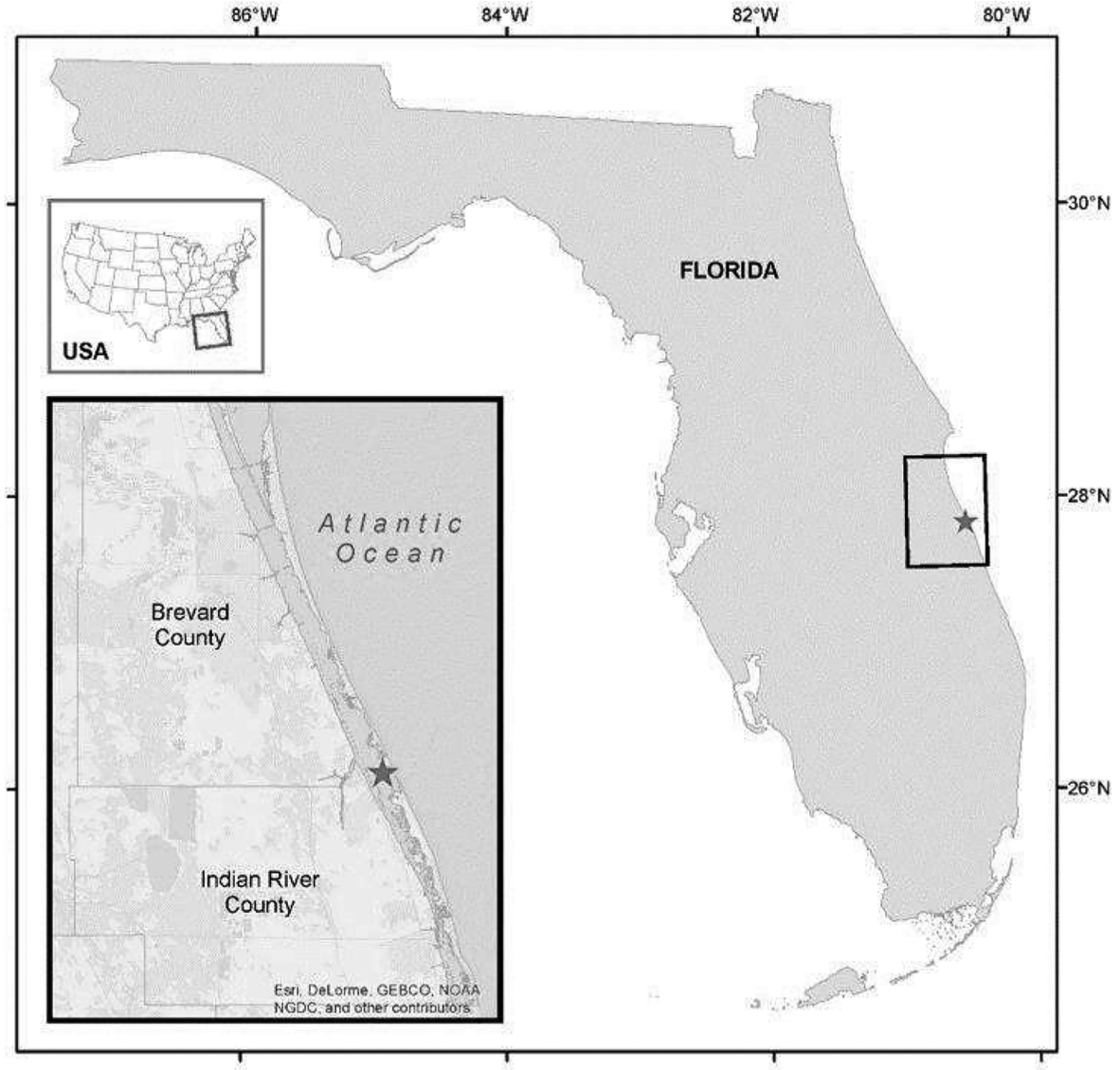

FIGURE 2 Map of Indian River Lagoon study location on the east, central coast of Florida, USA. This is the site of a long-term juvenile sea turtle sampling program conducted by UCFMTRG

capture was assigned to State 2. Any capture without enough information to determine State 0 or 2 was not assigned a value for those states (left as NA). The resulting dataset included binomial information (0, 1, or NA) for belonging to each disease state (State 0, pre-FP; State 1, FP; and State 2, post-FP) for each of the 4149 green turtle captures.

A diagram of the model system is in Figure 3 and the full model structure is shown in Table 1. The first level of the model is a logistic regression to predict whether an individual turtle will develop FP or not (Figure 3, Box A). This level of the model could also be used to assess the factors of interest that may impact whether or not a turtle develops FP, such as which nesting beach or oceanic habitat the turtle came from, diet, genetic factors, toxicology factors, immune factors like MHC genes (Martin et al., in review), and many others. However, in this study, we did not evaluate factors affecting FP development and assumed random FP development. The second level is a modified ordinal logistic regression to model the progression of FP through each disease state based on SCL (Figure 3, Box B). An ordinal logistic regression allows for ordered transition from disease State 0 to State 1, and then State 1 to State 2, with no backward movement. We used an ordinal logistic regression because there were no cases of an individual developing tumors again. If intermittent FP occurs, it likely only occurs during a brief period rather than many years later, and would not impact the general structure of the model. We made modifications to the standard ordinal logistic regression to allow for different slopes, which was necessary since transitions from State 0 to 1 and State 1 to 2 likely occurred at different rates.

