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Scavenging versus predation: shark-bite injuries in stranded sea turtles in the southeastern USA

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ABSTRACT: Injuries inflicted by sharks are a frequent observation in stranded sea turtles. Sharks prey on live turtles and scavenge carcasses, which can create uncertainty as to the cause of stranding when sea turtles are found dead with shark-bite wounds. Consequently, attributing the cause of stranding to a shark attack based purely on the presence of the characteristic wounds can overestimate predation by sharks as a cause of mortality. To better characterize the timing of shark-bite wounds relative to death of sea turtles in the southeastern USA, we performed necropsies on 70 stranded turtles that were found dead in which the predominant observation was bite wounds without any grossly evident vital responses (inflammation or healing). Postmortem examination included assessment for evidence of exsanguination and histopathological evaluation of skeletal muscle comprising wound margins. We characterized wounds as antemortem, perimortem, or postmortem based on specific criteria related to the presence or absence of supravital and intravital responses. Most (80%) shark-bite wounds were postmortem, 10% were antemortem, and 10% were perimortem. We found that antemortem and postmortem wounds were similar in extent and location except for wounds that primarily involved the shell, which were never found in cases of scavenging. For sea turtles found dead in the southeastern USA, our findings suggest that most shark-bite wounds without externally evident vital responses are due to scavenging. Additionally, this scavenging can significantly damage a carcass, potentially obscuring the detection of other causes of mortality. These findings should be considered when using data derived from stranded sea turtles to conduct mortality assessments.

KEY WORDS: Turtle · Shark · Bite · Intravital · Supravital · Postmortem · Antemortem

1. INTRODUCTION

All species of sea turtle are imperiled worldwide and are the focus of protective global and regional measures intended to promote recovery of their populations. Such measures require an understanding of causes of mortality in order to inform effective conservation strategies and actions. Dead, injured, or debilitated sea turtles found washed ashore or floating, i.e. stranded, are one of

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the few indicators of mortality at sea. Programs in many countries monitor sea turtle strandings as part of efforts to study threats within the marine environment.

Sharks of the orders Carcharhiniformes and Lamniformes are known to prey upon all species of sea turtle (reviewed by Stancyk 1981, Heithaus et al. 2008). The tiger shark *Galeocerdo cuvier* is a well-documented sea turtle predator and has been studied in multiple regions (Witzell 1987, Lowe et al. 1996, Heithaus et al. 2002, 2008, Bornatowski et al. 2012, Hammerschlag et al. 2015). Sharks also are facultative scavengers that feed on a variety of dead animals, including sea turtle carcasses (e.g. Dudley et al. 2000, Gallagher et al. 2011, Bornatowski et al. 2012).

The dual role of sharks as both sea turtle predators and scavengers can make it difficult to ascertain the nature of shark-inflicted wounds encountered in stranded turtles, particularly in those that are found dead (Bornatowski et al. 2012). A minimum number of stranded turtles depredated by sharks can be derived from those that are either found alive with characteristic injuries or that have survived long enough for inflammation or healing associated with these wounds to become evident. However, in our experience this approach has significant limitations because most stranded turtles with major wounds are dead upon discovery and the period of survival following fatal injuries is likely insufficient for vital responses to become readily apparent. For example, as part of an intensive effort from 2010 through 2017 to examine stranded sea turtles found in the northern Gulf of Mexico following the *Deepwater Horizon* oil spill, 6.7% (114/1697) had major shark-bite injuries, and only 5.3% (6/114) of these cases were found alive or exhibited obvious evidence of antemortem occurrence (B. A. Stacy unpubl. data). Moreover, scavenging of sea turtle carcasses by sharks not only confounds efforts to properly attribute the role sharks play in sea turtle mortality but may also obscure evidence of other causes of death.

Our objective was to determine the timing of shark-bite injuries without any external indications of wound vitality in relation to death for sea turtles that were found in the southeastern USA. Through postmortem examination, we evaluated turtles for evidence of exsanguination and examined the soft tissue wound margins for intravital and supravital responses. In addition, we compared the patterns of injuries based on determinations of antemortem or postmortem occurrence to evaluate whether certain wound characteristics were associated with predation or scavenging.

