FIBROPAPILLOMATOSIS IN STRANDED GREEN TURTLES (CHELONIA MYDAS) FROM THE EASTERN UNITED STATES (1980–98): TRENDS AND ASSOCIATIONS WITH ENVIRONMENTAL FACTORS

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ABSTRACT: We examined data collected by the US Sea Turtle Stranding and Salvage Network on 4,328 green turtles (Chelonia mydas) found dead or debilitated (i.e., stranded) in the eastern half of the USA from Massachusetts to Texas during the period extending from 1980 to 1998. Fibropapillomatosis (FP) was reported only on green turtles in the southern half of Florida (south of 29°N latitude). Within this region, 22.6% (682/3,016) of the turtles had tumors. Fibropapillomatosis was more prevalent in turtles found along the western (Gulf) coast of Florida (51.9%) than in turtles found along the eastern (Atlantic) coast of Florida (11.9%) and was more prevalent in turtles found in inshore areas (38.9%) than in turtles found in offshore areas (14.6%). A high prevalence of FP corresponded to coastal waters characterized by habitat degradation and pollution, a large extent of shallow-water area, and low wave energy, supporting speculation that one or more of these factors could serve as an environmental cofactor in the expression of FP. A high prevalence of FP did not correspond to high-density green turtle assemblages. Turtles with tumors were found most commonly during the fall and winter months, and the occurrence of tumors was most common in turtles of intermediate size (40-70-cm curved carapace length). Stranded green turtles with tumors were more likely to be emaciated or entangled in fishing line and less likely to have propeller wounds than were stranded green turtles without tumors. Turtles with and without tumors were equally likely to show evidence of a shark attack. The percent occurrence of tumors in stranded green turtles increased from approximately 10% in the early 1980s to over 30% in the late 1990s. Fibropapillomatosis was first documented in southernmost Florida in the late 1930s and spread throughout the southern half of Florida and the Caribbean during the mid-1980s. Because green turtles living in south Florida are known to move throughout much of the Caribbean, but are not known to move to other parts of the USA or to Bermuda, the spread and current distribution of FP in the western Atlantic, Gulf of Mexico, and Caribbean can be explained by assuming FP is caused by an infectious agent that first appeared in southern Florida. Aberrant movements of captive-reared turtles or of turtles that are released into areas where they were not originally found could spread FP beyond its current distribution.

Key words: Chelonia mydas, conservation, fibropapilloma, fibropapillomatosis, Florida, green turtle, strandings, tumors.

INTRODUCTION

Fibropapillomatosis (FP) occurs primarily in green turtles (*Chelonia mydas*), but it has been reported in loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), hawksbill (*Eretmochelys imbricata*), leatherback (*Dermochelys coriacea*), and flatback (*Natator depressus*) turtles (Herbst, 1994; Huerta et al., 2002). Fibropapillomatosis is a disease characterized by

single to multiple tumors ranging from 0.1 cm to greater than 30 cm in diameter (Herbst, 1994). The tumors arise from a proliferation of epidermal cells (papillomas), dermal fibroblasts (fibromas), or both (fibropapillomas) (Smith and Coates, 1938). Externally, these tumors most commonly appear on soft integumentary tissue but may also grow on the carapace or plastron, especially along suture lines (Jacob-

son et al., 1989). Tumor growth is often concentrated in the inguinal and axillary regions, at the base of the tail, around the neck, and on the conjunctiva of the eye (Smith and Coates, 1938). In the Hawaiian Islands (USA), about half of the green turtles with FP also have tumors that grow in the mouth (Aguirre et al., 2002). Internally, tumors ranging from 0.1 cm to over 20 cm in diameter have been found in the lungs, kidneys, heart, gastrointestinal tract, and liver in association with FP (Schlumberger and Lucké, 1948; Norton et al., 1990; Herbst, 1994).

Although some of the tumors present in FP have been suspected to represent malignant transformation, most appear to be benign (Herbst, 1994). Nevertheless, the size, location, and number of tumors can contribute to progressive debilitation and eventual death. Internal tumors can disrupt normal organ functions (Herbst, 1994). Tumors on the body, especially in the inguinal and axillary regions, can grow large enough to impair swimming activity (Jacobson et al., 1989). Tumors growing around the eyes can eventually occlude vision (Jacobson et al., 1989), and oral tumors can interfere with feeding and breathing (Aguirre et al., 2002). Herbst (1994) suggested that turtles with tumors are more susceptible to entanglement in monofilament fishing line than are those without tumors, but others question this susceptibility (Williams et al., 1994).

