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Cover image: The mudskipper *Periophthalmus argentilineatus* on the mangrove of Ulo Beach, Cabo Delgado, North Mozambique. © José Paula, 2006

Fibropapillomatosis infection in a population of green turtles at Watamu Bay, Kenya

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Anthropogenic stressors from onshore and offshore activities can act as driving factors of disease for a wide range of marine organisms. Green turtles (*Chelonia mydas*) are prominently afflicted with a tumour-causing disease known as fibropapillomatosis (FP) caused by the chelonid alphaherpesvirus ChHV5. Previous studies indicate that pathways of FP transmission may be genetic (vertical transmission) or linked to causal factors in a turtle's environment (horizontal transmission). In this paper patterns of FP prevalence were examined in 10,896 records of green turtles caught or found stranded around Watamu Bay, Kenya, between 2003 – 2020. Findings were focused on locational and seasonal factors that may potentially influence infection. The findings show that FP prevalence varies significantly on an annual basis. Location significantly influenced infection prevalence, with prevalence higher in open ocean sites than sites located within the creek. Infection prevalence was highest at sites around the creek mouth and north of the creek mouth, with both regions exhibiting disparate annual patterns of infection. This paper is the first to examine long-term trends of FP prevalence in-depth in this region and has implications for the health of turtles and marine biota found along the Kenyan coast, and potentially within the wider Western Indian Ocean region. The findings emphasize the need to distinguish the infection pathways of causative agents via: i) further examination of the links between infection and environmental and/or biont community factors; and ii) the collection of data pertinent to the genetic diversity of green turtles and associated ChHV5 viral strains occurring in the Western Indian Ocean.

Keywords: fibropapillomatosis, Watamu Bay, Kenya

Introduction

The marine biome is one of the largest and most influential on earth; it plays a significant role in global socio-economic health and also provides a range of ecosystem services (Costanza, 1999). However, exposure to anthropogenic stressors has led to the decline of ecosystem services, and caused phenomena such as dead zones and altered food web dynamics (Ravaglioli *et al*., 2019). Anthropogenic stressors also facilitate the exposure of marine biota to compromised ecosystem function, predation and infections (Diaz and Rosenberg, 2008). Unsustainable practices such as overfishing and habitat destruction can eventually threaten food security and unbalance coastal ecosystems (McClanahan and Muthiga, 1988). Coastal ecosystems especially highlight how food security and people's livelihoods are closely tied to ecological health. In these environments, marine biota have proven to be sound predictors of both ecosystem resilience and human health (Colin *et al*., 2015).

Sea turtles are long-lived and can cover vast expanses of ocean during different stages of their lives (Schofield *et al*., 2010; Rees *et al*., 2012). This exposure positions them as key indicators of ocean health and resilience (Aguirre and Lutz, 2004); however, the alternative consequence is that sea turtles are also exposed to a wide range of anthropogenic stressors. Turtles are often caught as by-catch, injured or killed during the course of fishing activities (Hazel

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and Gyuris, 2006; Wallace *et al.*, 2013). Additionally, various studies show that the ingestion of plastics and other debris discarded in the ocean can significantly impact turtle fecundity (Barnes *et al.*, 2009; Schuyler *et al.*, 2014). Currently all sea turtle species are listed on the red list created by the International Union for the Conservation of Nature (IUCN), in categories ranging from 'vulnerable' to 'critically endangered'. The green turtle (*Chelonia mydas*) is listed as endangered as a result of the continual degradation of their nesting and foraging habitats, as well as incidental mortalities from fishing activities (Seminoff, 2004).

In more recent years, increasing attention has been focused towards the impact of anthropogenic stressors on turtle health (Rees *et al.*, 2016). Fibropapillomatosis (FP), a virulent form of neoplasia, is an additional threat prevailing against the global green turtle population. Although reports on FP extend back to the late 1930s (Smith and Coates, 1938), it remains underreported in various regions of the ocean (Rao *et al.*, 2020). Currently, there are active investigations concerning: (i) the causal pathways leading to an outbreak; (ii) the dominant transmission pathways, i.e. hereditary (vertical) or environmental (horizontal); and (iii) whether pathways vary geographically or in different turtle populations (Greenblatt *et al.*, 2005). Although FP has been recorded in all turtle species (Herbst, 1994; Foley *et al.*, 2005), it is predominantly prevalent in green turtles. The causative agent is thought to be the chelonid alphaherpesvirus 5 (ChHV5) belonging to the family Herpesviridae (Herbst *et al.*, 1995; Jones *et al.*, 2016). A typical FP infection mostly manifests cutaneously in the form of masses or tumours anywhere on a turtle's skin, carapace or plastron. Masses can also occur in the ophthalmic tissue, as well as in the viscera (Schlumberger and Lucké, 1948). Tumour masses can interfere with turtle movements, compromise their feeding ability and increase their vulnerability to hazards, such as bycatch incidents and predators (Flint *et al.*, 2015).