2. MATERIALS AND METHODS

The study area encompassed much of the Atlantic and Gulf coasts of the southeastern USA, including the states of Florida, Alabama, Mississippi, Louisiana, and Texas. Stranded sea turtles found floating or onshore in these states were documented by participants in the Sea Turtle Stranding and Salvage Network (STSSN) according to established protocols (Foley et al. 2007). Straight carapace length (SCL) was measured from the nuchal notch to the caudal extent of the supracaudal scutes. For turtles that were found dead, the degree of decomposition was classified as minimal, moderate, or severe. Minimally decomposed turtles exhibited little to no autolysis or putrefaction. Turtles that were moderately decomposed were partially bloated, had a foul odor, and there was some detachment of the epidermis. Severely decomposed carcasses were prominently bloated or had erupted due to the internal expansion of gases, and the skeleton was beginning to disarticulate.

From 2010 through 2019, we performed necropsies on stranded sea turtles with shark-bite wounds that met our study criteria. Shark-bite wounds were recognized as injuries resulting in deep incision or removal of soft tissue, appendages, or the head with accompanying sharp incisions of the skin or scoring and gouging of bone or cartilage as created by shark teeth (Fig. 1). We only included cases in which (1) the turtle was dead upon discovery; (2) wounds were sufficiently extensive to have plausibly resulted in death, i.e. those that resulted in decapitation, amputation, or soft tissue injury that may have led to exsanguination or loss of other vital function; and (3) there was no externally evident vital response (e.g. hemorrhage, inflammation, re-epithelialization, or fibroplasia). These criteria comprise a typical scenario where injuries caused by sharks cannot be confidently attributed to predation or scavenging without a necropsy.

Postmortem examination consisted of evaluation of all organ systems to the extent feasible. All examinations were performed or attended by a board-certified pathologist (B. A. Stacy). We considered absence of blood within the heart and generalized pallor of the soft tissues without other apparent cause (e.g. concurrent injuries, emaciation, marine leech infestation, disease) as indications of exsanguination (Fig. 2). Samples of skeletal muscle were collected from the margins of the bite wounds, perpendicular to the wound, and if possible, along the longitudinal axis of the myofibers. Following fixation in 10% neutral phosphate