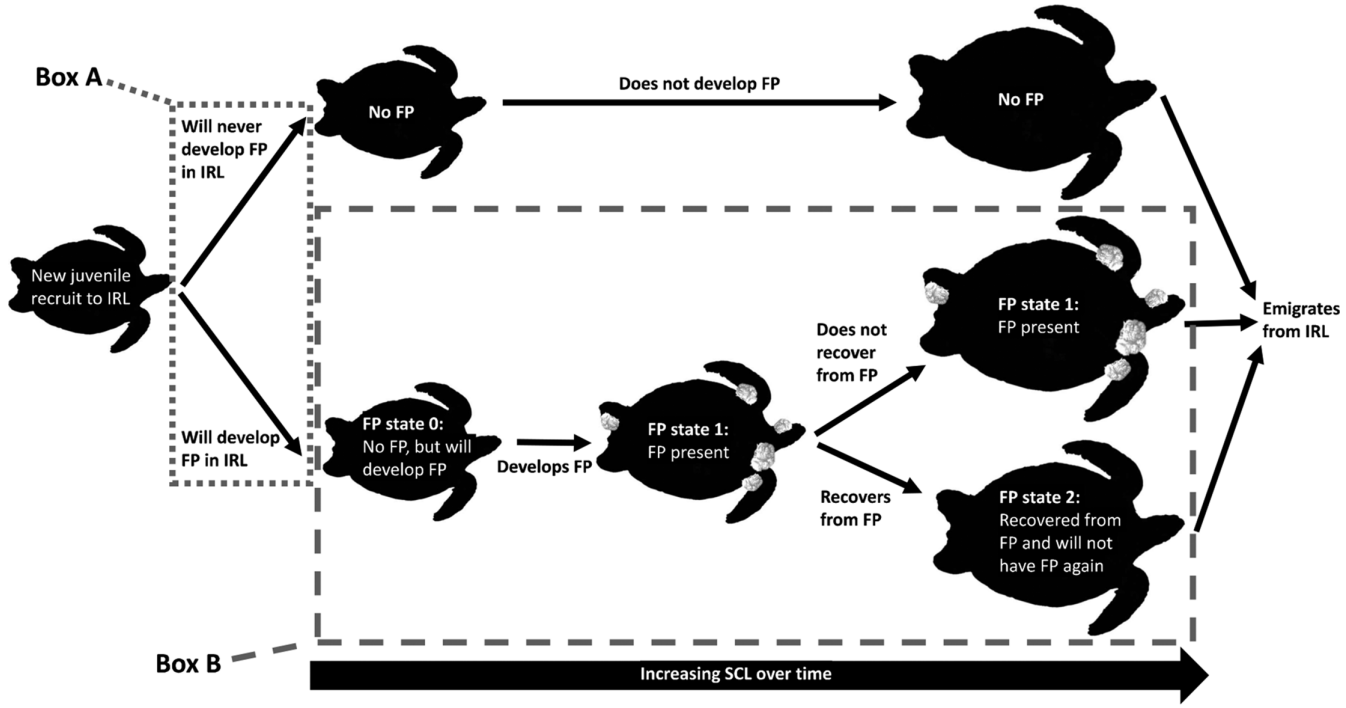

FIGURE 3 Diagram of the fibropapillomatosis (FP) system for green turtles in the Indian River Lagoon, FL as it relates to the hierarchical model of FP state. The first level of the model is a logistic regression that determines what happens in Box A. The second level of the model is a modified ordinal logistic regression that determines what happens in Box B. IRL, Indian River Lagoon

TABLE 1 Specification and structure of the Bayesian hierarchical model of fibropapillomatosis (FP) state for green turtles in the Indian River Lagoon (IRL)

Hierarchical levels	Model structure	Definition of terms
Level 1—Logistic regression for probability a turtle develops FP while in the IRL	$Z_{FP}[i] \sim \text{Bernoulli}(\psi_{FP}[i])$ $\text{logit}(\psi_{FP}[i]) < -\text{logit}(\text{int.FP})$	i, each turtle capture Z_{FP}, whether or not a capture develops FP while in the IRL ψ_{FP}, probability of a turtle developing FP while in the IRL
Level 2—Modified ordinal logistic regression for progression through FP states based on SCL	$Z_2[i] \sim \text{Bernoulli}(Z_{FP}[i] \times \psi_2[i])$ $\text{logit}(\psi_2[i]) < -\text{logit}(1 - \psi_{1cum}[i])$ $Z_1[i] \sim \text{Bernoulli}(Z_{FP}[i] \times \psi_1[i])$ $\text{logit}(\psi_1[i]) < -\text{logit}(\psi_{1cum}[i] - \psi_0[i])$ $\text{logit}(\psi_{1cum}[i]) < -\text{logit}(S_1 \times [1 - \text{int.psi0}] + \text{int.psi0}) - S_2 \times \beta_{SCL} \times \text{SCL}[i]$ $Z_0[i] \sim \text{Bernoulli}(Z_{FP}[i] \times \psi_0[i])$ $\text{logit}(\psi_0[i]) < -\text{logit}(\text{int.psi0}) - \beta_{SCL} \times \text{SCL}[i]$	Z_2, whether or not a capture is FP State 2 ψ_2, probability a capture is FP State 2, provided the turtle will develop FP in the IRL Z_1, whether or not a capture is FP State 1 ψ_1, probability a capture is FP State 1, provided the turtle will develop FP in the IRL ψ_{1cum}, cumulative probability a capture is FP State 0 or 1, provided the turtle will develop FP in the IRL Z_0, whether or not a capture is FP State 0; ψ_0, probability a capture is FP State 0, provided the turtle will develop FP in the IRL *Other terms*: int.FP and int.psi0 are intercept parameters between 0 and 1 S_1 and S_2 are scalars between 0 and 1; β_{SCL} is a positive coefficient SCL[i] is the straight carapace length of each capture

Note: Fibropapillomatosis State 0 is defined as never having had FP, State 1 is currently having FP, and State 2 is having recovered from FP.

We ran the model with OpenBUGS and R via the R package R2OpenBUGS. We used uninformed priors and set the MCMC settings to three chains of 80,000 iterations with a 20,000-iteration burn-in and chains thinned by two. We verified convergence of the model by inspecting trace plots and verifying Rhat values were less than 1.1 for all parameters. We evaluated goodness of fit by inspecting the graphical plots of posterior predictive checks.

Data and code access

All data used in this study are publicly available on Dryad (Mansfield, Kelley, et al., 2021a). Code is available from Zenodo (Mansfield, Kelley, et al., 2021b).

RESULTS

Data summarization and initial statistical analyses

The green turtle capture dataset from the IRL included 4149 captures of 3700 individuals, 388 of which were captured at least two times and 53 of which were captured at least three times. Of the 388 turtles captured at least twice, 53 were captured without FP and subsequently captured with FP, and 72 were captured with FP and subsequently captured without FP. Of the 53 turtles captured at least three times, there were no cases of recurring FP, where an individual had FP, recovered, and then was captured again with FP. For those turtles with three or more captures, four individuals were first captured without FP, then with FP, and then again recovered from FP; 12 individuals did not have FP at any capture; 15 individuals had FP at every capture; 9 went from not having FP to having FP; and 13 went from having FP to not having FP. The long-term annual average FP rate (proportion of green turtle captures with FP) was 0.49 (0.10 SD), and the overall FP rate of the entire dataset was 0.51. Green turtles captured in the IRL and included in this study ranged from 22.0 to 78.6 cm SCL, with most captures between 30 and 60 cm SCL (Figure 4). There was a positive skew in SCL of green turtle captures, which could represent variation in size at permanent emigration from the IRL and/or differences in size-specific capture rates. Fibropapillomatosis rates were highest for turtles between 30 and 50 cm SCL (Figure 5a). There were small fluctuations in FP rates over time, typically ranging between 0.4 and 0.6, with a small spike in FP rates during the late 1990s (Figure 5b). FP rates were highest in fall and winter (Figure 5c).