Data from various regions helps to establish an understanding of FP distribution patterns and prevalence globally (Jones *et al.*, 2016). Research on FP has focused on three main priorities: i) spatio-temporal patterns highlighting prevalence and global distribution; ii) the mechanics of vertical transmission (Duffy *et al.* 2018); and to a lesser extent iii) the horizontal transmission (dos Santos *et al.* 2010), although the evidence for this pathway is increasing (Jones *et al.*, 2020). The results of these studies have indicated that juvenile green turtles appear to be most vulnerable to FP, likely as a result of the significant time they spend in neritic environments, which are heavily impacted by anthropogenic activities and degradation (Ene *et al.*, 2005; Foley *et al.*, 2005). Turtles foraging in these habitats are subsequently more vulnerable to pollutants present in the water or incorporated in their algal-based diet (Komoroske *et al.*, 2011; Camacho *et al.*, 2014). Van Houtan *et al.* (2010) found a strong link between nutrient-rich waters and incidences of FP in juvenile turtles in Hawaii. The authors postulated that invasive macroalgae in nutrient-rich waters had higher levels of arginine (processed from anthropogenic nitrogen), which has been implicated in promoting the proliferation of viruses in the Herpesviridae family. Turtles ingesting these algae may be at higher risk of FP; furthermore, the observed elevated FP prevalence is a potential indicator of the habitat quality. Van Houtan *et al.* (2010) also reported great spatial and temporal variability in infection rates, further signalling that infection is triggered by local environmental factors. Similar research (Keller *et al.*, 2014) reported high concentrations of both man-made and organic pollutants in stranded turtles afflicted with FP. Although there was no evidence that these pollutants triggered FP, results indicated that a bio-accumulation of pollutants could be contributing to the progression of the disease. Further evidence for horizontal transmission pathways comes from a study by Greenblatt *et al.* (2004). Their study demonstrated high levels of FPTHV (a suspected causative virus for FP) in leeches and barnacles removed from stranded and free-ranging turtles. This raises the possibility that such organisms may be vector candidates furthering horizontal pathways of viral transmission.

The South Western Indian Ocean basin (which includes the Kenyan coast) is a biodiversity hotspot and is a foraging and nesting ground for a variety of megafauna including sea turtles (Obura *et al.*, 2019). Fishing activities are the predominant income generator for coastal communities in this region, with turtles typically constituting part of the fishing catch or by-catch (Temple *et al.*, 2017). The resilience of marine species in this region is further challenged by the negative impacts stemming from ocean-based industries (Jouffray *et al.*, 2020), onshore activities (the decimation of mangrove stands, influx of untreated effluent from agriculture and tourism) and the impacts of climate change (Obura, 2004; Kirui *et al.*, 2013; Aller *et al.*, 2019). Based on the increasing evidence linking environmental and community dynamics to FP infection, being able to identify the specific dynamics influencing infection patterns will provide a starting point for establishing causative factors and the scale at which they operate.

In this paper, trends of fibropapillomatosis infection observed in a green turtle population occurring in Watamu Bay, Kenya are presented. The focus was specifically on the effects of location and seasonal factors on infection patterns.