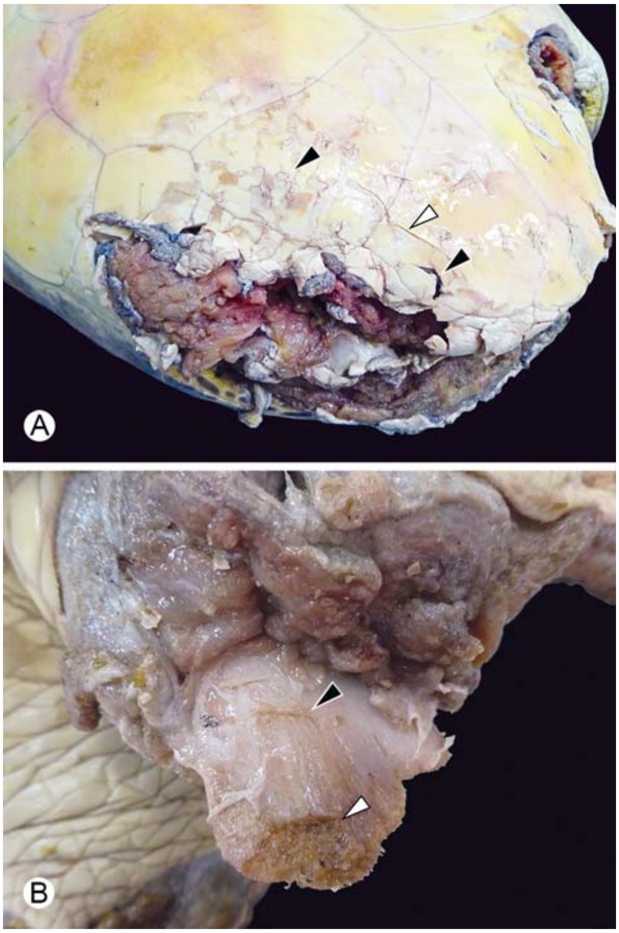

Fig. 1. Examples of shark-bite wounds in sea turtles. (A) Green turtle *Chelonia mydas* with the head and front flippers removed by bite wounds characterized by sharply incised tooth marks (black arrowheads) and rakes (white arrowhead). (B) Kemp's ridley turtle *Lepidochelys kempii* with amputation of a front flipper by shark bite. Note the scoring of bone by teeth (black arrowhead) and fracture of subchondral bone of the distal humerus (white arrowhead)

buffered formalin, the wound margins were processed into paraffin, sectioned by 5 µm, mounted onto glass slides, and stained with hematoxylin and eosin using routine methods. Sections were evaluated by histopathology for inflammation or myofiber disintegration, the latter being a supravital response indicative of contractile potential at the time of wounding (Henssge et al. 2002, Warther et al. 2012, Stacy et al. 2015) (Fig. 3).

Shark-bite injuries were categorized as antemortem (occurring prior to death) if wounds were accompanied by evidence of exsanguination or other intravital response (i.e. inflammation or hemorrhage). Wounds were considered perimortem (inflicted at or around the time of death) if indications of exsanguination were not observed or could not be evaluated, but myofiber disintegration was present (supravital response) without any intravital responses. Injuries were considered postmortem (occurring after death) if no supravital or intravital responses were found.

The injuries were categorized according to their location and extent (Table 1) and were compared with wound vitality determinations. Concurrent necropsy findings and ancillary information relevant to cause of death were also examined.

3. RESULTS

In total, 70 sea turtles met our study criteria, including 46 Kemp's ridley turtles *Lepidochelys kempii*, 8 loggerhead turtles *Caretta caretta*, and 16 green turtles *Chelonia mydas*. Median SCL by species was 45.8 cm (range: 17.9–64.0 cm) for Kemp's ridleys, 72.1 cm (65.6–87.2 cm) for loggerheads, and 35.2 cm (19.2–94.6 cm) for green turtles. With regard to postmortem condition, 7 were minimally decomposed, 42 were moderately decomposed, and 21 were severely decomposed. Twenty-four turtles were found in Louisiana, 20 in Florida, 16 in Texas, 6 in Alabama, and 4 in Mississippi.

We determined the injuries to be postmortem in 56 (80.0%) cases, antemortem in 7 (10.0%) cases, and perimortem in 7 (10.0%) cases. Four of the turtles with antemortem wounds and 4 with perimortem wounds were green turtles. Only 3 Kemp's ridleys had antemortem injuries; 3 had perimortem wounds. All bite wounds in loggerheads were postmortem.

The most common bite wound categories were decapitation with one or more flipper amputations (n = 29) and amputations of multiple flippers (n = 21) (Table 2). Amputations involved one or both front flippers (n = 22), one or both rear flippers (n = 15), or combinations of both front and rear flippers (n = 30). The head and flippers in most cases were removed by disarticulation (Fig. 4). Most skeletal fractures only involved the subchondral bone and vertebral articular facets. Diaphyseal fractures were only found in 11.1% (7/63) of turtles with amputations, including 5 Kemp's ridleys, 1 loggerhead, and 1 green turtle. Five of 7 turtles with diaphyseal fractures were under 30.0 cm SCL. We observed no apparent relationship between the extent and location of the bite wounds and wound vitality determination, except for injuries that primarily involved the carapace and plastron (Fig. 4). Only 2 turtles had wounds centered on the shell; both were antemortem (Fig. 5).