The most informative logistic regression model for FP occurrence based on DIC included interactive effects of SCL and season (Table 2). Fibropapillomatosis probability was higher during the fall season for turtles less than approximately 45 cm SCL, but there were no differences between seasons for larger turtles (Figure 6). For all seasons, FP probability increased with SCL until about 35–40 cm SCL and decreased thereafter (Figure 6).

Hierarchical modeling of FP state

The Bayesian hierarchical model of FP state reached convergence, and graphical plots of posterior predictive checks indicated good fit of the model and data. From Level 1 of the model, an estimated 99.8% (95% credibility intervals 99.1%–100%) of juvenile green turtles in the IRL developed FP, indicating that nearly every individual in the IRL is affected by FP. Level 2 of the model indicated that turtles quickly develop FP upon recruitment to the IRL and then recover at different rates, with most completely recovering before permanently emigrating from the IRL. The smallest turtles (<30 cm SCL) had a relatively high probability of being FP State 0, but by approximately 35 cm SCL there was a very low probability of a turtle being FP State 0 (Figure 7a). Small- to intermediate-sized turtles (approximately 35–45 cm SCL) were most likely to be FP State 1, and this tracked very closely to the results of logistic regression analysis (Figure 7b). Fibropapillomatosis State 2 probability steadily increased with SCL (Figure 7c). The model predicts that almost every turtle (approximately 93%) will develop FP by 40 cm SCL, and over 90% fully recover by 65 cm SCL (Figure 7d).

DISCUSSION

This study presents a modeling approach to assess the FP disease system in juvenile green turtles, revealing insights into FP dynamics. We found that almost every resident

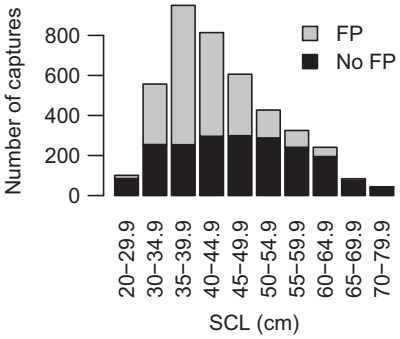

FIGURE 4 Histogram of straight carapace length (SCL) and fibropapillomatosis (FP) status for juvenile green turtles captured in the Indian River Lagoon, FL from 1983 to 2018

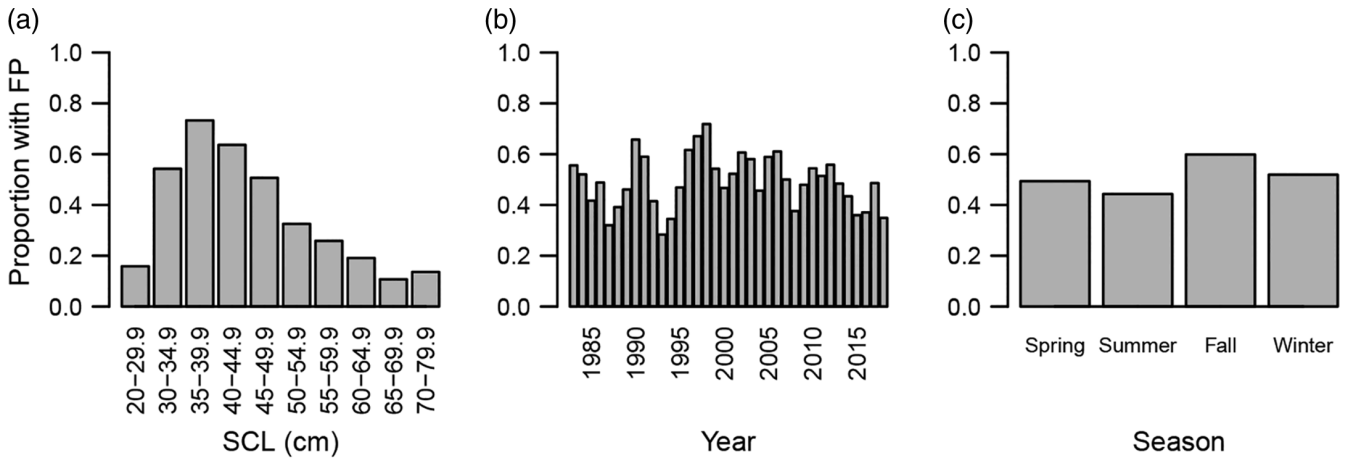

FIGURE 5 Proportions of juvenile green turtles with fibropapillomatosis (FP) captured in the Indian River Lagoon, FL from 1983 to 2018 based on (a) straight carapace length (SCL), (b) year, and (c) season

TABLE 2 Comparison of deviance information criterion (DIC) values of logistic regression models for fibropapillomatosis (FP) status with covariates straight carapace length (SCL) and season

Model	DIC
FP ~ $(\log SCL)^2$ + log SCL + $(\log SCL)^2$: Season + log SCL:Season + Season	5141
FP ~ $(\log SCL)^2$ + log SCL + Season	5148
FP ~ $(\log SCL)^2$ + log SCL	5184
FP ~ Season	5715

Note: For these models, the covariate SCL was considered as the quadratic of the logarithm transform of SCL. The top model included the interactive effects of SCL and season.

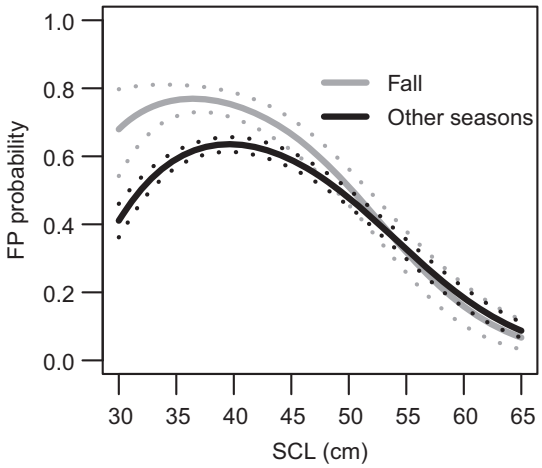

FIGURE 6 Results of a logistic regression model of fibropapillomatosis (FP) probability based on interactive effects of season and the quadratic of logarithm-transformed straight carapace length (SCL). Dotted lines represent 95% credibility intervals. Fall was the only season that significantly affected FP probability, so this model grouped all other seasons besides fall for better visual representation of the results. Fibropapillomatosis probability was higher in fall for smaller turtles (<45 cm SCL)

juvenile green turtle in the IRL study site likely develops FP and subsequently recovers, at least from visible FP (we did not evaluate turtles for the presence of internal, nonvisible tumors). This is the first analysis of long-term sea turtle data that suggests nearly every turtle in an aggregation develops and recovers from FP.