Physiologic changes ascribed to FP include anemia, hypoproteinemia, hypoal-buminemia, uremia, electrolyte imbalances, elevations in liver enzymes, low cholesterol and triglyceride values, and increases or decreases in various white blood cells (Norton et al., 1990; Aguirre et al., 1995; Adnyana et al., 1997; Work and Balazs, 1999; Aguirre and Balazs, 2000). The increasing severity of FP (as determined by the size and number of tumors) correlates with deteriorating physiologic condition (Work and Balazs, 1999), and green turtles with severe cases of FP grow more slowly in the wild than do their counterparts

without tumors (Balazs et al., 1998). Green turtles with FP are also chronically stressed and immunosuppressed (Aguirre et al., 1995) and are more likely to have systemic bacterial infections (Work et al., 2003) than are green turtles without FP.

Evidence from recent studies on FP continually points to an infectious etiology involving a virus or a number of viruses (Herbst et al., 1995, 1996; Quackenbush et al., 1998). These viruses might then be spread by biological vectors (Lu et al., 2000) or may become more tumorigenic because of biotoxins (Landsberg et al., 1999). The reoccurring association of FP with shallow, inshore areas (especially areas with poor water circulation) and pollution has led to speculation on the potential role of these environmental factors in the distribution or prevalence of FP (Limpus and Miller, 1990; Ehrhart et al., 1996; Adnyana et al., 1997). Herbst and Klein (1995) also suggested that the spread of FP might be related to the density of turtle assemblages. Fibropapillomatosis was first reported at very low levels (<2%) on green turtles captured around the southern tip of Florida (USA) during the late 1930s (Lucké, 1938; Smith and Coates, 1938). Since then, FP has been reported throughout much of the worldwide range of the green turtle. Local rates of occurrence have reached levels as high as 92%, making it the most significant neoplastic disease of reptiles (Herbst, 1994).

Although in-water studies of green turtle populations in the eastern USA have provided valuable data on the local occurrence of FP (Ehrhart et al., 1996; Schmid, 1998; Schroeder et al., 1998), these studies have been limited to relatively small geographic or temporal scales. The US Sea Turtle Stranding and Salvage Network (STSSN) has been collecting data from stranded (i.e., dead or debilitated) turtles throughout the eastern half of the USA (along almost 6,000 km of coastline) since 1980. In the present study, we used these data to discern spatial and temporal trends in the distribution and prevalence of FP in

stranded green turtles in the eastern USA from 1980 to 1998. To better understand the potential impact of FP, we also compared the percent occurrences of emaciation, entanglement, and wounds from propellers or shark attacks between stranded green turtles with and without tumors. Lastly, we examined the distribution and prevalence of FP in the eastern USA to determine if either corresponded to the environmental conditions that have been suspected of playing a role in this disease.

MATERIALS AND METHODS

Data from stranded green turtles were collected during the period extending from 1980 to 1998 by the STSSN, which comprises participants from 18 states extending from Maine to Texas. Strandings included carcasses that were found washed ashore or floating and live turtles that were found debilitated by injury or disease. Although some stranded turtles were found floating far from shore, most (>99%) were found beached along shorelines or floating close to shore. Observers used a standardized form to document data from each stranded turtle. The data used in our analyses included date, species, location, curved or straightline carapace length (CCL and SCL, respectively; both measured from the nuchal notch to the posterior marginal tip), and documentation of fibropapilloma-like tumors. In the area where FP occurred (the southern half of Florida, south of 29°N latitude), our analyses also included observations of emaciation, entanglement in fishing line, propeller wounds, and shark attacks. These anomalies were not assumed to be the cause of death.