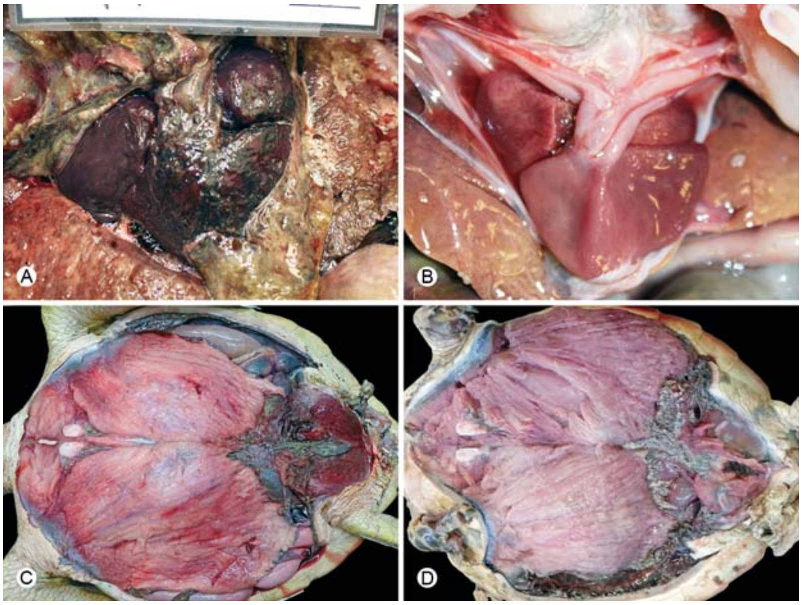

Fig. 2. Examples of sea turtle with shark-bite wounds with and without evidence of exsanguination. (A) Heart of a Kemp's ridley turtle *Lepidochelys kempii* full of blood, the typical postmortem state of a healthy turtle without major blood loss. (B) Green turtle *Chelonia mydas* in which the heart is pale and devoid of blood due to exsanguination. (C) Green turtle with pink pectoral muscle typical of the postmortem appearance without exsanguination. (D) Prominent pallor of the pectoral muscle in a green turtle suggestive of severe blood loss. The visceral organs also were pale and blood was absent from the heart and major vessels (not shown)

Of those turtles with postmortem shark-bite wounds, 67.9% (38/56) did not have any other identifiable abnormalities, 17.9% (10/56) had concurrent unrelated injuries (mostly vessel strikes), 8.9% (5/56) had significant disease states and/or were in poor nutritional condition, 1 (1.8%) was found during a red tide with associated sea turtle mortality, and 2 (3.6%) could not be further evaluated due postmortem state. Among those without other abnormalities, nutritional condition was within normal limits for free-ranging turtles based on robustness of muscle and fat. Food items were present in the esophagus or stomach in 83.8% (25/30) in which evaluation was possible. Gastrointestinal contents of 48.1% (13/27 examined) of the Kemp's ridleys included finfish (n = 10), penaeid shrimp (n = 1), or both fish and shrimp (n = 2). Fish and penaeid shrimp were not found in green turtles (n = 2) or loggerheads (n = 3) with postmortem wounds and examinable digestive tracts.

In turtles with perimortem bite wounds, 5 did not have other apparent abnormalities and 2 had vessel-strike injuries. In 5 cases, we could not determine whether there was exsanguination resulting from the shark-bite wounds because the visceral organs and other soft tissues were missing or exposed (n = 2), there were concurrent major injuries (n = 2), or unrelated anemia could not be excluded (n = 1). Two turtles, both Kemp's ridleys with perimortem shark-bite wounds, did not have evidence of exsanguination or any other evident abnormalities; both had been feeding on fish.

We attributed death to a shark attack for all 7 turtles with antemortem injuries based on the potential lethality of the wounds and concurrent gross evidence of exsanguination. All had supravital muscle responses without histologically evident hemorrhage or inflammation.

4. DISCUSSION

Aquatic animals with traumatic injuries present several challenges to forensic assessments of wound vitality. Water can wash away hemorrhage from antemortem wounds (DiMaio & DiMaio 2001, Lu-