Potential for differential capture probability to affect hierarchical model

One major assumption of our hierarchical modeling approach was that there must be no differences in capture probabilities between FP and non-FP turtles of the same size. If the presence of FP tumors affects capture probability, it could bias model results if not accounted for because capture data would be skewed toward whichever group has higher capture probabilities. Therefore, it is important to consider potential differences in capture probabilities among FP and non-FP turtles. Due to the nature of our dataset, we were unable to statistically assess capture probabilities. Instead, we conceptually reviewed the capture process for our study and carefully considered where differences could occur before proceeding with our hierarchical modeling approach.

Capture probability in this system could be described by two processes: the probability of being available for capture (in the IRL and near the net) and the probability of getting tangled in the net. The process of getting tangled in the net could be biased if FP turtles are more likely to be captured due to the tendency for FP tumors to get tangled in or snagged by the net. Other factors may

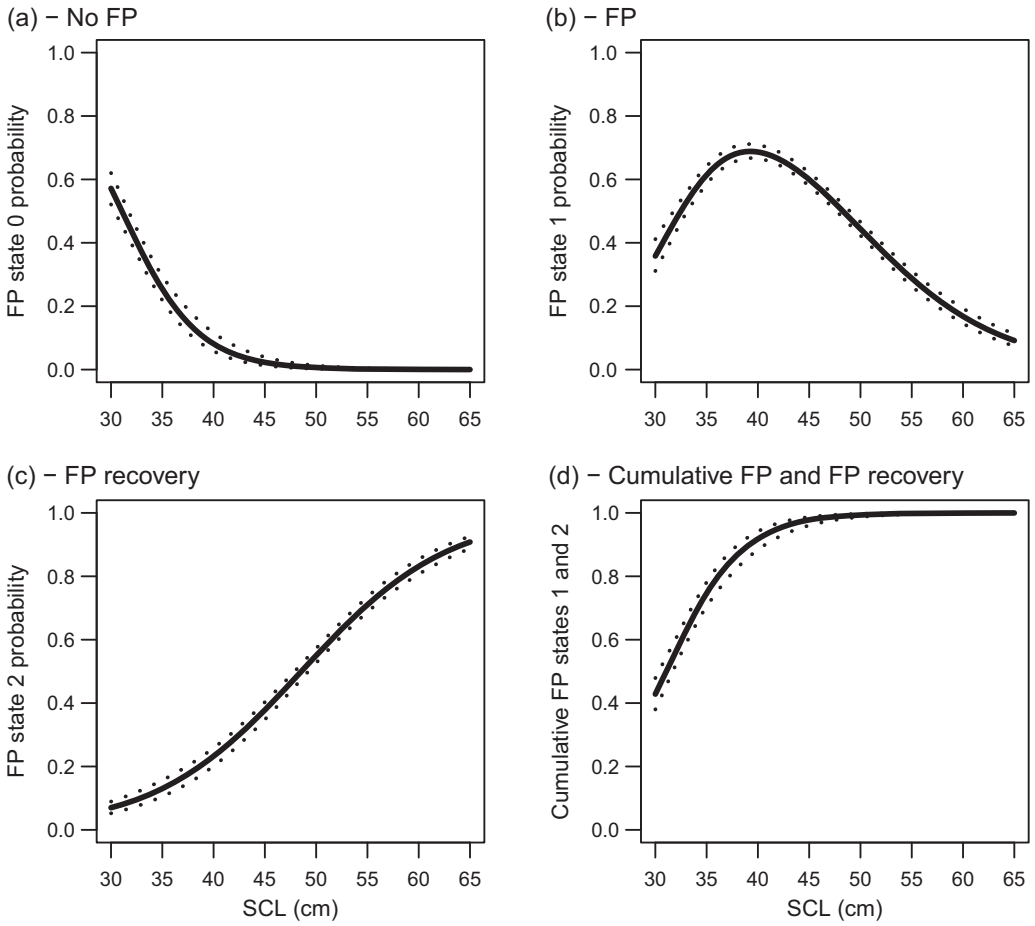

FIGURE 7 Results of the Bayesian hierarchical model of fibropapillomatosis (FP) state for green turtles in the Indian River Lagoon, FL. Dotted lines represent 95% credibility intervals. Each panel represents the probability of a turtle being in a particular FP state based on straight carapace length (SCL), including (a) FP State 0 (never had FP), (b) FP State 1 (FP present), (c) FP State 2 (recovered from FP), and (d) the cumulative probabilities of FP states 1 and 2 (has FP or has had FP). Turtles quickly transition from State 0 to State 1, with about 80% of turtles developing FP by 35 cm SCL. Then turtles recover from FP at different rates, resulting in gradual transition from State 1 to State 2 (recovered). Over 90% of turtles fully recover from FP by 65 cm SCL

also contribute to differences in getting tangled between FP and non-FP turtles, including potential differences in turtle activity, vision, and swimming ability. However, tangling probability is a relatively insignificant process compared to availability probability. Recapture rates were very low (<10% overall, estimated 4% annual recapture probability; Borrowman, 2008) for green turtles in the IRL, likely because the IRL is large and the probability of an individual turtle being available for capture at the discrete netting site is very low. Therefore, availability is the driving factor in capture probability, so much so that differences in getting tangled are likely negligible in overall capture probability within our study.

Another question is whether FP status causes differences in availability at the sampling site. Differences in behavior, survival, and size at permanent emigration among FP and non-FP turtles could lead to differences in availability. However, previous research suggests FP does not have a major effect on growth rates or survival, including in the IRL (Borrowman, 2008). There is currently no evidence to suggest there are differences in size at emigration for FP and non-FP turtles, and FP is rare to nonexistent in subadult/adult foraging sites, suggesting turtles generally do not have FP at the time of emigration. Distinct behavioral differences between FP turtles and non-FP turtles have never been documented, except for severe cases of FP which are relatively uncommon in IRL captures (Hirama & Ehrhart, 2007). However, there may still be a subset of turtles that are severely affected by FP in the IRL and are rarely captured due to behavioral differences, and therefore not included in this analysis.

The fact that the IRL is an open system where turtles are free to come and go could affect availability at the study site based on FP status, particularly if there are transient turtles from other sites with differing FP dynamics.