Point location data for each stranded turtle in Florida were further classified as either Florida Atlantic or Florida Gulf and as either offshore or inshore. Florida Atlantic and Florida Gulf represented the Atlantic (eastern) coast and Gulf (western) coast of Florida, respectively, separated by a line at 80°30'W longitude (Fig. 1). Offshore locations included any points in the Atlantic Ocean or Gulf of Mexico or along shorelines that were directly adjacent to either of these bodies of water. Inshore locations included any points in bays, bayous, bights, channels, cuts, coves, creeks, intracoastal waterways, lagoons, lakes, passes, rivers, or sounds or along shorelines that were directly adjacent to any of these bodies of water.

The CCL was used in size analyses because the SCL was taken less often. About 75% of the records had a CCL and about 50% of the records had an SCL. For records with an SCL but no CCL (about 8% of the records), the SCL was converted to CCL using the following formula from Teas (1993): $SCL=0.294+(0.937\times CCL)$.

Sea Turtle Stranding and Salvage Network observers were asked to note any carcass anomalies on the data forms. The anomalies that were analyzed in this study were defined by specific criteria. A turtle was determined to have fibropapilloma-like tumors when at least one verrucose tumor was present. Typically, these tumors were easily detectable, but observers may have failed to report or notice tumors on some turtles, especially if tumors were small and few. The observers typically noted the locations of tumors and the general sizes of tumors, but a standardized methodology for scoring the severity of the FP (a combination of size and number of tumors) was not widely implemented in the Florida STSSN until 2000. Emaciation was determined by appraising the overall body condition of the turtle. Typically, only severe cases of emaciation (i.e., turtles with a distinctly concave plastron and a prominent supraoccipital) were noted. Propeller wounds included parallel gashes across the head, carapace, or plastron. Shark attacks were indicated by crescent-shaped wounds that were usually most distinct on the carapace or plastron. Numerous cuts forming a crescentshaped "dotted line" also indicated a shark attack. Missing flippers or missing parts of flippers alone were not accepted as evidence of propeller wounds or shark attacks.

Sea Turtle Stranding and Salvage Network observers ranged from professional sea turtle biologists to volunteers with no prior data-collection training. Nevertheless, as a condition of the Endangered Species Act permits required to conduct work with the STSSN, individuals had to first gain adequate expertise (in the opinion of the permitting agency) in the standardized data-collection methodology of the STSSN before being permitted to participate.

We served as national or Florida coordinators of the STSSN and as observers in Florida throughout almost the entire study period (1983–98). As STSSN coordinators, we conducted periodic training workshops for STSSN observers to keep the quality and consistency of the data collected as high as possible. We also reviewed and edited all stranding reports as they were submitted. If there were questions or inconsistencies regarding the reliability of the species identification, carapace measurements, anomalies, or location, we contacted the original observer and asked for additional documentation or information. Any data fields that



FIGURE 1. The Florida counties where fibropapillomatosis (FP) was found on stranded green turtles (*Chelonia mydas*) during 1980–98. Green turtles with FP were found in every coastal county south of 29°N latitude. The line of longitude at 80°30′W is the Sea Turtle Stranding and Salvage Network demarcation between the Florida Atlantic and the Florida Gulf. The 200-m offshore contour represents the varying width of the continental shelf around Florida.

we felt were not adequately documented were left blank or marked unknown.

Despite defining criteria, observer training, and scrutiny of stranding reports, distinguishing anomalies (especially emaciation) in stranded green turtles involved a certain degree of subjectivity. This may have biased the absolute values of the reported prevalences of anomalies.

However, we avoided much of this bias when we compared the prevalences of anomalies between turtles with tumors and without tumors because the same observers (those in the southern half of Florida) collected data from both groups of turtles. If an observer tended to underestimate or overestimate the prevalence of an anomaly, that observer was likely to do so equally for turtles with tumors and without tu-

We examined the distribution of FP in the eastern half of the USA to determine if the presence of this disease corresponded to coastal areas with the poorest ecological health as determined by the US Environmental Protection Agency (USEPA). The USEPA rated the condition of coastal areas based on water clarity, dissolved oxygen, loss of coastal wetlands, eutrophic condition, sediment contamination, benthic condition, and accumulation of contaminants in fish tissue (USEPA, 2001). We also examined the differences in the prevalence of FP between the Florida Gulf and the Florida Atlantic to determine if the highest prevalence of this disease corresponded to the coastal area with the poorest ecological health (as determined in USEPA, 2001), greatest extent of shallow-water area (as determined by the width of the continental shelf at 200 m), lowest wave energy (as determined by Tanner, 1960), and highest density of green turtles (as determined by stranding numbers and the extent of suitable habitat).