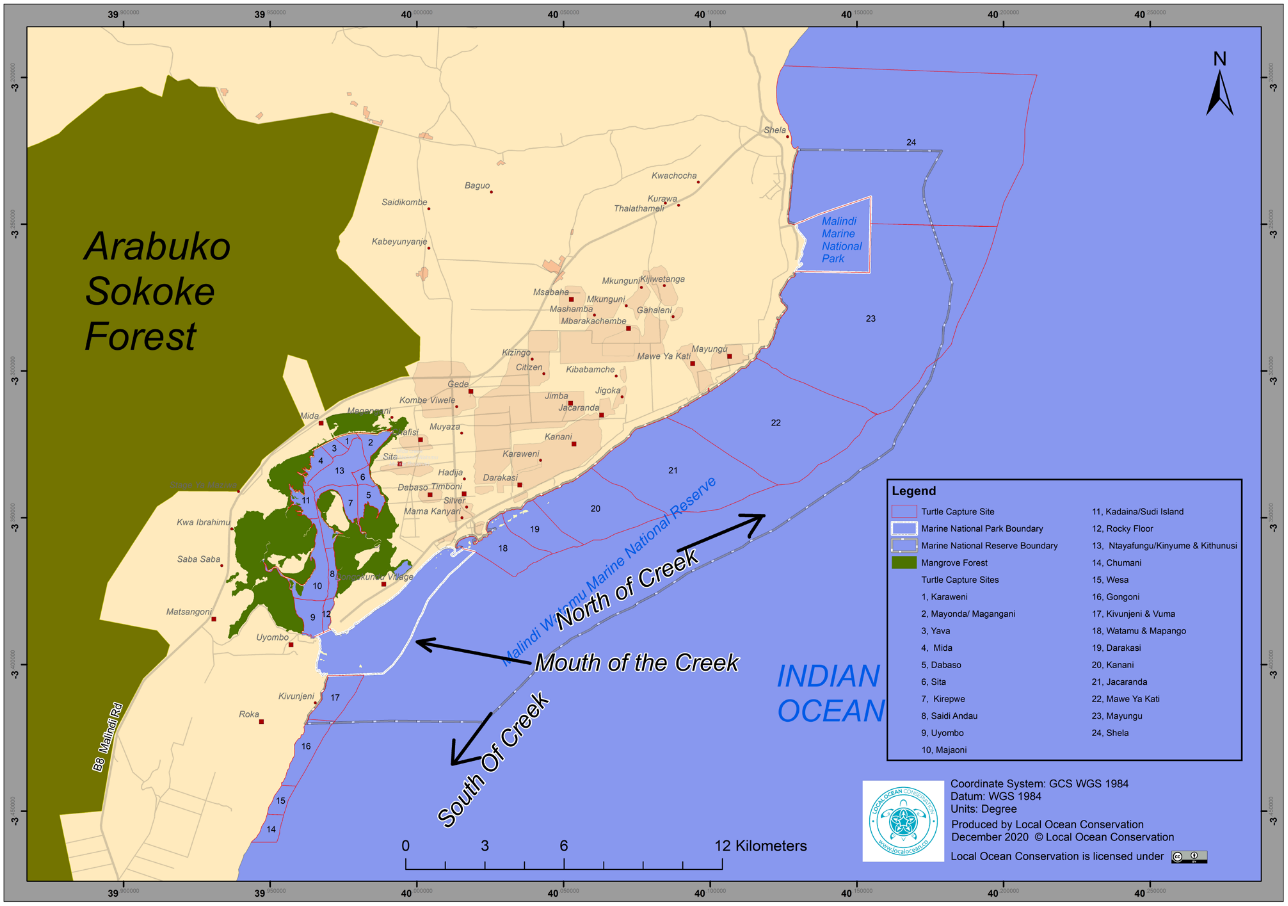

Figure 1. Map of the Watamu area, indicating key marine parks and reserves and capture sites (produced by Local Ocean Conservation).

Methods

Study area

Watamu is a coastal town occurring in the Malindi district of Kenya, located 88 km north of Mombasa and 25 km south of Malindi. Watamu Marine Park and Mida Creek are located in the area, and feature among the marine protected areas of Kenya (Tuda and Omar, 2012; Fig. 1). Both ecosystems are a part of the Malindi/Watamu Marine Reserve. Watamu Marine Park is one of Kenya's oldest marine protected areas (Muthiga, 2009). It forms a conservation area of open ocean approximately 32 km^2 in size that is patrolled and monitored by Kenya Wildlife Services (KWS). The Mida Creek extends inland for approximately 9 km and covers an area of 31.2 km^2. The creek is bordered by mangrove forests on either side covering more than 2000 hectares of land (Kairo *et al.*, 2002). The climate in Watamu Bay adheres to established regional patterns (McClanahan, 1988) influenced by North Eastern monsoon tradewinds (October to March) and South Eastern winds (March to October).

Watamu Bay provides nesting sites for several turtle species including green turtles, and breeding females return to the beaches to lay their eggs.

Data collected by Local Ocean Conservation (LOC), a locally founded marine conservation organization (https://localocean.co/) founded in 1997 was used in this study. LOC operates one of the oldest turtle rehabilitation centres in Africa. It is based in Watamu, Kenya, and runs under the flagship programme of Watamu Turtle Watch. One of the organization's core mandates is to monitor and mitigate activities threatening local turtle nesting sites and populations. LOC routinely receives turtles brought in as by-catch or found stranded in locations around Watamu and other locations along the Kenyan coast.

Data collection

Infection diagnostics

Turtles with visible tumours (on the eyes, body or shell) that were caught in by-catch or found stranded, were brought into the LOC rehabilitation clinic for assessment by a veterinarian. FP tumours typically exhibit a distinct morphology (colour, texture and location) and can manifest on a turtle's skin, carapace, plastron; also on the eye and ocular region (Herbst, 1994). In cases of suspected infection, samples of the tumour(s) were sent to a laboratory for histological analysis. Upon a positive diagnosis of FP, the veterinarian proceeded to cauterize the tumour(s) if possible. Turtles were released after the veterinarian cleared them for release.

Turtle by-catch and stranding data

Standard metric measurements are taken for all captured turtles caught in bycatch and/or found stranded around Watamu Bay. Metric measurements include carapace length and width, weight and turtle ID (tag number). A juvenile turtle was defined as any turtle caught between the curved carapace length (CCL) of 20 - 80 cm, whereas an adult was defined as any turtle with a CCL exceeding 80 cm, as per Kubis *et al.* (2009). New captures are tagged with a titanium metal tag using standard tagging protocols (Limpus, 1992; Heidemeyer *et al.*, 2018). Each tag has a unique identifier number, which can be used to identify turtle individuals upon recapture. For turtles with existing tags, only the tag number and metric measurements were recorded. All tag numbers are recorded, after which turtles are released back into the Watamu Marine National Park. Although LOC occasionally received turtles from other locations along the Kenyan coast, all FP infection records used in this study were restricted to green turtles recorded around Watamu Bay.

Data analysis

Data sorting

Incidents of FP recorded in green turtles from 2003 to 2020 were compiled. This timespan constituted the period of the most reliable data records compiled from the LOC bycatch and rehabilitation programmes. As all FP infections in this time period occurred only in green turtles, other turtle species were excluded from infection analysis. Turtles were counted by cross-checking individual entries in the database using tag numbers (for individual counts), date captured and location (for seasonal and locational counts). In addition to tag number, each turtle was also assigned a unique turtle ID to keep track of their appearance in the database independent of tag replacements. Unique turtle IDs, date and size were used to sort recaptures, whereby turtles with a recurring ID were counted as a recapture whereas turtles that were not tagged or assigned an ID prior were assumed to be unique.

Recaptures were sorted and calculated by year, season and site. Recapture data was taken into account in order to: i) standardize annual and monthly turtle counts (and avoid pseudo replication); and ii) as an indirect indicator of preferred foraging sites around Watamu Bay, to further determine the influence of location (and environmental aspects that turtles are exposed to) on FP prevalence.

Prevalence

Infection prevalence was defined as the sum of turtles infected with FP divided by the total number of turtles captured per unit time or location. Captured refers to turtles recorded as bycatch, stranded, or admitted to the rehabilitation centre. Annual and seasonal infection prevalence were calculated for all capture sites with FP infections. Locational infection prevalence was calculated for capture sites with locational data only.