The effects of nonresident transient turtles on our model results would depend on the source and number of such animals. For example, if large numbers of turtles with FP briefly enter the IRL from other sites, that would likely result in an overestimation of the proportion of turtles that get FP in the IRL. However, if large numbers of turtles without FP are transient in the IRL, it would have minimal effect on our results because the bias would underestimate FP rates of resident IRL turtles and our results already suggest high FP incidence. There are also reasons to assume the IRL is a relatively closed system for juvenile turtles with minimal effects of nonresident turtles. The IRL is connected to the Atlantic Ocean by very few, relatively narrow inlets, which likely restricts free movement in and out of the lagoon system. Another site on the ocean side of the IRL site (~2 km straight line distance, separated by a narrow barrier island) was also monitored by UCFMTRG from 1989 to 2010 and was comprised of almost entirely different turtles (<1% of individuals captured at both locations) of overlapping size ranges with completely different FP rates (Hirama & Ehrhart, 2007). Juvenile green turtles often display foraging site fidelity within coastal habitats (Colman et al., 2015; Hancock et al., 2018; Mendonça, 1983; Pilcher, 2010; Shimada et al., 2014; Siegwalt et al., 2020). A short-term tracking study in the IRL showed most turtles had small home ranges at the IRL site (Redfoot & Ehrhart, 2008), but there are no long-term studies on site fidelity in the IRL. Relatively low recapture rates in the IRL (~8%; Long et al., 2021) bring site fidelity into question, but the study site is very small (~1 km^2) relative to the useable area of the IRL, which may lead to low recapture rates when considering the broader IRL system as a single foraging aggregation. Additionally, many turtles in this study were recaptured across long periods of time (average time between recaptures was about 1.9 years, with 25 turtles recaptured at least 5 years apart, UCFMTRG, unpublished data), implying some level of long-term site fidelity may exist. Thus, while it is possible that differences in FP capture probability could bias our model results, there is no evidence to suggest substantial differences exist. Future research could focus on evaluating long-term site fidelity and habitat use in the IRL, which would also help clarify the validity of our model of FP state.

Fibropapillomatosis disease dynamics

This study showed that nearly every resident juvenile green turtle in the IRL develops and recovers from FP. While this is the first report of near ubiquity of FP in a group of sea turtles, other pathogens and diseases in wild, captive, and human populations have similarly high incidences with minimal effects on populations, with examples including *Mycoplasma* in tortoises and birds (Jacobson et al., 2014; Sawicka-Durkalec et al., 2021), *Batrachochytrium dendrobatidis* in bullfrogs (Garner et al., 2005; Peterson et al., 2007; Schloegel et al., 2009), and herpesviruses in turtles, elephants, and humans (Hardman et al., 2011; Hidalgo-Vila et al., 2020; Prober, 2005). There are likely many other green turtle aggregation sites that are also heavily affected by FP, but do not have available data or data have not yet been analyzed. The IRL has a 49% FP rate, and other sites have had similar or higher apparent FP rates, with examples including Hawaii (42%–65%; Aguirre & Lutz, 2004), Espírito Santo Bay, Brazil (58%; dos Santos et al., 2010), Lake Worth Lagoon, Florida (49%; Gorham et al., 2016), and Crystal River, Florida (68%; Chabot et al., 2021). Those sites may also have every resident green turtle affected by FP, for at least a period of time, with older residents having already recovered. But other sites still maintain no FP, low FP, or extremely variable FP rates compared to the IRL, with some examples including Trident Submarine Basin, Florida (~0%–23%; Hirama & Ehrhart, 2007; UCFMTRG, unpublished data), the worm-rock reef near the IRL site (~0%–33%; Hirama & Ehrhart, 2007; UCFMTRG, unpublished data), Corisco Bay, Gulf Guinea (~10%–27%; Formia et al., 2007), Hawaii (~0%–60%; Chaloupka et al., 2009), and sites in Puerto Rico (~0%–80%; Patrício et al., 2016). Future comparisons of factors affecting FP dynamics within and among these different sites could help clarify the epidemiology of FP.

What makes the IRL a hotspot for FP in green turtles? We developed several hypotheses for this question based on previous research and results from this study: (1) High levels of ChHV5 are maintained in the IRL, leading to quick infections and FP development for green turtles in the IRL. High environmental ChHV5 loads may be maintained by a consistent source of FP turtles or superspreader turtles described in Work et al. (2014), and may also be facilitated by leeches which commonly parasitize IRL turtles and can harbor ChHV5 at high viral loads (Rittenburg et al., 2021). In addition, relatively low water turnover rates in inshore habitats (like the IRL) compared to coastal habitats could allow for accumulation of ChHV5 particles. (2) Poor water and habitat qualities due to runoff from nearby developed areas and attenuation of pollutants lead to green turtles consistently developing FP in the IRL. Environmental pollutants have been suggested as potential contributing factors for FP development, and FP rates are associated with inshore habitats with lower water quality (dos Santos et al., 2010; Foley et al., 2005; Herbst, 1994; Van Houtan et al., 2010). Additionally, stress from ontogenetic habitat and diet shifts that occur when juvenile green turtles recruit from offshore to nearshore habitats (Bolten, 2003; T. T. Jones & Seminoff, 2013) may be more severe in the IRL due to

poor habitat quality, thereby promoting FP development. (3) Turtles that use the IRL are genetically more susceptible to developing FP than those from other sites. Though this hypothesis is unlikely since most juvenile green turtle foraging aggregations are mixed-stock populations, it could contribute to some extent given individual-level variation in immune system genotypes (Martin et al., in review). And finally, (4) viral variants of ChHV5 in the IRL are more virulent or more transmissible than those from other sites, leading to more infections and higher FP incidence in the IRL. There are viral variants that are more common in the IRL than other sites (Ene et al., 2005), but the complete extent of ChHV5 variation is not well-understood. All of our proposed hypotheses are not mutually exclusive and could be valid in conjunction with one another. The IRL system is ideal for future research to test these hypotheses on the etiology of FP, particularly with comparisons of other juvenile green turtle foraging sites.

Aside from the high prevalence of FP in the IRL, this study also revealed other aspects of FP dynamics in the IRL, including the progression of FP as a disease. Based on Level 2 of the hierarchical model, turtles appeared to quickly develop FP upon recruitment to the IRL. For smaller turtles, FP probability was highest in fall. Turtles may develop FP over the summer and into the fall while temperatures are high (Herbst, 1994), and by fall the tumors have developed enough to be seen. Then turtles could recover at different rates, which would explain the positive skew in FP rates with SCL. Future work should investigate whether turtles recover at different rates and assess what factors affect differential recovery rates, such as resource availability, environmental factors, immune genes, or other genetic factors. Our model also suggests that nearly every turtle completely recovers from FP in the IRL before typical permanent emigration size (90% at 65 cm SCL); this makes sense given that FP is rare in adults (Work et al., 2004, reviewed in K. Jones et al., 2016). Also of note were the relatively stable observed FP rates over time, with annual FP rates typically ranging between 0.4 and 0.6. With green turtle populations growing and a key finding of this study being that smaller green turtles in the IRL were more likely to have FP, it might be expected that FP rates would increase over time as the size structure of the IRL shifts toward a higher proportion of small turtles. However, our data did not show an increase in FP rates over time, and notably there was no trend in size structure over time in the IRL during this study (Long et al., 2021).