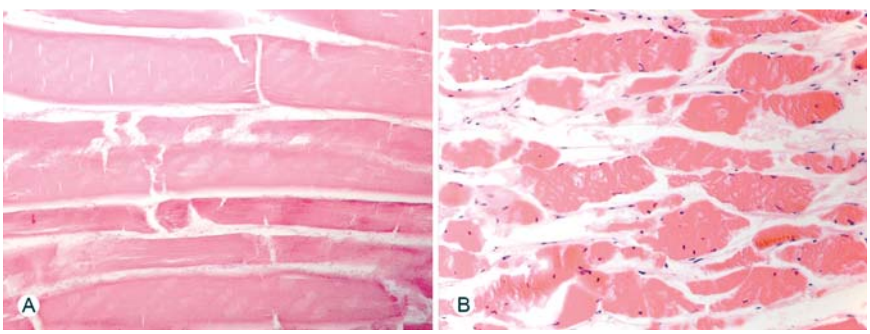

Fig. 3. Photomicrographs of skeletal muscle comprising shark-bite wounds in sea turtles. (A) Myofibers in a Kemp's ridley turtle *Lepidochelys kempii* exhibiting no supravital or intravital changes, indicative of postmortem wounds resulting from scavenging. (B) Myofibers in a green turtle *Chelonia mydas* exhibiting disintegration, a supravital response characterized by band-shaped condensation and segmental disruption of the sarcoplasm with loss of cross striations

Table 1. Patterns of shark-bite wounds observed in stranded sea turtles evaluated for wound vitality

Category	Predominant wound features
A	Amputation of single flipper
B	Amputation of 2 or more flippers
C	Decapitation only
D	Decapitation with one or more amputations
E	Bite wound(s) with soft tissue loss without amputation or decapitation
F	Bite wound primarily involving carapace/plastron ± amputation

Table 2. Categories of shark-bite wound patterns (see Table 1 for wound category definitions) observed in stranded sea turtles and wound vitality results

Wound vitality determination	Wound category A	B	C	D	E	F	Total
Antemortem	0	3	0	1	1	2	7
Perimortem	1	4	1	1	0	0	7
Postmortem	10	14	0	27	5	0	56
Total	11	21	1	29	6	2	70

netta & Modell 2005), the duration of survival post-injury may be insufficient for development of a demonstrable inflammatory response (Foley et al. 2019), and scavenging or decomposition may limit evaluation or confidence in some observations. The ecological roles of sharks as both predators and facultative scavengers contests assumptions about the circumstances of injury. As a result, the timing of shark-bite wounds relative to death and the nature of the wounds in terms of predation or scavenging often are not confidently determined in stranded sea turtles (Bornatowski et al. 2012).

By employing a combination of consistent gross postmortem evaluation during necropsy coupled with wound histology, we were able to confidently characterize wound vitality in most cases. Histopathological evaluation of skeletal muscle comprising the margins of bite wounds was a critical tool to determine wound vitality because this may be otherwise difficult to determine due to decomposition, missing visceral organs, or postmortem leaching of blood from the exposed tissues by seawater. Skeletal muscle maintains its histological integrity better than most other tissues, and supravital changes can remain observable for days after death (Stacy et al. 2015). Although myofiber disintegration alone does not indicate antemortem trauma, its absence is indicative of a postmortem injury such as scavenging.

We most often classified injuries as perimortem when we could not confidently evaluate sea turtles for intravital responses, but observed myofiber disintegration in the wound margins. It is unsurprising that we documented 2 cases with supravital responses without evidence of exsanguination or other intravital responses given that myofiber disintegration may occur until contractile potential is lost with the onset of rigor mortis (Stacy et al. 2015). We interpreted the findings in these cases as consistent with postmortem scavenging prior to rigor mortis.

The most frequent injury among our cases was decapitation in combination with one or more flipper amputations, which was similar to the finding of a previous study in Brazil (Bornatowski et al. 2012). We did not detect any differences in the location or extent of injuries between those that were antemortem and those that were postmortem except for bite wounds centered on the shell. Although only 2 such wounds were represented in our study (both were antemortem), we never saw these shell-centered wounds among numerous cases of scavenging. Additionally, we have frequently seen shell-centered wounds in live turtles attacked by sharks. For example, of the 21 sea turtles with bite wounds that we excluded from our study because they were either found alive or had an externally evident vital response, 6 (28.6%) had injuries that primarily involved the shell.