Location

Location data was obtained from records provided by LOC and organized using allotted capture blocks as shown in Fig. 1. Turtles with no capture site data and capture sites with no cases of infection were omitted from locational analysis.

Sites were allocated into two sets representing broad and finer scale influences: i) broad scale - sites occurring within Mida creek ("creek sites") and sites onshore to the open ocean ("ocean sites"); ii) finer scale – ocean sites north of the creek mouth ("Nocean"; blocks 18 - 22; n = 11); ocean sites south of the creek mouth ("Socean"; block 17; n = 4); sites around the mouth of Mida Creek ("CMS"; blocks 8 - 10, including the marine park; n = 6) and sites within Mida creek ("ICS"; blocks 2 - 7, 11 and 13; n = 11).

QGIS software (Hannover version 3.16) was used to map monthly FP prevalence within Watamu Bay sites. Onshore site coordinates were used for turtles found beached or stranded on onshore sites (n = 5), since in these cases, it was difficult to pinpoint the actual foraging location of stranded turtles. GPS coordinates of FP cases were imported and mapped onto a google earth satellite layer (96 DPI resolution) in QGIS at a scale of 1: 100,000 km. A heatmap was generated using a kernel density algorithm (quartic renderer), with a radius of 1 km representing the approximate range of occurrence for each incident, and using FP monthly prevalence as a weighting measure.

Seasonal and epibiont data

Season has been shown to significantly affect marine environmental variables, such as pollutants and nutrient levels and tidal cycles (Espino and Medina, 1993; Li *et al.*, 2016). Seasonal factors were accounted for in this study to determine the influence of associated environmental variables on FP prevalence.

Seasonal data was organized using localized seasons described in Richmond (2011), as Kaskazi (December to March), Kusi (April to mid-September), and Matalai (mid-September to November). The presence of epibionts was accounted for based on evidence indicating that certain species may act as candidate vectors that transmit causative agents for FP (Greenblatt *et al.*, 2004). The presence of epibionts (leeches and barnacles) was accounted for using presence/absence records, both for infected and non-infected green turtles.

Statistical analysis

Statistical analysis was conducted using Python (v3.7) with pingouin (v0.3.8) statistical package and R (v. 6.3.2).

The extent of variation in infection prevalence was determined using Fisher's exact test and ANOVA. Mantel tests (using the vegan 2.5-7 package in R) were used to assess whether there was a spatial correlation between recapture rates and infection prevalence (Oksanen *et al.*, 2020). Matrices for annual infection prevalence and recapture rates were created across all Watamu sites. Matrices were standardized for comparability (by subtracting the mean and dividing by the standard deviation), and an arbitrary constant of 1 added to avoid negative values (for computation using the Bray-Curtis dissimilarity matrix).

Potential effects of seasonality on FP prevalence were tested for using chi-square tests. Logistic regression (using leech and barnacle counts as predictor variables) was used to assess the potential influence of the presence of epibionts (leeches and barnacles) on infection prevalence.

An independent t-test was used to determine the extent of variation in infection prevalence between creek and ocean sites, and Freedman's test was used to determine the extent of variation in infection prevalence between capture sites. A similar approach was applied for seasonal analysis, where an independent t-test was used to determine variation in infection prevalence between monsoon seasons, whereas an ANOVA was used to determine variations between local oceanic seasons.

Results

Annual prevalence

Between 2003 - 2020, 10,869 unique green turtles were brought into the rehabilitation programme or captured as by-catch from 88 sites within Watamu Bay, with a mean of 605 (SD ± 161) turtles captured annually. A further 103 turtles were captured and/or brought in from sites outside of Watamu (n = 10). Juvenile turtles were the most prominently caught age group (n = 10,694), followed by adults (n = 130) and post-hatchlings (n = 45).

A total of 236 turtles (2.4 %) from 40 sites in Watamu Bay exhibited visible FP tumours; of this number, 108 cases (44 %) subsequently died during this time period. Watamu Bay cases showed an annual mean prevalence of 2.9 % during the 2003 - 2020 period. FP prevalence displayed significant annual variation ($F_{1,15}$ = 8.38; p = 0.01), with the number of cases peaking during 2013 (n = 53) and 2019 (n = 52) respectively (Fig. 2).

Although recapture rates across sites did not vary notably, there was a significant discrepancy between ocean and creek sites (x^2 = 446.6; $p < 0.01$) which had recapture rates of 0.6 % and 4 % respectively. High recapture rates were particularly evident at three sites within the creek, which had recapture rates greater than 10 %. FP prevalence and recapture rates displayed a weak negative association (r = -0.3; $p > 0.05$), where FP prevalence decreased with higher recapture rates.

Location influence

A total of 194 incidents of FP were recorded around Watamu Bay. Cases of FP were recorded in 19 blocks and at 39 specific capture sites. Overall, FP infection across sites recorded a monthly mean of 24 %.