The results of this study have potential positive and negative implications for sea turtle conservation. Our model suggests that a prominent juvenile foraging site has almost all resident green turtles affected by FP. The long-term effects of this are unclear because most work in the IRL has been conducted after the emergence of FP in the region. For other sites with low or no FP, introduction of ChHV5 and/or changes in environmental conditions could lead to similarly high FP incidence. However, despite the prominence of FP in the IRL, green turtle populations are showing exponential growth within regional rookeries, including those (e.g., Florida) rookeries with stocks represented in the IRL (Seminoff et al., 2015). This could suggest that widespread mild-to-moderate FP rates like we see in the IRL may have little impact on current population trajectories, though further work is certainly required to fully characterize the conservation impacts of FP on sea turtle populations.

Overall, there are still many unknowns in the FP disease system. The hierarchical model structure presented here can be adapted and extended to other sites. For the purposes of this study, we assumed FP randomly develops within the IRL juvenile aggregation; however, covariates can (and likely should) be added to Level 1 to assess factors affecting whether or not turtles get FP. More generally, the practice of modeling a system piecewise in a hierarchical modeling framework can be applied to many biological systems to provide more insightful results (Direnzo & Campbell Grant, 2019; Maunder & Punt, 2013; Zipkin & Saunders, 2018).

ACKNOWLEDGMENTS

The authors thank Llewellyn "Doc" Ehrhart and all past UCFMTRG staff, students, and interns for establishing the long-term IRL dataset used in this study. They especially thank their fellow UCFMTRG laboratory members (in alphabetical order) Ryan Chabot, Tiffany Dawson, Chris Long, Katrina Phillips, and Gustavo Stahelin for continued advice and support on this project. They thank Pedro Quintana-Ascencio for endless back-and-forth on the statistics that greatly improved this study. They also thank the anonymous reviewers for presenting relevant questions and suggestions for clarifying some aspects of this study. This work was funded in part by the Sea Turtle Grants Program which is funded by the proceeds of the Florida Sea Turtle License Plate. Article processing charges were provided in part by the UCF College of Graduate Studies Open Access Publishing Fund. All works were conducted in accordance with institutional IACUC protocols and federal and state protected species permits (National Marine Fisheries Service #19508, Florida Marine Turtle Permit 231 and all predecessors).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Mansfield, Kelley, et al., 2021a) are available from Dryad: https://doi.org/10.5061/dryad.ttdz08kzn.

ORCID

Anna E. Savage https://orcid.org/0000-0002-4917-8358
Kate L. Mansfield https://orcid.org/0000-0002-6568-2861

REFERENCES

Aguirre, A. A. 1991. "Green Turtle Fibropapilloma: An Epidemiologic Perspective." In *Research Plan for Marine Turtle Fibropapilloma*, edited by G. H. Balazs and S. G. Pooley, 107–13. Honolulu, Hawaii: U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service. NOAA-TM-NMFSSWFSC-156.

Aguirre, A. A., and P. L. Lutz. 2004. "Marine Turtles as Sentinels of Ecosystem Health: Is Fibropapillomatosis an Indicator?" *EcoHealth* 1: 275–83.

Bagley D. A. 2003. "Characterizing Juvenile Green Turtles (*Chelonia mydas*), from Three East Central Florida Developmental Habitats." MS diss., University of Central Florida, Orlando, FL.

Balazs, G. H. 1999. "Factors to Consider in the Tagging of Sea Turtles." In *Research and Management Techniques for the Conservation of Sea Turtles*, edited by K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly, 101–9. Washington, DC: IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Bolten, A. B. 1999. "Techniques for Measuring Sea Turtles." In *Research and Management Techniques for the Conservation of Sea Turtles*, edited by K. L. Eckert, K. A. Bjorndal KA, A. Abreu-Grobois, and M. Donnelly, 110–4. Washington, DC: IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Bolten, A. B. 2003. "Variation in Sea Turtle Life History Patterns: Neritic vs. Oceanic Developmental Stages." In *The Biology of Sea Turtles*, Vol II, edited by P. L. Lutz, J. A. Musick, and J. Wyneken, 243–57. Boca Raton, FL: CRC Press.

Borrowman K. M. 2008. "Prevalence and Severity of Fibropapillomatosis in Juvenile Green Turtles (*Chelonia mydas*) in Three Habitats on Florida's East Coast." MS diss., University of Central Florida, Orlando, FL.

Brooks, D., P. Ginn, T. Miller, L. Bramson, and E. Jacobson. 1994. "Ocular Fibropapillomas of Green Turtles (*Chelonia mydas*)." *Veterinary Pathology* 31: 335–9.

Chabot, R. M., R. C. Welsh, C. R. Mott, J. R. Guertin, B. M. Shamblin, and B. E. Witherington. 2021. "A Sea Turtle Population Assessment for Florida's Big Bend, Northeastern Gulf of Mexico." *Gulf and Caribbean Research* 32: 19–33.

Chaloupka, M., T. Work, G. Balazs, S. Murakawa, and R. Morris. 2008. "Cause-Specific Temporal and Spatial Trends in Green Sea Turtle Strandings in the Hawaiian Archipelago (1982–2003)." *Marine Biology* 154: 887–98.

Chaloupka, M., G. Balazs, and T. Work. 2009. "Rise and Fall over 26 Years of a Marine Epizootic Hawaiian Green Sea Turtles." *Journal of Wildlife Diseases* 45(4): 1138–42.

Colman, L. P., A. R. C. Patrício, A. McGowan, A. J. B. Santos, M. Â. Marcovaldi, C. Bellini, and B. J. Godley. 2015. "Long-Term Growth and Survival Dynamics of Green Turtles (*Chelonia mydas*) at an Isolated Tropical Archipelago in Brazil." *Marine Biology* 162(1): 111–22.

Direnzo, G. V., and E. H. Campbell Grant. 2019. "Overview of Emerging Amphibian Pathogens and Modeling Advances for Conservation-Related Decisions." *Biological Conservation* 236: 474–83.

dos Santos, R. G., A. S. Martins, E. Torezani, C. Baptistotte, J. D. Farias, P. A. Horta, T. M. Work, and G. H. Balazs. 2010. "Relationship between Fibropapillomatosis and Environmental Quality: A Case Study with *Chelonia mydas* off Brazil." *Diseases of Aquatic Organisms* 89: 87–95.

Ehrhart, L. M. 1991. "Fibropapillomas in Green Turtles of the Indian River Lagoon, Florida: Distribution over Time and Area." In *Research Plan for Marine Turtle Fibropapilloma*. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-156, edited by G. H. Balazs and S. G. Pooley, 59–61. La Jolla, CA: US Department of Commerce.

Ehrhart, L. M., W. E. Redfoot, and D. A. Bagley. 2007. "Marine Turtles of the Central Region of the Indian River Lagoon System, Florida." *Florida Scientist* 70: 415–34.