Possible explanations for a lack of shell-centered wounds among the dead turtles in our study are that carcasses with these penetrating shell injuries are less likely to become buoyant and wash ashore, reflecting bias inherent to stranded turtles, or that injuries involving the shell more commonly result from predation. The behavioral responses of sea turtles and sharks to one another also could explain why injuries involving the shell were disproportionally antemortem in our study. Sea turtles are known to position themselves with their carapace oriented towards an approaching shark (Bostwick et al. 2014), potentially resulting in bite wounds involving the shell. Obviously, dead sea turtles do not exhibit such movements. Also, sharks may approach live turtles differently than carcasses, thus influencing the probability of the shell being bitten.

Decapitation and amputation in our cases most often occurred by disarticulation, not by fracturing of bones. The bites associated with these injuries could damage the articular cartilage or fracture the subchondral bone or the relatively delicate articular facets of the cervical vertebrae, but diaphyseal fractures were less common and most were in smaller

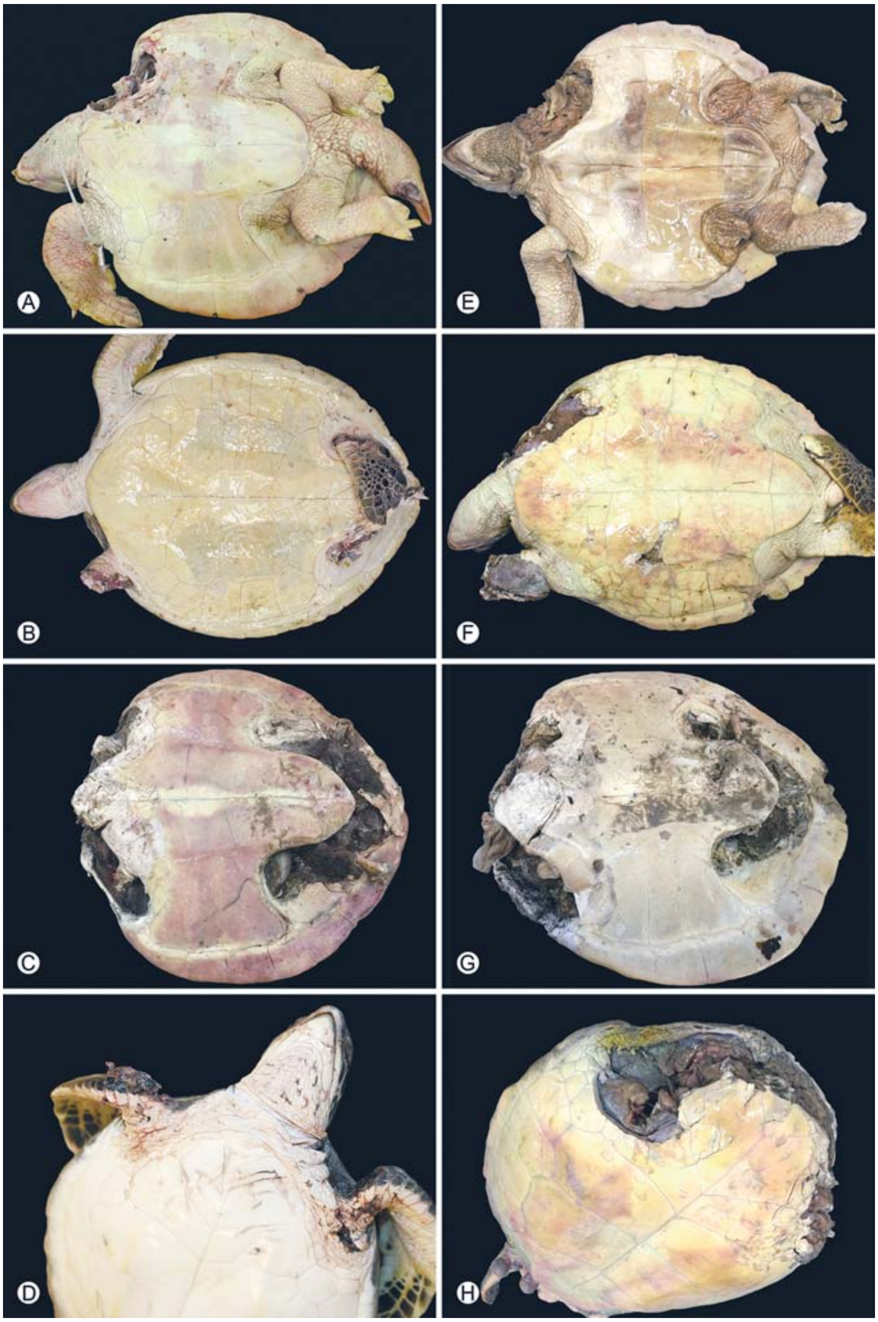

Fig. 4. Examples of antemortem and postmortem shark-bite wounds in sea turtles showing similarity in patterns of injury associated with probable predation and scavenging. (A–D) Sea turtles that were either (B,D) found alive or (A,C) had evidence of antemortem injury upon necropsy, whereas (E–H) injuries determined to be postmortem were based on lack of associated intravital or supravital responses. Note that the missing appendages have been removed by disarticulation

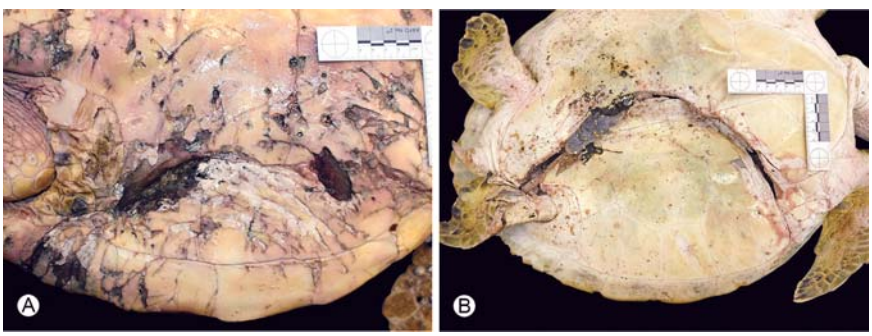

Fig. 5. Shark-bite wounds primarily involving the shell in sea turtles. (A) Loggerhead turtle *Caretta caretta* that was found alive with extensive bite wounds involving the plastron. (B) A similar bite wound in a green turtle *Chelonia mydas* that was found dead with evidence of exsanguination accompanied by myofiber disintegration within the damaged muscle