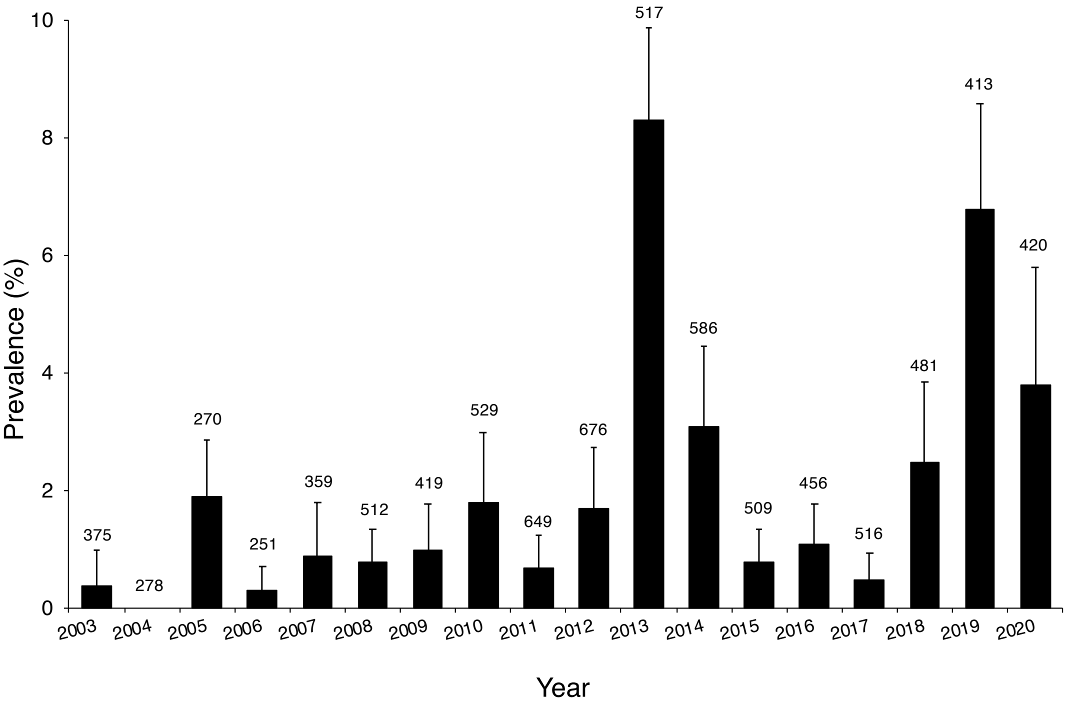

Figure 2. Mean annual prevalence of FP across sites within Watamu Bay (2003 - 2020). Numbers above bars indicate the total number of turtles caught (from by-catch and rehabilitation combined); error bars represent annual (monthly) standard deviation.

Site location significantly affected FP infection prevalence; at a broad scale, ocean sites located offshore or in open ocean displayed a higher infection prevalence per site than sites located within the creek ($F_{1,196}$ = 12.29; p < 0.01; Table 1). Block size did not affect FP incidents or prevalence.

At a finer local scale, variation in infection prevalence became more significantly pronounced within localised regions of Watamu Bay ($F_{3,\ 194}$ = 34.76; p < 0.01; Fig. 3b). Sites located around the creek mouth displayed the highest average prevalence, whereas sites located within the creek had the lowest average prevalence (Fig. 4). Sites around the creek mouth and ocean sites south of the creek also exhibited similar fluctuations in annual prevalence, with infections peaking during the same years. Although FP infections were first observed in the creek, with the first case recorded in 2003, sites within the creek recorded the lowest mean annual prevalence throughout the period of study. Annual infection prevalence patterns in ocean sites north of the creek varied in a pattern that was contrasting to those observed in the other regions of Watamu Bay (Fig. 4).

Seasonal and environmental data

FP prevalence showed seasonal variance, with prevalence lowest during the Matalai season, whereas Kaskazi and Kusi seasons showed comparable mean prevalence (Table 2). FP prevalence (x^2 = 17.7; p = 0.47) and recapture rates (x^2 = 24; p = 0.35) also displayed similar variance with season, although these were not significant.

Table 1. Turtles infected with FP across sites in Watamu (N = 131; SD = standard deviation). Turtles without capture site data are excluded (n = 8). Turtles caught are figures adjusted to account for recaptures.

Site Location	Total no. sites	No. of sites with infections	Mean Block Size (km)	Turtles Infected	Turtles Caught	Mean FP Prevalence
Creek	34	19	4.44 (SD ± 2.78)	131 (SD ± 8.5)	8386 (SD ± 690.6)	0.08 (SD ± 0.22)
Ocean	48	22	5.31 (SD ± 2.93)	124 (SD ± 13)	3067 (SD ± 245.6)	0.12 (SD ± 0.15)