All statistical analyses were performed using SigmaStat for Windows, Version 2.03 (SPSS Inc., Chicago, Illinois, USA). The Yates correction for continuity was used in all chi-square tests.

RESULTS

During the period extending from 1980-98, 4,328 stranded green turtles were documented by the STSSN in the eastern half of the USA from Texas to Massachusetts. Tumors that characterize FP were observed on 682 green turtles, and all of these were found in the southern half of Florida (south of 29°N latitude, Fig. 1). Six hundred and seventy-three green turtles were found from southern Texas to northwest Florida (north of 29°N latitude), and 639 green turtles were found from Massachusetts to northeast Florida (north of 29°N latitude), and none of these turtles had tumors. Within the southern half of Florida, 22.6% (682/3,016) of the green turtles had tumors. The prevalence of FP in Florida by county is given in Table 1. The frequency of FP in green turtles that were found in the Florida Gulf (51.9%, 418/806) was greater than the frequency of FP in green turtles that were found in the Florida Atlantic (11.9%, 264/2,210;

TABLE 1. Numbers of stranded green turtles (Chelonia mydas) by county in Florida south of 29°N latitude during 1980–98 and frequency of fibropapillomatosis. Most of Volusia County and some of Citrus County are north of 29°N, but the data given are only for turtles found south of 29°N. A map of Florida with these counties is shown in Figure 1. In Monroe County, 42 of the turtles were in the Florida Atlantic (east of 80°30′W longitude) and 458 of the turtles were in the Florida Gulf (at or west of 80°30′W longitude).

County	Total number of turtles	Number with tumors	Number without tumors	Percent with tumors
Citrus	11	2	9	18
Hernando	3	1	2	50
Pasco	18	12	6	67
Pinellas	187	100	87	53.5
Hillsborough	7	5	2	71
Manatee	21	14	7	67
Sarasota	33	16	17	49
Charlotte	11	3	8	27
Lee	44	17	27	39
Collier	13	3	10	23
Monroe	500	258	242	51.6
Miami-Dade	194	40	154	20.6
Broward	282	3	279	1.1
Palm Beach	289	37	252	12.8
Martin	203	31	172	15.3
St. Lucie	476	61	415	12.8
Indian River	410	48	362	11.7
Brevard	296	30	266	10.1
Volusia	18	1	17	6
Total	3,016	682	2,334	22.6

chi-square, P<0.001). The frequency of FP in green turtles that were found in inshore areas (38.9%, 387/996) was greater than the frequency of FP in green turtles that were found in offshore areas (14.6%, 294/2,013; chi-square, P<0.001).

The mean CCLs of stranded green turtles from the eastern USA in the area where FP was found and in the areas where FP was not found are given in Table 2. In the southern half of Florida, the frequencies of various size-classes (by 10-cm increments) of green turtles with tumors was different from that of green turtles without tumors (chi-square, P<0.001; Fig. 2), and the percent occurrence of turtles with tumors was greatest in the intermediate size-classes (40–70-cm CCL; Fig. 2). The frequency by month of stranded

Table 2. The mean curved carapace lengths (CCL, from the nuchal notch to the posterior marginal tip) of stranded green turtles (*Chelonia mydas*) from the area where fibropapillomatosis (FP) was found (Florida south of 29 $^{\circ}$ N latitude) and from the areas where FP was not found (Texas to northwest Florida and Massachusetts to northeast Florida) during 1980–98. In cases in which the straight line carapace length (SCL) of a turtle was determined instead of the CCL, the equation of Teas (1993) was used to convert the SCL to CCL. Not all turtles were measured for carapace length. The mean carapace length is different for turtles from each area (analysis of variance, P<0.001; Tukey Test for pairwise multiple comparisons, all P<0.001).