Ene, A., M. Su, S. Lemaire, C. Rose, S. Schaff, R. Moretti, J. Lenz, and L. H. Herbst. 2005. "Distribution of Chelonid Fibropapillomatosis-Associated Herpesvirus Variants in Florida: Molecular Genetic Evidence for Infection of Turtles Following Recruitment to Neritic Developmental Habitats." *Journal of Wildlife Diseases* 41: 489–97.

Flint, M., J. C. Patterson-Kane, C. J. Limpus, and P. C. Mills. 2010. "Health Surveillance of Stranded Green Turtles in Southern Queensland, Australia (2006–2009): An Epidemiological Analysis of Causes of Disease and Mortality." *EcoHealth* 7: 135.

Foley, A. M., B. A. Schroeder, A. E. Redlow, K. J. Fick-Child, and W. G. Teas. 2005. "Fibropapillomatosis in Stranded Green Turtles (*Chelonia mydas*) from the Eastern United States (1980–98): Trends and Associations with Environmental Factors." *Journal of Wildlife Diseases* 41: 29–41.

Formia, A., S. Deem, A. Billes, S. Ngouesssono, R. Parnell, T. Collins, G. P. Soundguet, et al. 2007. "Fibropapillomatosis Confirmed in *Chelonia mydas* in the Gulf of Guinea, West Africa." *Marine Turtle Newsletter* 116: 20–2.

Garner, T. W. J., M. W. Perkins, P. Govindarajulu, D. Seglie, S. Walker, A. A. Cunningham, and M. C. Fisher. 2005. "The Emerging Amphibian Pathogen *Batrachochytrium dendrobatidis* Globally Infects Introduced Populations of the North American Bullfrog, *Rana catesbeiana*." *Biology Letters* 2(3): 455–9.

Gorham, J. C., M. J. Bresette, J. R. Guertin, B. M. Shamblin, and C. J. Nairn. 2016. "Green Turtles (*Chelonia mydas*) in an Urban Estuary System: Lake Worth Lagoon, Florida." *Florida Scientist* 79(1): 14–27.

Hancock, J. M., S. Vieira, V. Jimenez, J. C. Rio, and R. Rebelo. 2018. "Stable Isotopes Reveal Dietary Differences and Site Fidelity in Juvenile Green Turtles Foraging around Sao Tome Island, West Central Africa." *Marine Ecology Progress Series* 600: 165–77.

Hardman, K., A. Dastjerdi, R. Gurrala, A. Routh, M. Banks, F. Steinbach, and T. Bouts. 2011. "Detection of Elephant Endotheliotropic Herpesvirus Type 1 in Asymptomatic Elephants Using TaqMan Real-Time PCR." *Veterinary Record* 170(8): 205.

Hargrove S. A., T. M. Work, S. Brunson, A. M. Foley, and G. H. Balazs. 2016. Proceedings of the 2015 International Summit on Fibropapillomatosis: Global Status, Trends, and Population Impacts. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC54, 1–87.

Herbst, L. H. 1994. "Fibropapillomatosis of Marine Turtles." *Annual Review of Fish Diseases* 4: 389–425.

Herbst, L. H., E. R. Jacobson, R. Moretti, T. Brown, J. P. Sundberg, and P. A. Klein. 1995. "Experimental Transmission of Green Turtle Fibropapillomatosis Using Cell-Free Tumor Extracts." *Diseases of Aquatic Organisms* 22: 1–12.

Hidalgo-Vila, J., A. Martinez-Silvestre, N. Perez-Santigosa, L. Leon-Vizcaino, and C. Diaz-Paniagua. 2020. "High Prevalence of Diseases in Two Invasive Populations of Red-Eared Sliders (*Trachemys scripta elegans*) in Southwestern Spain." *Amphibia-Reptilia* 41(4): 509–18.

Hirama, S., and L. M. Ehrhart. 2007. "Description, Prevalence and Severity of Green Turtle Fibropapillomatosis in Three Developmental Habitats on the East Coast of Florida." *Florida Scientist* 70: 435–48.

Jacobson, E. R., M. B. Brown, L. D. Wendland, D. R. Brown, P. A. Klein, M. M. Christopher, and K. H. Berry. 2014. "Mycoplasmosis and Upper Respiratory Tract Disease of Tortoises: A Review and Update." *The Veterinary Journal* 201(3): 257–64.

Jones, T. T., and J. A. Seminoff. 2013. "Feeding Biology: Advances from Field-Based Observations, Physiological Studies, and Molecular Techniques." In *The Biology of Sea Turtles*, Vol III, edited by J. Wyneken, K. J. Lohmann, and J. A. Musick, 211–48. Boca Raton, FL: CRC Press.

Jones, K., E. Ariel, G. Burgess, and M. Read. 2016. "A Review of Fibropapillomatosis in Green Turtles (*Chelonia mydas*)." *The Veterinary Journal* 212: 48–57.

Lawrance, M. F., K. L. Mansfield, E. Sutton, and A. E. Savage. 2018. "Molecular Evolution of Fibropapilloma-Associated Herpesviruses Infecting Juvenile Green and Loggerhead Sea Turtles." *Virology* 521: 190–7.

Long, C. A., R. M. Chabot, M. N. El-Khazen, J. R. Kelley, C. Mollet-Saint Benoit, and K. L. Mansfield. 2021. "Incongruent Long-Term Trends of a Marine Consumer and Primary Producers in a Habitat Affected by Nutrient Pollution." *Ecosphere* 12(6): e03553.

Lucké B. 1938. "Studies on Tumors in Cold-Blooded Vertebrates." Annual Report of the Tortugas Laboratory of the Carnegie Institute, 92–94.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. "WinBUGS — A Bayesian Modelling Framework: Concepts, Structure, and Extensibility." *Statistics and Computing* 10: 325–37.

Lutz, P. L., J. A. Musick, and J. Wyneken. 1997. *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press.

Machado Guimarães, S., H. Mas Gitirana, A. Vidal Wanderley, C. Monteiro-Neto, and G. Lobo-Hajdu. 2013. "Evidence of Regression of Fibropapillomas in Juvenile Green Turtles *Chelonia mydas* Caught in Niterói, Southeast Brazil." *Diseases of Aquatic Organisms* 102: 243–7.

Mansfield K. L., J. Kelley, A. Savage, and K. Kelley. 2021a. "Novel Disease State Model Finds most Juvenile Green Turtles Develop and Recover from Fibropapillomatosis." Dryad. Dataset. https://doi.org/10.5061/dryad.ttdz08kzn.

Mansfield, K. L., J. Kelley, A. Savage, and K. Kelley. 2021b. "Novel Disease State Model Finds most Juvenile Green Turtles Develop and Recover from Fibropapillomatosis." Zenodo. Code. https://doi.org/10.5281/zenodo.5822712.

