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Forensic determination of shark species as predators and scavengers of sea turtles in Florida and Alabama, USA

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ABSTRACT: Sharks are the primary predator of large immature and mature sea turtles, yet the shark species responsible for both lethal and non-lethal injuries are rarely identified. Forensic analysis of bite wounds can be used to accurately assess size and potential shark species when combined with observations on species-specific feeding behavior, geographic distribution, and habitat preference. The objective of this study was to use forensic analysis of bite damage on sea turtles to infer shark size and species. Photographs from 13 cases of documented shark predation (n = 10) and scavenging (n = 3) attempts on sea turtles were retrospectively analyzed, including nesting, free-ranging, and/or dead stranded loggerhead *Caretta caretta*, green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii*, and leatherback *Dermochelys coriacea* sea turtles in Florida and Alabama, USA, from 2010–2020. Mean interdental distance (IDD) and bite circumference (BC) of wound marks on sea turtles suggest that wounds were generated by white sharks *Carcharodon carcharias* in 3 cases, tiger sharks *Galeocerdo cuvier* in 3 cases, and bull shark(s) *Carcharhinus leucas* in one case. For 3 cases with less distinct wound patterns, 2 likely shark species were identified and thereafter narrowed down to a single species based on bite mark characteristics (e.g. punctures). Due to indistinct IDD and BC ranges of the bite patterns, a single shark species was not identified in 3 cases. Forensic analysis enables more accurate evaluations of which shark species prey on and scavenge sea turtles and is a useful technique for studying the behavioral interactions of sharks and turtles.

KEY WORDS: Marine turtle · Forensic analysis · Injury · Shark bite · Predator–prey

1. INTRODUCTION

One of the most fundamental interactions between species is the predator–prey relationship. Predators inhabit every ecosystem on Earth and play an important role in shaping the evolution, ecology, life history, and behavior of organisms (Estes et al. 2001, Heithaus et al. 2002). Because predation can be highly variable in time and space, trophic information remains scarce for highly migratory species with wide distributions (Wetherbee & Cortés 2004, Barnett et al. 2010). Sharks of all sizes are known to prey upon a wide range of organisms, including plankton, teleost fishes, other elasmobranchs, and cephalopods

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(Wetherbee & Cortés 2004). Larger sharks, specifically tiger sharks *Galeocerdo cuvier*, white sharks *Carcharodon carcharias*, bull sharks *Carcharhinus leucas*, larger hammerhead species *Sphyrna* spp., lemon sharks *Negaprion brevirostris*, and oceanic whitetip sharks *Carcharhinus longimanus* are the primary predators of large immature and mature sea turtles (Stancyk 1983, Witzell 1987). Tiger sharks occupy coastal and offshore tropical habitats as well as warm temperate climates that overlap with several sea turtle species, and their broad, flat head, kinetic jaws, and specialized serrated teeth allow them to commonly consume large prey like sea turtles (Witzell 1987, Randall 1992, Motta & Wilga 2001, Heithaus et al. 2008a,b, Heithaus 2013). White sharks also frequently prey upon large marine animals; however, sea turtles likely comprise only a very small percentage of their diet (Heithaus et al. 2008b). Bull sharks have been documented feeding on smaller sea turtle species (i.e. juvenile and subadult green turtles) in coastal tropical waters (Cliff et al. 1989, Heithaus et al. 2008b).

Adult sea turtles have relatively high survivorship due to protection afforded by their large size and hard carapace (Frazer 1983, Stancyk 1983, Chaloupka & Limpus 2002, 2005, Whiting & Whiting 2011, Bornatowski et al. 2012). As a result, predation risks have largely been overlooked in large sea turtles because of low rates of predator-induced mortality compared to immature sea turtles, even though accounts show that large immature and mature sea turtles are susceptible to some predators (Heithaus et al. 2007). For example, saltwater crocodiles *Crocodylus porosus* have been observed preying on nesting olive ridley *Lepidochelys olivacea* and flatback *Natator depressus* sea turtles in Cape Van Diemen, Australia (Whiting & Whiting 2011), while killer whales *Orcinus orca* have been observed preying on leatherbacks *Dermochelys coriacea* in northern California (Pitman & Dutton 2004). Shark predation by a suite of species large and capable enough to exceed carapace durability may influence the spatial distribution and population size of large immature and mature sea turtles, yet formal studies on this subject are minimal (Heithaus et al. 2002, Wirsing et al. 2008, Bornatowski et al. 2012).