turtles. In contrast, bite wounds involving the carapace and plastron frequently deeply abraded or cut through the relatively robust dermal and appendicular bone. The tiger shark *Galeocerdo cuvier* is known for its ability to bite through turtle bone using its serrated teeth and saw-like jaw motions (Witzell 1987). Bite wounds penetrating the protective shell may reflect injury by those sharks that are adapted to prey on cheloniid turtles. Conversely, decapitation and amputation might result from removal of the most readily accessible and easily separated aspects of the body, whether during predatory attack or scavenging.

Our findings indicate that most shark-bite wounds resulting in amputation, decapitation, or other major tissue loss observed in dead stranded sea turtles in the southeastern USA without evident intravital responses are the result of sharks scavenging turtles that died from other causes. The cause of death for some of the turtles in the present study was attributable to other factors, the most frequent of which was from injuries caused by vessel strikes. However, 67.9% (38/56) of the turtles with postmortem shark-bite wounds did not have other abnormalities, their nutritional condition was within normal limits for healthy wild turtles, and most had food within their esophagus or stomach indicating recent feeding. Nearly half (48.1%, 13/27) of examined Kemp's ridleys had ingested finfish and/or penaeid shrimp, organisms that are not considered natural food items and are generally associated with opportunistic foraging on dead, captured, or discarded fish and shrimp, such as that related to fishing activities or other sources (Shaver 1991, Seney & Musick 2007). This combination of postmortem findings indicates a sudden cause of death and is observed when sea turtles drown from being forcibly submerged or entrapped underwater, as results from capture in fishing gear or under similar circumstances (Shoop & Ruckdeschel 1982, Work & Balazs 2010). In these cases, without careful examination, scavenging by sharks would have obscured indications of probable anthropogenic mortality.