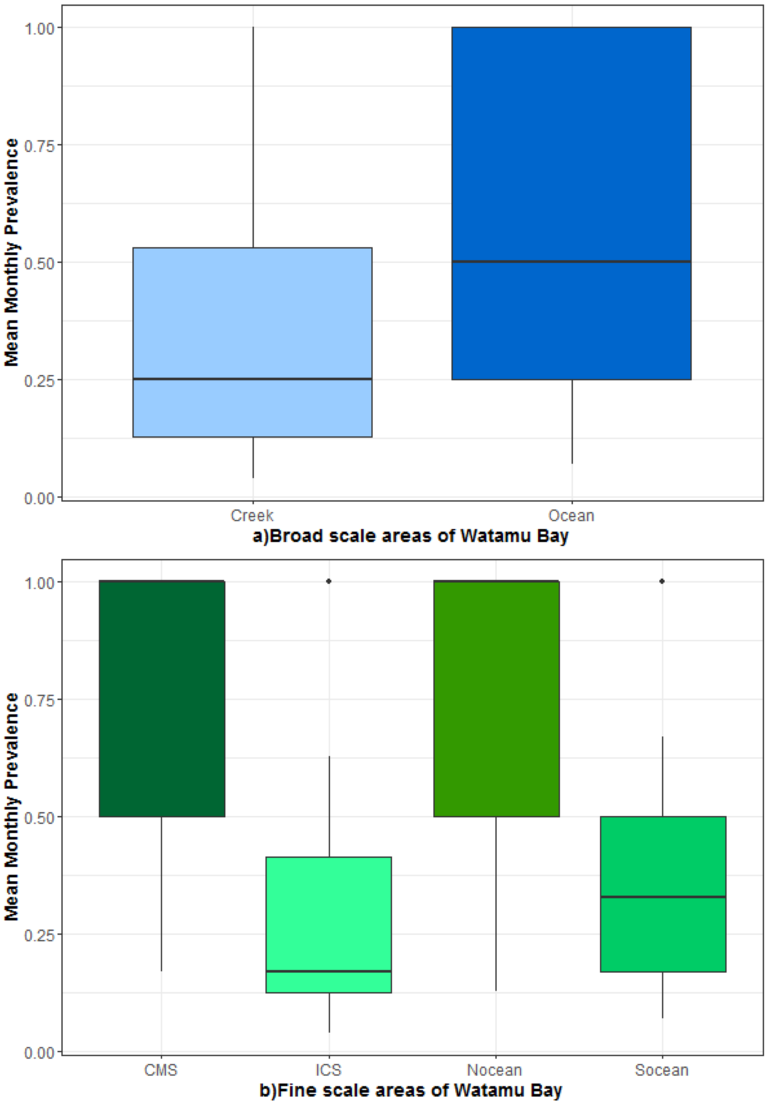

Figure 3. Mean monthly prevalence in Watamu Bay sites at: a) broad scale (creek or ocean); and b) fine scale (CMS = creek mouth; ICS = inner creek; Nocean = northern ocean; Socean = southern ocean).

Logistic regression indicated that barnacle presence increased with a reducing frequency of FP cases while the presence of leeches was correlated with a higher chance of FP (Table 3).

Discussion

Previous studies have shown that FP infections trends can vary temporally (Jones *et al.*, 2016). The finding in the current study are consistent with that variation, as patterns of FP infection prevalence showed prominent annual variation during the period of 2003 - 2020 (Fig. 2). Annual infection patterns indicated the occurrence of two significant outbreaks of FP infection in the Watamu green turtle population, with FP cases peaking during the years of 2013 and 2019 in particular. This suggests that there may have been specific events or significant disruptions within the marine habitat during those years or in the year(s) prior, which triggered an uptick in infection prevalence. Our findings showed that juvenile turtles were the age group most commonly caught around Watamu Bay, and were also the age group most afflicted with FP tumours. As juvenile green turtles remain mostly in neritic habitats during this life stage (Makowski *et al.*, 2006), it is likely that they were the group most exposed to changes in their environment in these years. Annual peaks in infection, especially in sites located around the creek mouth and southern ocean (Fig. 4) may be indicative of a time lag, whereby a period of time lapses between the cause of infection or event triggering infection, and the visible manifestation of infection. An in-depth experimental study by Herbst (1995) demonstrated the presence of a