		Curved carapace length (cm)	
Area	Mean ± SD	Range	n
Texas to northwest Florida South Florida	41.0 ± 15.8 46.3 ± 17.4	10.7–121.9 10.2–125.0	581
Massachussetts to northeast Florida	46.3 ± 17.4 36.2 ± 13.3	10.2–125.0 14.0–106.7	2,489 482

green turtles with tumors was also different from that of stranded green turtles without tumors (chi-square, P<0.001; Fig. 3). Green turtles with tumors were found more often in the fall and winter, and green turtles without tumors were found

more often in the spring and summer (Fig. 3).

Tumors were reported on the eyes, neck, tail, carapace, plastron, inguinal and axillary regions, and the dorsal and ventral surfaces of all flippers. Only one oral tu-

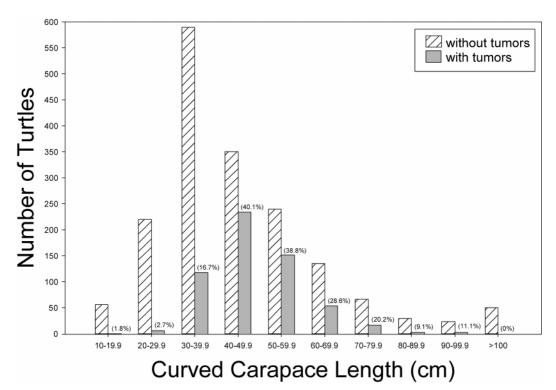


FIGURE 2. Size-class distributions of stranded green turtles (*Chelonia mydas*) found in the southern half of Florida (south of 29° latitude) during 1980–98 with and without the tumors associated with green turtle fibropapillomatosis. The percentage of turtles with tumors is also presented for each size-class. Carapace length was measured from the nuchal notch to the posterior marginal tip, but not all stranded turtles were measured for carapace length. In cases in which the straight carapace length (SCL) of a stranded turtle was determined instead of the curved carapace length (CCL), the equation of Teas (1993) was used to convert SCL to CCL.

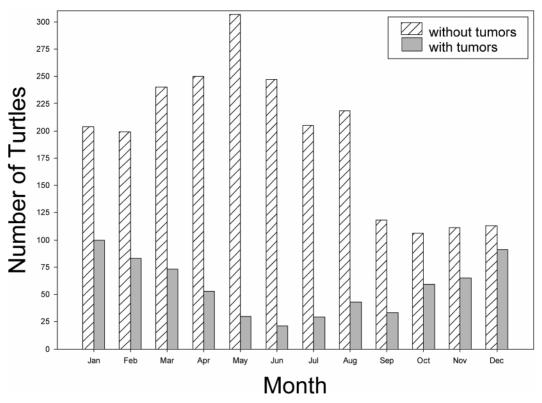


FIGURE 3. The number of stranded green turtles (*Chelonia mydas*) with and without the tumors associated with green turtle fibropapillomatosis found each month in the southern half of Florida (south of 29° latitude) during 1980–98.

mor was found in a green turtle with FP (Bresette et al., 2003). Stranded green turtles with tumors were more likely to be emaciated or entangled in fishing line and less likely to have propeller wounds than were stranded green turtles without tu-

TABLE 3. The percent occurrence of selected anomalies (not necessarily the cause of death) in stranded green turtles (*Chelonia mydas*) found from 1980–98 along the coast of Florida south of 29°N latitude with (n=682) or without (n=2,334) the tumors that characterize green turtle fibropapillomatosis. The frequencies of all anomalies except shark attacks are different for turtles with and without tumors (chisquare with Yates correction for continuity, P<0.001).

Anomaly	% Turtles with tumors (n)	% Turtles without tumors (n)
Propeller wounds	7.9 (54)	20.4 (477)
Emaciated	17.7(121)	4.6(108)
Entangled in fishing line	10.9(74)	3.3(76)
Shark attack	2.1(14)	3.0(71)

mors; the two groups were equally likely to show evidence of a shark attack (Table 3).