Our observations are not necessarily applicable to other regions where there may be differences in predator–prey dynamics as well as other contributing causes of sea turtle mortality. However, our findings show that consistent gross examination during necropsy coupled with wound histology can be used to resolve uncertainties about the nature of shark-bite wounds in stranded sea turtles, including those cases where some aspects of diagnostic evaluation are limited by postmortem condition.

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LITERATURE CITED

Bornatowski H, Heithaus MR, Batista CMP, Mascarenhas R (2012) Shark scavenging and predation on sea turtles in northeastern Brazil. Amphib-Reptil 33:495–502

Bostwick A, Higgins BM, Landry AM Jr, McCracken ML (2014) Novel use of a shark model to elicit innate behavioral responses in sea turtles: application to bycatch reduction in commercial fisheries. Chelonian Conserv Biol 13:237–246

DiMaio VJ, DiMaio D (2001) Forensic pathology, 2nd edn. CRC Press, Boca Raton, FL

Dudley SF, Anderson-Reade MD, Thompson GS, McMullen PB (2000) Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks, *Galeocerdo cuvier*. Fish Bull 98:646–649

Foley AM, Singel KE, Dutton PH, Summers TM, Redlow AE, Lessman J (2007) Characteristics of a green turtle (*Chelonia mydas*) assemblage in northwestern Florida determined during a hypothermic stunning event. Gulf Mex Sci 25:131–143

Foley AM, Stacy BA, Hardy RF, Shea CP, Minch KE, Schroeder BA (2019) Characterizing watercraft-related mortality of sea turtles in Florida. J Wildl Manag 83:1057–1072

Gallagher AJ, Jackson T, Hammerschlag N (2011) Occurrence of tiger shark (*Galeocerdo cuvier*) scavenging on avian prey and its possible connection to large-scale bird die-offs in the Florida Keys. Fla Sci 74:264–269

Hammerschlag N, Broderick AC, Coker JW, Coyne MS and others (2015) Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. Ecology 96:2117–2126

Heithaus MR, Frid A, Dill LM (2002) Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. Mar Biol 140:229–236

Heithaus MR, Wirsing AJ, Thomson JA, Burkholder DA (2008) A review of lethal and non-lethal effects of predators on adult marine turtles. J Exp Mar Biol Ecol 356:43–51

Henssge C, Wang H, Hoppe B (2002) Light microscopical investigations on structural changes of skeletal muscle as artifacts after postmortem stimulation. Forensic Sci Int 125:163–171

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Environ Biol Fishes 47:203–211

Lunetta P, Modell J (2005) Macroscopical, microscopical, and laboratory findings in drowning victims — a comprehensive review. In: Tsokos M (ed) Forensic pathology reviews, Vol 3. Humana Press, Totowa, NJ, p 3–77

Seney EE, Musick JA (2007) Historical diet analysis of loggerhead sea turtles (*Caretta caretta*) in Virginia. Copeia 2007:478–489

Shaver DJ (1991) Feeding ecology of wild and head-started Kemp's ridley sea turtles in South Texas waters. J Herpetol 25:327–334

Shoop CR, Ruckdeschel C (1982) Increasing turtle strandings in the southeast United States: a complicating factor. Biol Conserv 23:213–215

Stacy BA, Costidis AM, Keene JL (2015) Histologic changes in traumatized skeletal muscle exposed to seawater: a canine cadaver study. Vet Pathol 52:170–175

Stancyk SE (1981) Nonhuman predators of sea turtles and their control. In: Bjorndal KA (ed) Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, DC, p 139–152

Warther S, Sehner S, Raupach T, Püschel K, Anders S (2012) Estimation of the time since death: post-mortem contractions of human skeletal muscles following mechanical stimulation (idiomuscular contraction). Int J Legal Med 126:399–405

Witzell WN (1987) Selective predation on large cheloniid sea turtles by tiger sharks (*Galeocerdo cuvier*). Jap J Herpetol 12:22–29

Work TM, Balazs GH (2010) Pathology and distribution of sea turtles landed as bycatch in the Hawaii-based North Pacific pelagic longline fishery. J Wildl Dis 46: 422–432

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