Forensic analysis is a tool to identify the total length (TL) and species of sharks involved in bites on humans (Lowry et al. 2009, Clua & Séret 2010, Clua & Reid 2017), and it is gaining broader use to study ecological interactions between sharks and their prey (van den Hoff & Morrice 2008, Bornatowski et al. 2012, Serres et al. 2022). Because shark size directly influences swimming speed, bite force capacity, and hunting behavior, reliable estimates of size and species are needed to better understand sharks' hunting and feeding behavior, dietary composition, and ecological interactions (Stillwell & Kohler 1982, Cortés 1999, Heithaus et al. 2002, Lowry et al. 2009). Comparison of bite damage metrics known to correlate with shark species and size has been used to examine the commonality of serrations in shark teeth relative to their position within the jaw (Nambiar et al. 1996), profile sharks responsible for fatal attacks on humans (Clua & Reid 2017), and analyze approach behavior and possible feeding motivation in sharks (Ritter & Levine 2004).

To better understand predator–prey relationships between sharks and sea turtles, the goal of this study was to apply the forensic methods of Lowry et al. (2009) to identify the species and estimated size of sharks preying on or scavenging sea turtles in the coastal waters of Florida and Alabama, USA. This method employs species-specific regressions of tooth spacing and jaw circumference, combined with shark distribution and known behavioral patterns, to identify likely candidate shark species capable of generating specific bite damage to sea turtle prey (Lowry et al. 2009).

2. MATERIALS AND METHODS

2.1. Data collection

Photographs and first-hand accounts associated with 13 cases of sea turtles bearing wound patterns consistent with predation, attempted predation, or scavenging by sharks were retrospectively evaluated (Corkeron et al. 1987, Woolgar et al. 2001). Predation and scavenging events were documented via complete postmortem examination of turtle carcasses (after Stacy et al. 2021), including gross examination of all organ systems and histopathological evaluation of sections of skeletal muscle associated with the bite wound(s). Incidents of attempted predation that did not result in turtle mortality were evaluated using the same methods, though these injuries were less severe and precluded examination of internal organs. Cases were collected in Florida and Alabama, USA, and shared by collaborators at NOAA Fisheries–Office of Protected Resources, Inwater Research Group, and Loggerhead Marinelife Center (see Fig. 1). The evaluated turtles were either encountered nesting on the beach (n = 2), examined while being removed from a coastal power plant intake canal (n = 5), or had died and were examined at necropsy (n = 6). Each case involved a turtle with definitive shark bite wounds characterized by either (1) an arced array of regularly spaced puncture wounds, with or without associated injuries extending from the initial puncture sites (e.g. see Fig. 2A); or (2) crescent-shaped, rough-edged wound(s) from which a portion of peripheral plastron, carapace, or flipper tissue had been excised (e.g. see Fig. 3A). Furthermore, all wounds included sharply incised tooth marks and/or scoring of bones typical of those caused by shark teeth (e.g. see Fig. 4). None had chop wounds or other sharp or blunt features attributable to vessel strikes (Foley et al. 2019, Stacy et al. 2021). For all cases, standard straight or curved carapace length and width measurements were collected, and digital photography was used to document each wound with a scale bar (standard 8 or 15 cm ruler) upon stranding or during physical examination of the animal (Klingshirn 2021, Page-Karjian & Perrault 2021, Stacy et al. 2021). When available, detailed measurements of wounds collected at the time of turtle encounter (Ataman et al. 2021, Klingshirn 2021) were also used to inform forensic analysis. Shark bites were attributed to predation versus scavenging based on postmortem examination findings following Stacy et al. (2021). Specifically, shark bite injuries were categorized as antemortem if lesions had evidence of exsanguination or other intravital responses (e.g. inflammation, hemorrhage) and postmortem if no supravital (e.g. myofiber disintegration) or intravital responses were found. Postmortem wounds were, thus, determined to result from scavenging behavior on deceased turtles, while antemortem wounds resulted from predation events on live turtles.