Mansfield, K. L., J. Wyneken, and J. Luo. 2021. "First Atlantic Satellite Tracks of 'Lost Years' Green Turtles Support the Importance of the Sargasso Sea as a Sea Turtle Nursery." *Proceedings of the Royal Society B* 288: 20210057.

Martin, K., A. E. Savage, and K. L. Mansfield. in review. "Functional immune gene variation in sea turtles predicts fibropapillomatosis tumor development and regression."

Maunder, M. N., and A. E. Punt. 2013. "A Review of Integrated Analysis in Fisheries Stock Assessment." *Fisheries Research* 142: 61–74.

Mendonça, M. T. 1983. "Movements and Feeding Ecology of Immature Green Turtles (*Chelonia mydas*) in a Florida Lagoon." *Copeia* 1983: 1013–23.

Page-Karjian, A., T. M. Norton, B. Ritchie, C. Brown, C. Mancia, M. Jackwood, and N. L. Gottdenker. 2015. "Quantifying Chelonid Herpesvirus 5 in Symptomatic and Asymptomatic Rehabilitating Green Sea Turtles." *Endangered Species Research* 28: 135–46.

Patrício, A. R., X. Vélez-Zuazo, and C. Diez. 2011. "Survival Probability of Immature Green Turtles in Two Foraging Grounds at Culebra, Puerto Rico." *Marine Ecology Progress Series* 440: 217–27.

Patrício, A. R., C. E. Diez, R. P. van Dam, and B. J. Godley. 2016. "Novel Insights into the Dynamics of Green Turtle Fibropapillomatosis." *Marine Ecology Progress Series* 547: 247–55.

Peterson, J. D., M. B. Wood, W. A. Hopkins, J. M. Unrine, and M. T. Mendonca. 2007. "Prevalence of *Batrachochytrium dendrobatidis* in American Bullfrog and Southern Leopard Frog Larvae from Wetlands on the Savannah River Site, South Carolina." *Journal of Wildlife Diseases* 43(3): 450–60.

Pilcher, N. 2010. "Population Structure and Growth of Immature Green Turtles at Mantanani, Sabah, Malaysia." *Journal of Herpetology* 44(1): 168–71.

Prober, C. 2005. "Sixth Disease and the Ubiquity of Human Herpesviruses." *The New England Journal of Medicine* 352(8): 753–5.

Quackenbush, S. L., T. M. Work, G. H. Balazs, R. N. Casey, J. Rovnak, A. Chaves, L. DuToit, et al. 1998. "Three Closely Related Herpesviruses Are Associated with Fibropapillomatosis in Marine Turtles." *Virology* 246: 392–9.

Quackenbush, S. L., R. N. Casey, R. J. Murcek, T. A. Paul, T. M. Work, C. J. Limpus, A. Chaves, et al. 2001. "Quantitative Analysis of Herpesvirus Sequences from Normal Tissue and Fibropapillomas of Marine Turtles with Real-Time PCR." *Virology* 287(1): 105–11.

R Core Development Team. 2018. "RStudio: Integrated Development Environment for R (Version 0.96.122) [Computer Software]." Boston, Massachusetts.

Redfoot W. E., and L. M. Ehrhart. 2008. "Determining Home Ranges and the Use of Habitat by Juvenile Green Turtles in the Central Region of the Indian River Lagoon System, Florida." Final Report submitted for US Fish and Wildlife Service Agreement No. 401815G053.

Rittenburg, L. T., J. R. Kelley, K. L. Mansfield, and A. E. Savage. 2021. "Marine Leech Parasitism of Sea Turtles Varies across Host

Species, Seasons, and the Tumor Disease Fibropapillomatosis." *Diseases of Aquatic Organisms* 143: 1–12.

Sawicka-Durkalec, A., O. Kursa, L. Bednarz, and G. Tomczyk. 2021. "Occurrence of *Mycoplasma* spp. in Wild Birds: Phylogenetic Analysis and Potential Factors Affecting Distribution." *Scientific Reports* 11: 17065.

Schloegel, L. M., C. M. Ferreira, T. Y. James, M. Hipolito, J. E. Longcore, A. D. Hyatt, M. Yabsley, et al. 2009. "The North American Bullfrog as a Reservoir for the Spread of *Batrachochytrium dendrobatidis* in Brazil." *Animal Conservation* 13(1): 53–61.

Seminoff, J. A., C. D. Allen, G. H. Balazs, P. H. Dutton, T. Eguchi, H. L. Haas, S. A. Hargrove, et al. 2015. "Status Review of the Green Turtle (*Chelonia mydas*) Under the U.S. Endangered Species Act." NOAA Technical Memorandum NOAANMFS-SWFSC:539–571.

Shimada, T., S. Aoki, K. Kameda, J. Hazel, K. Reich, and N. Kamezaki. 2014. "Site Fidelity, Ontogenetic Shift and Diet Composition of Green Turtles *Chelonia mydas* in Japan Inferred from Stable Isotope Analysis." *Endangered Species Research* 25(2): 151–64.

Siegwalt, F., S. Benhamou, M. Girondot, L. Jeantet, J. Martin, M. Bonola, P. Lelong, et al. 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.

Smith, G. M., and C. W. Coates. 1938. "Fibro-Epithelial Growths of the Skin in Large Marine Turtles, *Chelonia mydas* (Linnaeus)." *Zoologica* 23: 93–8.

Sturtz, S., U. Ligges, and A. Gelman. 2005. "R2WinBUGS: A Package for Running WinBUGS from R." *Journal of Statistical Software* 12(3): 1–16.

Van Houtan, K. S., S. K. Hargrove, and G. H. Balazs. 2010. "Land Use, Macroalgae, and a Tumor-Forming Disease in Marine Turtles." *PLoS One* 5(9): e12900.

Work, T. M., G. H. Balazs, R. A. Rameyer, and R. A. Morris. 2004. "Retrospective Pathology Survey of Green Turtles *Chelonia mydas* with Fibropapillomatosis in the Hawaiian Islands, 1993–2003." *Diseases of Aquatic Organisms* 62: 163–76.

Work, T. M., J. Dagenais, G. H. Balazs, N. Schettle, and M. Ackermann. 2014. "Dynamics of Virus Shedding and In Situ Confirmation of Chelonid Herpesvirus 5 in Hawaiian Green Turtles with Fibropapillomatosis." *Veterinary Pathology* 52: 1195–201.

Zipkin, E. F., and S. P. Saunders. 2018. "Synthesizing Multiple Data Types for Biological Conservation Using Integrated Population Models." *Biological Conservation* 217: 240–50.

How to cite this article: Kelley, Jake R., Kayla L. Kelley, Anna E. Savage, and Kate L. Mansfield. 2022. "Novel Disease State Model Finds Most Juvenile Green Turtles Develop and Recover from Fibropapillomatosis." *Ecosphere* 13(3): e4000. https://doi.org/10.1002/ecs2.4000