During the first 2 yr of work by the STSSN (1980 and 1981), tumors were reported only on green turtles that were found in the Florida Keys (Fig. 1). Of the 14 stranded green turtles documented in the Florida Keys during those years, six had tumors. Throughout the rest of the southern half of Florida (south of 29°N latitude), STSSN observers documented 42 stranded green turtles during 1980 and 1981, and none were reported with tumors. From 1982 to 1985, fibropapillomalike tumors on stranded green turtles were reported from both coasts north to the approximate present-day distribution of FP in Florida. From 1985 to 1994, the only geographic gap in the occurrence of tumors in stranded green turtles in the

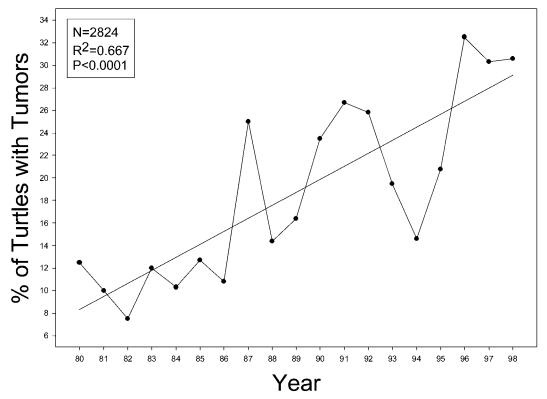


FIGURE 4. Yearly percent occurrence of tumors associated with green turtle fibropapillomatosis in stranded green turtles (*Chelonia mydas*) found in the southern half of Florida (south of 29° latitude) during 1980–98.

southern half of Florida was in Broward County (Fig. 1). Of the 204 stranded green turtles documented in Broward County through 1996, none had tumors. The percentage of stranded green turtles found in Florida each year with FP has been increasing at a rate of 1.2% per year (linear regression, r^2 =0.660, P<0.001; Fig. 4) and has risen from around 10% in the early 1980s to over 30% in the late 1990s.

The presence of FP in the eastern half of the USA did not necessarily correspond to the coastal areas with the poorest ecological health. Fibropapillomatosis occurred in a coastal area with relatively poor ecological health (Florida Gulf), but it also occurred in a coastal area with relatively good ecological health (Florida Atlantic) and did not occur in other coastal areas with relatively poor ecological health (Virginia to Massachusetts and Texas) (USE-PA, 2001). However, within the area where

FP did occur, the highest prevalence was found in the Florida Gulf, which, when compared to the Florida Atlantic, had coastal waters with the poorest ecological health (USEPA, 2001), largest extent of shallow-water area (Fig. 1), and lowest wave energy (Tanner, 1960).

The highest prevalence of FP did not correspond to the green turtle assemblage with the highest density. During the period extending from 1980–98, 806 stranded green turtles were found in the Florida Gulf, and 2,210 stranded green turtles were found in the Florida Atlantic (both south of 29°N latitude). The Florida Gulf has a longer coastline, more shallow-water area, and almost nine times more acreage of seagrass (Sargent et al., 1995) than the Florida Atlantic does. Considering the smaller number of strandings and a greater amount of habitable area, the green turtle assemblage in the Florida Gulf was likely

less dense than the green turtle assemblage in the Florida Atlantic. Nevertheless, the prevalence of FP was higher in the Florida Gulf than it was in the Florida Atlantic.

DISCUSSION

By all accounts, the green turtle stranding data accurately portrayed the distribution of FP in the eastern USA during 1980-98. In-water studies in east Florida (Ehrhart et al., 1996; Provancha et al., 1998), the southern tip of Florida (Schroeder et al., 1998), and west Florida (Schmid, 1998) also documented the occurrence of FP among green turtles in the southern half of Florida (although the latter study also found FP in green turtles that were slightly north of our boundary at 29°10′). Studies of green turtle populations in Texas (Shaver, 2000) and North Carolina (Epperly et al., 1995) did not report any cases of FP. On a finer scale, the absence of FP that we detected in Broward County (Fig. 1) mirrored the results of an in-water study of green turtles in that area (Wershoven and Wershoven, 1992).