2.2. Forensic analysis of shark bite wounds

Each digital photo was independently assessed by 2 expert reviewers using the methods of Lowry et al. (2009). Photos were imported into Image J image processing software, and wound length was calibrated using the field scalar provided (Schneider et al. 2012). For arced arrays of puncture wounds, the straight-line distance between a pair of consecutive punctures was measured 3 times and the mean value was recorded. This was repeated for each pair of adjacent wounds along the array to produce a series of values describing all visible puncture lesions. The mean value of this spacing was then calculated as mean interdental distance (IDD), which has been shown to correlate with size for various species of sharks (Shimada 2002, Lowry et al. 2009). Furthermore, species-specific relationships exist between shark size and the mean IDD in the upper and lower jaws as a consequence of differences in tooth morphology and spatial arrangement (Lowry et al. 2009). Injuries radiating from the tooth punctures were ignored because such wound tracts tend to converge as a shark rotates its head during a bite and are thus a poor indicator of tooth spacing.

After all puncture wound pairs were evaluated, the cumulative length of the array of lesions was calculated by summing the IDD for all pairs of adjacent punctures and projecting the ends of the array along a curved path to the extent of the tissue continuous with the array. This estimate of bite circumference (BC) has been shown to correlate with subadult and adult shark size and species (Lowry et al. 2009), though it often produces an underestimate of TL because sharks frequently employ only the anterior portion of their jaw when biting. Here, we relied upon IDD as the primary indicator of shark size, with BC providing a secondary confirmation of minimum size. If bite wounds were present on both the dorsal and ventral aspects of the turtle, measurements of IDD and BC were made on each side, and the array with the smaller BC was assumed to have been generated by the lower jaw of the shark. For wounds with substantial tissue loss, the same procedure was used to measure and calculate IDD and BC, but estimates of IDD were often limited because sharks typically remove tissues through head shaking, tooth sawing, and jaw repositioning behaviors. This tends to obscure the damage produced by any single tooth or tooth pair and necessitates reliance upon BC measured as the length of the arc along which tissue was removed. For any cases in which the IDD and BC measures calculated by reviewers differed by >5%, the 2 reviewers would conduct a cooperative assessment and the results of this evaluation were considered final. This occurred in only one of the 13 cases, in which degradation of the tissue created a rounded edge that did not translate well into a planar photograph.

Once IDD and BC measurements were determined for each case study, these values were entered into the electronic supplementary material of Lowry et al (2009), a tool that provides species-specific regression equations for 14 shark species (see 'Calculator' in the Supplement at www.int-res.com/articles/suppl/m703p145_supp.xlsx). This application was developed after measuring dozens of preserved jaws over a range of shark sizes and 14 shark species to estimate the TL of a specimen capable of generating observed bite damage (Lowry et al. 2009). While the application is not comprehensive, the species included in the electronic supplementary material of