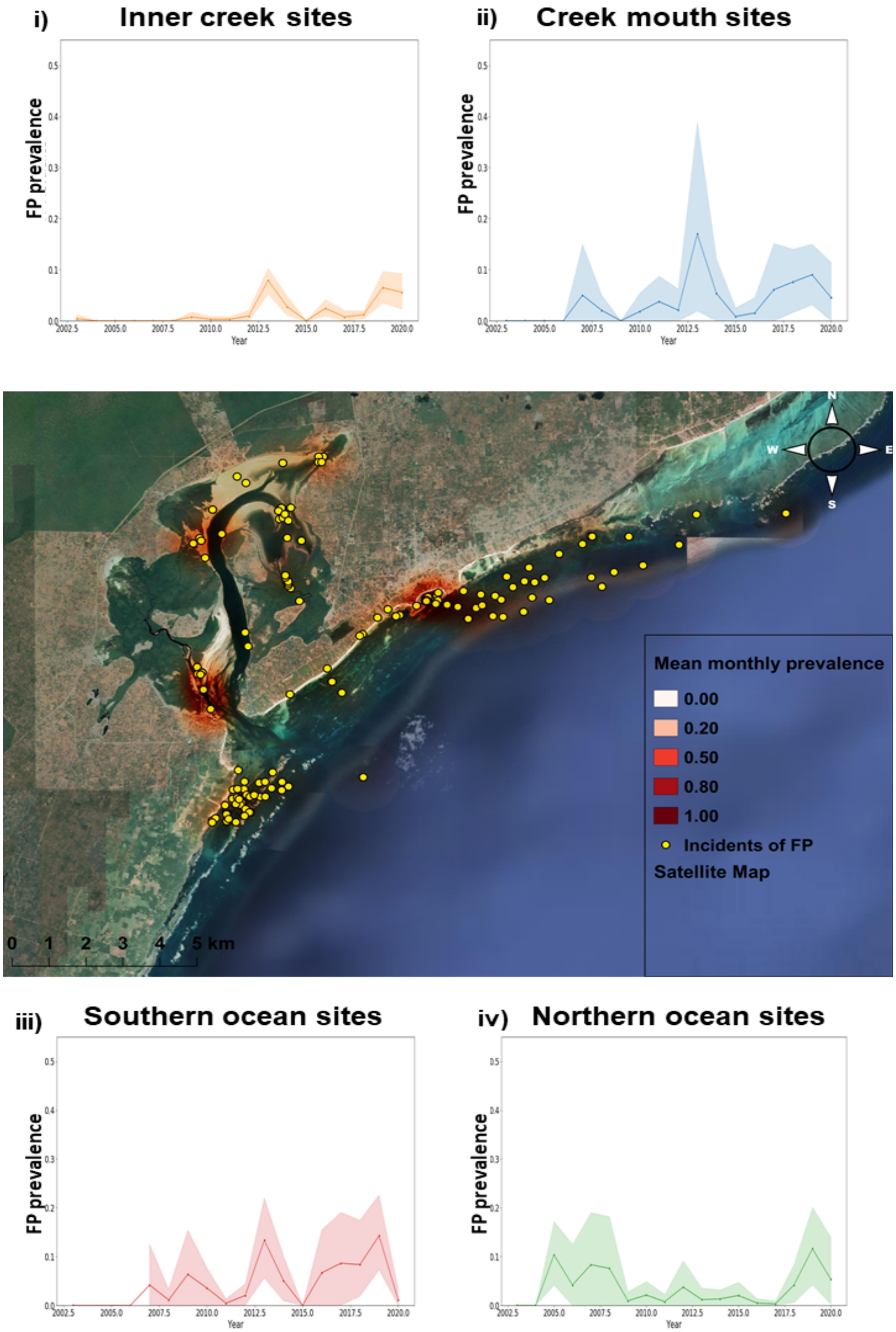

Figure 4. A heatmap depicting monthly incidents of FP infection in sites in and around Watamu Bay (n = 40). Infection intensity is weighted by monthly prevalence; shaded areas depict 95 % confidence intervals derived from annual prevalence in each location. Graphs i - iv show annual variation of infection prevalence in: i) locations around the creek mouth (mean 0.22 ± 0.27); ii) locations within the creek (mean = 0.02 ± 0.016); iii) locations south of the marine park (mean = 0.03 ± 0.02); and iv) locations north of the marine park (mean = 0.12 ± 0.14).

Table 2. Infection prevalence across seasons in positive sites with FP cases in the period between 2003 - 2020 (*n* = 10,896; SD = standard deviation).

Season	Season Length	Turtles Infected	Turtles Caught	FP Prevalence Range	Mean FP Prevalence
Kaskazi	Nov - Mar	121 (SD ± 8.6)	4400 (SD ± 72.9)	0.00 - 0.10	0.02 (SD ± 0.03)
Kusi	Apr - Aug	99 (SD ± 6.2)	3219 (SD ± 47.2)	0.00 - 0.12	0.03 (SD ± 0.03)
Matalai	Sep - Oct	36 (SD ± 3.1)	1814 (SD ± 35.1)	0.00 - 0.14	0.02 (SD ± 0.04)

lag period between infection and the development of visible tumours ranging between 15 - 43 weeks. However, little remains known about the course of the disease from field studies, such as this one; especially since influential factors are multiple, including the health and age of the turtle, surrounding environmental factors, and the load or type of the infectious agent (Herbst *et al.*, 1994; Greenblatt *et al.*, 2005). The time periods between prominent annual peaks in infection were not consistent, suggesting that the causal agents of infection are diverse and subsequently triggered by various causal factors. Therefore, peaks in infection may also be attributable to various forms or stages of the infection manifesting (Kang *et al.*, 2008).

The other notable outcome of this study was the strong influence of location on FP prevalence in and around Watamu Bay. Additionally, the pattern of annual infection observed across sites in the northern region of Watamu Bay was in contrast to infection patterns observed around the creek mouth and southern ocean regions (Fig. 4). It is possible that infections in the northern ocean may have another underlying factor, such as a different causal agent, or different event. A recent report from Jones *et al*. (2020), demonstrated the diversity of viral strains causing FP occurring at six sites along the Australian coast. Previous studies have found that location plays a significant role on infection - even within the same region, due to the diversity of viral variants that may occur in the same region (Ene *et al*., 2005). Although the locations of observed FP tumours observed were not a focal point for this study, a closer examination of tumour forms observed on turtles in the region, as well as genetic sampling of the viral strains will help determine whether the peaks in infection are attributable to more than one causative viral strain.

Alternatively, specific onshore events occurring during the course of the years with peak infections may help explain the increases in FP incidents, and also the prominent fluctuations in infection observed at the creek mouth and in surrounding southern ocean locations (Fig. 4). It is likely that the marine habitats at these locations were specifically impacted or exposed to environmental triggers. In Watamu, creek sites are bordered by villages, residential areas, fishing docks and moorings on both sides. Subsequently, onshore discharge from activities such as agriculture and untreated sewage may be washed towards the creek mouth and open ocean and affect neritic habitats in these areas. Mida creek is bordered on either side by extensive mangrove forests, which help with the regulation of ecosystem function and maintenance of water quality (Owuor *et al.,* 2019; Owuor *et al*., 2017). The dense mangrove habitat bordering the creek may help to explain why FP infection prevalence was consistently lower at sites in the inner creek sites throughout the period of this study.

Although Mida creek (which recorded the lowest overall FP infection prevalence) is affected by tidal ebbs and flows, its ecosystem functions can be viewed

Table 3. Logistic regression model showing the influence of turtle epibionts and algal presence (on shell or body) on FP infection prevalence.