Relative variations in the prevalence of FP depicted by the stranding data were probably accurate. For example, the finding that FP was more common in turtles from inshore areas than in turtles from offshore areas was also supported by data from an in-water study (Ehrhart et al., 1996). Determining absolute values of the prevalence of FP were more problematic. Herbst (1994) suggested that stranding data may overestimate the prevalence of a severely debilitating disease such as FP. However, the stranding data did not indicate a higher prevalence of FP than did the data from some concurrent in-water studies. The frequency of FP in green turtles captured in southwest Florida Bay (at the southern tip of the mainland) during 1990-98 (62%, 31/50; Schroeder et al., 1998) was the same as that in stranded green turtles documented in Florida Bay over the same time period within 30 km of the in-water study site (48.5%, 48/99;

chi-square, P>0.05). The frequency of FP in green turtles captured in the central part of the Indian River Lagoon (on the east-central coast) during 1982–96 (47.1%, 454/964; Ehrhart et al., 1996; Bagley, unpubl. data) was greater than that in stranded green turtles found in the Indian River Lagoon during the same time period within 30 km of the in-water study site (34.5%, 48/139; chi-square, P<0.01).

The in-water studies of green turtles in Florida Bay and the Indian River Lagoon depended primarily upon the capture of turtles with entangling nets. Because green turtles with tumors may become more easily entangled than green turtles without tumors, entanglement capture methodologies could lead to an overestimate of the prevalence of FP. A green turtle capture methodology not based on entanglement netting was employed incidental to operations of the St. Lucie Power Plant on Hutchinson Island (St. Lucie County, Fig. 1). Three large intake pipes 365 m offshore draw water into an intake canal. Sea turtles are also incidentally drawn into the canal, where they are captured, studied, and then released (Bresette et al., 1998). From 1980 to 1998, 1,927 green turtles were captured in this manner, and 99 (5.1%) had tumors (Bresette, pers. comm.). During this same time period, 278 stranded green turtles were found on the ocean side of Hutchinson Island, and 26 (9.2%) had tumors. In this case, the frequency of FP as determined by the stranding data was greater than that determined by an in-water study (chisquare, P = 0.007).

Tumors in the present study were most common on green turtles in the intermediate size-classes (40–70-cm CCL), a trend also found in Australia (Limpus and Miller, 1990) and Hawaii (Murakawa et al., 2000). The rarity of tumors in the smallest size-class (20–30-cm CCL) of neritic green turtles supports the hypothesis that the agent responsible for FP is either acquired or is triggered by some factor or combination of factors that the turtles are exposed to after

they recruit to nearshore environments (Balazs, 1986; Ehrhart, 1991). The rarity of tumors in the largest size-classes (>80-cm CCL) results from the mortality of green turtles with FP before they reach a large size, from tumor regression, or from a combination of both.

In Florida, dead or debilitated green turtles with FP were found most commonly during the fall and winter months. Herbst (1994) speculated that tumors grow most rapidly during the warmest time of year, so the tumors of many turtles simultaneously reach a debilitating size by the end of the summer. This scenario would also explain why no seasonal pattern in the prevalence of stranded green turtles with FP occurs in Hawaii (Murakawa et al., 2000), where there is less seasonal change in water temperatures than in Florida and, thus, less opportunity for the synchronization of fast tumor growth.

As expected, stranded green turtles with tumors were more likely than those without tumors to show external signs of chronic debilitation (emaciation). The cause of death in the stranded green turtles was not determined, but only 18% of the turtles with tumors were considered to be emaciated. The clinical course of FP is prolonged and there is a possibility of recovery (Herbst, 1994). Stranded green turtles with FP may have died as a result of a mortality factor that was not directly related to physiologic deterioration. The presence of tumors along with the increasing lethargy that may occur as FP progresses could increase the risk of a green turtle being killed by something else before succumbing to, or recovering from, FP. For example, in the southern half of Florida, stranded green turtles with tumors were more likely to be entangled in fishing line than stranded green turtles without tumors. Although fishing line entanglement does not necessarily lead to death, it increases the risk of death due to trauma, ingestion of the fishing line, or entrapment underwater. Because green turtles may become less able to move about

as FP progresses (either because of physiologic deterioration or because tumors interfere with sight or motion), we expected turtles with FP to be generally less likely than turtles without FP to evade boats and predators. However, the behavior of green turtles with FP apparently does not put them at greater risk of being attacked by a shark or of being hit by a propeller.