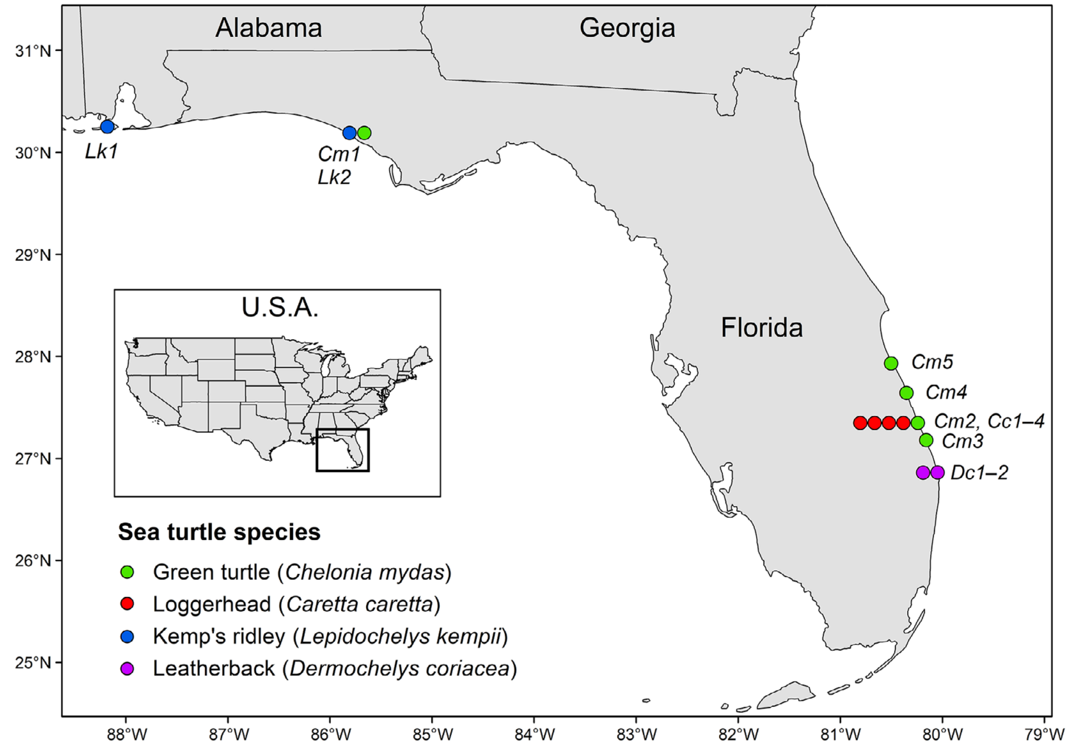

Fig. 1. Locations of the 13 cases of shark–sea turtle interactions. Twelve cases originated in Florida and one (*Lk1*) originated in Alabama. Inwater Research Group provided 5 cases (*Cm2*, *Cc1–4*) at the St. Lucie Nuclear Powerplant intake canal, 2 cases (*Dc1*, *Dc2*) were provided by Loggerhead Marinelife Center, and 6 cases (*Cm1*,*3–5*, *Lk1–2*) were provided by NOAA Fisheries, Office of Protected Resources

Lowry et al. (2009) represent most nearshore shark species capable of preying on turtles in tropical and temperate waters in the Gulf of Mexico and off the west and east coast of the USA. The electronic supplemetary material of Lowry et al. (2009) annotates instances in which IDD and BC measurements are outside the range of values used to generate a given regression, or when the resulting TL estimate exceeds the known maximum TL for that species. Shark species and size estimates generated via the electronic supplementary material of Lowry et al. (2009) were combined with reviewer knowledge of species-specific feeding behavior, geographic distribution, and habitat preference to narrow the candidate list of specimens likely involved in each predation event. In nearly every case, this resulted in no more than 2 putative species identifications for the size and species of shark involved.

3. RESULTS

In total, 13 cases were included in this study, including 5 green *Chelonia mydas*, 4 loggerhead *Caretta caretta*, 2 Kemp's ridley *Lepidochelys kempii*, and 2 leatherback sea turtles that were encountered nesting, stranded on Florida's east coast or in the northern Gulf of Mexico, or hand-captured in a nuclear powerplant intake canal (Fig. 1). Ten turtles exhibited evidence of predation or attempted predation and 3 exhibited evidence of scavenging. Data from turtles were collated and summarized, including species, year encountered, sex (when known), capture method, size and life-stage class, and timing of inflicted wound (i.e. predation versus scavenging, for deceased turtles only). Data from sharks include IDD and BC measurements, likely species that inflicted the wound, and estimated linear natural TL measured in meters (Table 1).