Names	coefficient	Standard error	*p*
Intercept	-3.6	0.07	-
Barnacles	-0.78	0.16	< 0.001
Leech	1.5	0.75	0.046

as distinct to those occurring in the ocean. For example, activities such as the overharvesting of mangroves and pollution have been noted as prominent threats, which potentially also impact the quality of neritic habitats frequented by turtles within the creek (Alamayehu *et al.*, 2014).

It was predicted that a high recapture rate would be an indicator of preferred foraging sites; and that subsequently, habitats with a higher recapture rate would be more commonly frequented by turtles as found by Diez and van Dam (2002). More turtles were caught in capture sites within Watamu creek than in the open ocean (Table 1), with creek sites also reflecting a much higher recapture rate than ocean sites ($p < 0.01$). Foraging trends for green turtles indicate that the species show a preference for seagrass and near-shore habitats (Burgett *et al.*, 2018; Stokes *et al.*, 2019). The findings presented here suggest a higher abundance of preferred foraging habitats in the creek than in the open ocean. However, this finding is confounded by the fact that sites with higher recapture rates in the creek are also frequently visited by fishermen due to their high biodiversity and abundance of marketable species (LOC, personal communication). Recapture is also a measure that carries some potential bias due to realities such as turtles losing their tags over the course of their lives (Heidemeyer *et al.*, 2018) or a lack of available tags. Tag loss is further influenced by tag location, tag type or species tagged (Limpus, 1992; Eckhert *et al.*, 1999). Possible links between FP prevalence and habitat quality indicators (e.g. water quality, nutrient load) is a promising area for deeper consideration, as this study lacked the data to investigate this.

The findings from this study indicated that season was not influential to FP prevalence, with little to no effect on oceanic seasons on FP prevalence (Table 2.) This is similar to the findings of Hirama and Ehrhart (2007), which found that seasonality was weakly associated with FP prevalence. However, as factors pertaining to possible lag periods in infection were not accounted for in this study, there is further opportunity to explore the effects of seasonality in more detail. Overall, findings here indicate that factors more intimately related to green turtle life history traits, such as foraging behaviour, diet and/or turtle community composition, are more likely to act as indirect driving factors for FP.

The incidence of epibionts in this study was varied; the first pattern indicated that barnacle incidence reduces with increased FP prevalence. Barnacle abundance on turtles has been linked with reduced body condition index (Nájera-Hillman *et al.*, 2012), which contrasts with the findings in this study. Turtles not infected with FP were more likely to have barnacles, which indicates a minimal association of barnacle presence with FP prevalence (Table 3). However, this study did find that the presence of leeches increased concurrently with FP prevalence. Prior recent studies have also reported similar findings, where patterns of FP prevalence and the abundance of specific leech species were correlated (Lockley *et al.*, 2020); supporting the potentiality of leeches to act as FP vectors. Observed links between leech infestation and FP prevalence in this study can be further investigated to determine whether: i) leeches, or specific leech species, act as vectors for FP causative pathogens in the Western Indian Ocean region; and ii) whether leech infestations may increase a turtle's susceptibility to FP infection. Further investigations may also determine the range of potential leech vectors, given that the home range of green turtles can vary significantly on an individual scale (Seminoff *et al.*, 2006; Schofield *et al.*, 2015). Therefore, determining the foraging ranges of the Watamu turtle population will be key in helping identify potential environmental factors that turtles are exposed to and which may be driving infection.

Conclusion

The multiple issues facing marine life are widely acknowledged in the sustainable development goals (SDG 14) listed by the United Nations Development Program (UNDP, 2015). There exists an important opportunity to develop knowledge and understanding of turtle populations along the Kenyan coast on multiple levels, with a view to understanding their role as indicators of marine health, and as a priority for their conservation. Besides a lone documented case of FP in the Western Indian Ocean turtle population (Leroux *et al.*, 2010), information pertaining to this disease in this region remains anecdotal. Particularly along the East African coast, information is needed concerning the diversity and type of infectious agents of FP, as well as causal environmental driving factors. This study is the first attempt at an investigation of FP infection patterns in this region. Sites considered in this study were restricted to those within Watamu Bay. However, the emerging associations between location and FP prevalence in this study are highly indicative of the potential influence of environmental factors in the progression of FP, and supports arguments for horizontal transmission of FP. This outcome provides a foundation for further studies examining other sites along the coast to: i) compare whether potential causative conditions are similar; and ii) to determine whether other unique factors are also contributing towards incidences of FP. Subsequently, the findings from this study are also subject to variations in onshore human activities and threats. Watamu is a popular tourist destination along the Kenyan coast, and a majority of the residents derive their income from the tourism industry. It will be important to investigate whether there are any direct or lag impacts from annual population fluxes in residency; factors such as hotel residency rates, new constructions and marine traffic (boat excursions, snorkelling and fishing), can all adversely affect neritic habitats in and around Watamu, especially those located directly offshore. Therefore, factors for further consideration may be related to habitat quality; its influence on turtle ranges and habitat usage; and the level of exposure of various turtle populations to triggers of FP infection. Finally, there is also a need to consider and assess the genetic diversity of turtles along the Kenyan coast as: i) this plays a key role in resilience; and ii) may provide clues to the life-stage at which ChHV5 is transmitted. Such research transcends FP, as characterising the genetic diversity of turtles in Kenya has broader implications for green turtle management as a whole.

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