The tumors that characterize FP were first found to occur in a small percentage (<2%) of green turtles from southernmost Florida in the late 1930s (Lucké, 1938; Smith and Coates, 1938). Even though many green turtles were captured in studies along the west coast and east coast of Florida (where FP would eventually become common) during the next 40 yr (Carr and Caldwell, 1956; Ehrhart et al., 1986), FP was not reported again in Florida until STSSN observers documented tumors on stranded green turtles from southernmost Florida in 1980. By 1985, FP was documented throughout most of the southern half of Florida, but the northward spread of FP appeared to stop at that time. Green turtles with FP were also found throughout the Caribbean, beginning in the mid-1980s (Williams et al., 1994). FP has not been reported in any of the more than 1,500 green turtles that have been captured in Bermuda since 1992 (Meylan, pers. comm.).

The most likely cause of FP is an infectious agent, probably a virus (Herbst et al., 1995). Fibropapillomatosis could be spread through direct contact with infected individuals or through contact with an agent that is shed into the water by infected individuals (Curry et al., 2000). Numerous tag-and-recapture studies of wild green turtles in south Florida have revealed that these turtles move throughout the southern half of Florida (north to 29°N latitude) and throughout the Caribbean but not to any other part of the eastern USA or Bermuda (Ehrhart et al., 1996; Redfoot et al., 1996; Bresette et al., 1998; Schmid, 1998; Schroeder, unpubl. data). Green turtles in other parts of the eastern USA and Bermuda are known to move into south Florida or the Caribbean (Epperly et al., 1995; Meylan, pers. comm.). The most likely explanation for the distribution of FP in the western Atlantic, Gulf of Mexico, and Caribbean is that the disease began in southernmost Florida and was subsequently spread by infected individuals throughout the southern half of Florida (north to 29°N latitude) and throughout the Caribbean. Fibropapillomatosis did not spread to other areas of the eastern USA or Bermuda because infected turtles did not move into those areas.

In the southern half of Florida, FP was most prevalent in the area with the greatest degree of marine habitat degradation and pollution, largest extent of shallow-water area, and lowest wave-energy level. This supports the supposition that one or more of these conditions may be an environmental cofactor in the expression of FP. In contrast, a high prevalence of FP did not correspond to a high density of green turtles. The latter was also true for an in-water study conducted in the Florida Atlantic. As determined from catch perunit effort, the density of the green turtle assemblage on a sabellariid worm reef, offshore of Indian River County, was greater than the density of the green turtle assemblage at a site in the nearby Indian River Lagoon, but the prevalence of FP at the lagoon site was greater than that at the reef site (Guseman and Ehrhart, 1990; Ehrhart et al., 1996).

If the natural behavior of green turtles is preventing the further spread of FP in the western Atlantic, then some conservation practices have the potential to breach the containment of this disease. Green turtles that strand alive along the Atlantic coast of the USA north of Florida (where FP does not occur) have been rehabilitated and then released in southern Florida (where FP does occur) because of warmer water temperatures (Foley, pers. obs.). Immature green turtles can exhibit strong fidelity to a specific foraging area (Medonca, 1983; Coyne and Landry, 1994;

Limpus et al., 1994; Renaud et al., 1995) and if displaced, have been known to return (Carr and Caldwell, 1956; Limpus et al., 1994). Rehabilitated turtles could return to foraging grounds north of Florida after being released in south Florida.

Sea turtles that are raised in captivity and then released have also been known to make aberrant movements. An immature green turtle that was raised in captivity for 1 yr and then released in south Florida in 1985 as part of a headstart program (Huff, 1989) was captured in Bermuda in 1990 in the company of other green turtles (Meylan, pers. comm.). These examples emphasize the need to carefully consider where sea turtles are released to reduce the risk of aberrant movements and the possible spread of infectious agents.

ACKNOWLEDGMENTS

We are grateful for the dedicated efforts of the state stranding coordinators and participants in the US Sea Turtle Stranding and Salvage Network. The manuscript was improved by reviews from J. Leiby, A. Meylan, J. Quinn, S. Rommel, B. Witherington, and two anonymous reviewers. Funding for this study was provided by the Nongame Wildlife Program of the Florida Game and Freshwater Fish Commission (grant NG92-100), the National Marine Fisheries Service (NOAA), and the Florida Sea Turtle License Plate.

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Received for publication 2 June 2003.