3.1. Green sea turtles *Chelonia mydas*

Five juvenile green turtle cases were recorded in Florida (Fig. 1) during 2010–2019. Case *Cm1* was captured and released at the St. Lucie Nuclear Powerplant intake canal on Hutchinson Island. It exhibited a 280 mm, crescent-shaped bite wound on the

Table 1. Case data on sea turtles that were preyed/scavenged upon by sharks. For turtles, included are the year of stranding, life-stage class, sex (if known), capture method, standard straight carapace length (SCL) and straight carapace width (SCW), and timing of the wound (i.e. antemortem or postmortem). For sharks, data are also provided on the most likely predator(s), including mean interdental distance (IDD), bite circumference (BC), and estimated total length. CND: could not determine; NA: not available. Case IDs correspond to turtle scientific names: *Cm*: *Chelonia mydas* (green turtle); *Cc*: *Caretta caretta* (loggerhead); *Lk*: *Lepidochelys kempii* (Kemp's ridley); *Dc*: *Dermochelys coriacea* (leatherback). Shark species: bull shark *Carcharhinus leucas*; dusky shark *C. obscurus*; longfin mako shark *Isurus paucus*; mako species *Isurus* spp.; sandbar shark *C. plumbeus*; shortfin mako shark *I. oxyrinchus*; tiger shark *Galeocerdo cuvier*; white shark *Carcharodon carcharias*

	Sea turtles						Sharks			
Case	Year	Life-stage class/sex	Capture method	SCL (cm)	SCW (cm)	Bite timing	Mean IDD (mm)	Mean BC (mm)	Likely species	Total length (m)
(1) *Cm1*	2010	Juvenile/unknown	Hand-captured	49.5	39.5	Antemortem	12	CND	Bull shark	1.9
(2) *Cm2*	2013	Juvenile/unknown	Stranded	47.4	37.4	Antemortem	12	310	Bull shark	1.9–2.2
(3) *Cm3*	2016	Juvenile/unknown	Stranded	41.1	NA	Postmortem	16	316	Tiger shark	2.3–2.4
(4) *Cm4*	2018	Juvenile/unknown	Stranded	19.2	17.2[a]	Antemortem	19	467	White shark	2.3–2.7
(5) *Cm5*	2019	Juvenile/unknown	Stranded	45.0[a]	29.3[a]	Antemortem	8	238	Dusky shark	1.6–1.7
(6) *Cc1*	2014	Adult/female	Hand-captured	83.2	67.0	Antemortem	20	412	White shark	2.3–2.4
(7) *Cc2*	2017	Adult/female	Hand-captured	83.2	67.5	Antemortem	25	CND	Mako shark	2.6
(8) *Cc3*	2017	Adult/unknown	Hand-captured	68.8	56.6	Antemortem	52	CND	White shark	6.3–6.4
(9) *Cc4*	2019	Adult/unknown	Hand-captured	65.3	56.3	Antemortem	19	294	Tiger shark	2.8
(10) *Lk1*	2011	Adult/female	Stranded	60.7	59.7	Postmortem	15	317	White shark	1.8–1.9
									Bull shark	2.3–2.5
(11) *Lk2*	2015	Adult/unknown	Stranded	63.2	62.8	Postmortem	11	212	Bull shark	1.4–1.7
									Sandbar shark	1.6–2.0
(12) *Dc1*	2019	Nesting/female	Nesting	155.6[a]	114.0[a]	Antemortem	29.2	250–280	Tiger shark	4.2
(13) *Dc2*	2020	Nesting/female	Nesting	154.6[a]	111.4[a]	Antemortem	Head: 31	Head: CND	Head injury:	
									Longfin mako shark	3.3
									White shark	3.8
							Carapace: 28	Carapace: CND	Carapace injury:	
									White shark	3.4
									Longfin mako shark	3.0
									Shortfin mako shark	3.0

[a]Measurements are standard (*Cm5*) and minimum (*Dc1–2*) curved carapace length and curved carapace width

plastron (Fig. 2A, white arrowhead), partial amputation (~10%) of the trailing edge of the right hind limb, and 3 healing notches on the left hind limb (Fig. 2A, yellow arrowhead). A mean IDD of 12 mm and BC of 310 mm suggest that the predator was a 1.9 m bull shark. Other potential predators include a 1.9 m tiger shark or a 1.4 m white shark. Tiger sharks typically grab the carapace and attempt to consume the entire turtle (of which there was no evidence, as only the extremities were targeted); therefore, we suggest a bull shark as the most likely predator.

Case *Cm2* was a moderately decomposed turtle found in Bay County. The turtle had been decapitated and its left front flipper was partially amputated (Fig. 2B, yellow arrowhead). BC measurements could not be determined due to wound severity, but a mean IDD of 12 mm suggests a tiger or bull shark, and the lack of evidence of tiger shark feeding behavior (e.g. sawing, twisting) points to a 1.9–2.2 m bull shark as the most likely predator. Other possible predators included a 1.9–2.2 m tiger shark or a 1.4–1.8 m white shark; however, these juvenile

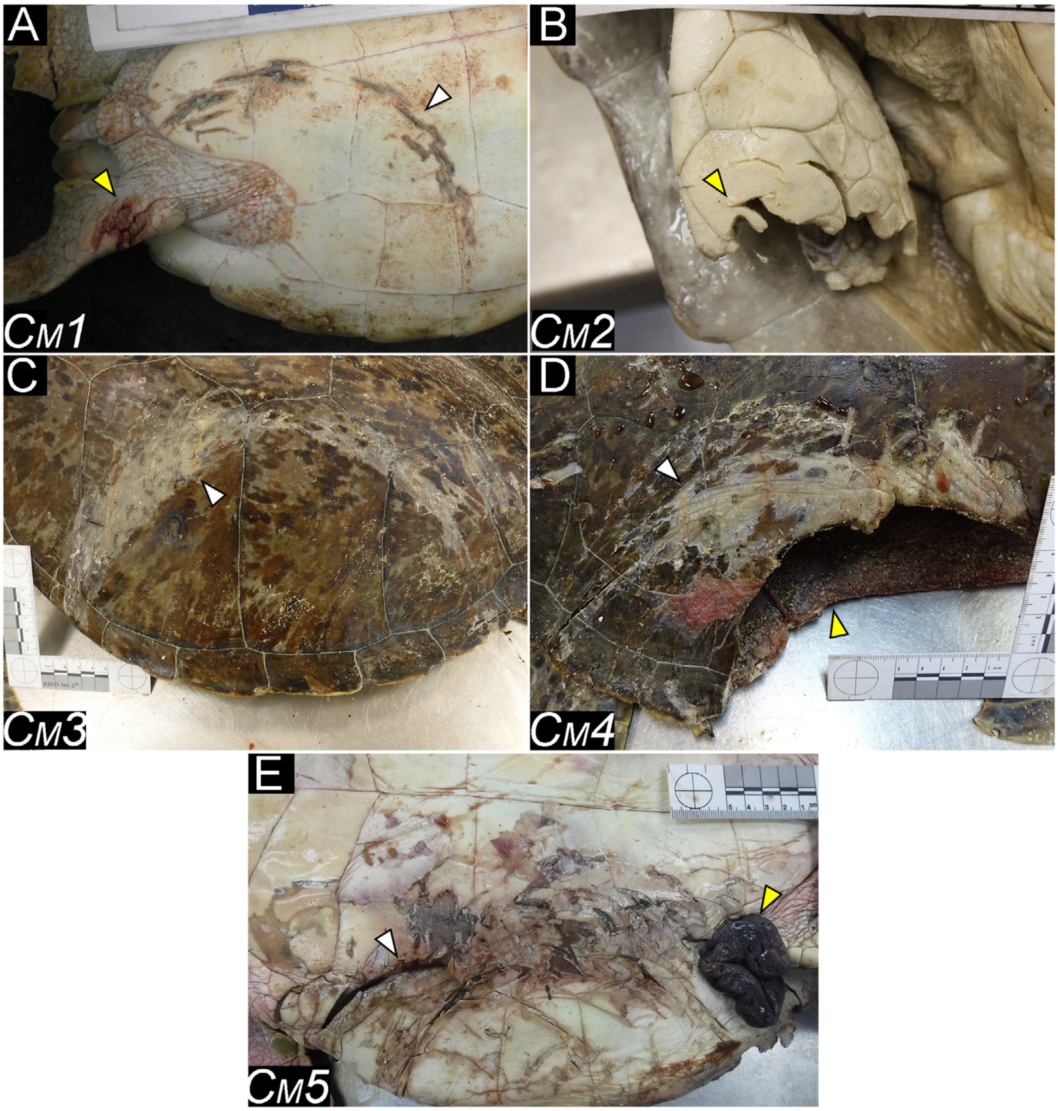

Fig. 2. Shark bite wounds on 5 green sea turtles *Chelonia mydas* used in the forensic analysis. Common bite wound patterns were (A) crescent-shaped bite wound on the plastron (white arrowhead), partial amputation (~10%) of the trailing edge of the right hind limb, and 3 healing notches on the left hind limb (yellow arrowhead); (B) a partially amputated right front flipper (yellow arrowhead); (C) typical semi-circular bite pattern (white arrowhead); (D) evidence of sawing (white arrowhead) along a semi-circular bite (yellow arrowhead); and (E) a crescent-shaped bite wound that penetrated the plastron (white arrowhead) and a related bite with perforation and disembowelment into the coelom (yellow arrowhead). Photos from Inwater Research Group (*Cm1*) and National Oceanic Atmospheric Administration (*Cm2–5*)

sharks would most likely target fish rather than large prey due to their small size. Additionally, the wound had a broad arc and marks suggesting that the teeth were serrated, further indicating a bull shark as the predator.

Case *Cm3* was found stranded in Vero Beach. The turtle had a typical semi-circular bite pattern made by serrated teeth (Fig. 2C, white arrowhead) on its carapace. A mean IDD of 19 mm and BC of 467 mm is consistent with a 2.3–2.4 m tiger shark. Mako *Isurus* spp. and white sharks were possible candidates because both can excise tissues from the turtle; however, the small size estimate makes these 2 candidates unlikely.

Case *Cm4* was found stranded on Hutchinson Island and had evidence of sawing (Fig. 2D, white arrowhead) along the 230 mm bite (Fig. 2D, yellow arrowhead) that removed a portion of the carapace. A 16 mm mean IDD and 316 mm BC suggest predation by a 2.3–2.7 m white shark. A tiger shark is another possible predator; however, one this large would have cut through the carapace rather than sawed it.

Case *Cm5* was found stranded in Melbourne Beach and presented with a crescent-shaped bite wound that penetrated the plastron (Fig. 2E, white arrowhead) and a related bite with perforation and disembowelment into the coelom (Fig. 2E, yellow arrowhead). The high degree of cutting and penetration into the plastron, combined with a mean IDD of 8 mm and a BC of 238 mm, indicate a 1.6–1.7 m dusky shark *Carcharhinus obscurus* as the most likely predator.

3.2. Loggerhead sea turtles *Caretta caretta*

Four adult loggerhead turtle cases were recorded in the intake canal of the St. Lucie Nuclear Power Plant on Hutchinson Island, Florida (Fig. 1), during 2014–2019. Case *Cc1* had a 60 × 140 mm shark bite wound (Fig. 3A, white arrowhead) and a 280 mm,

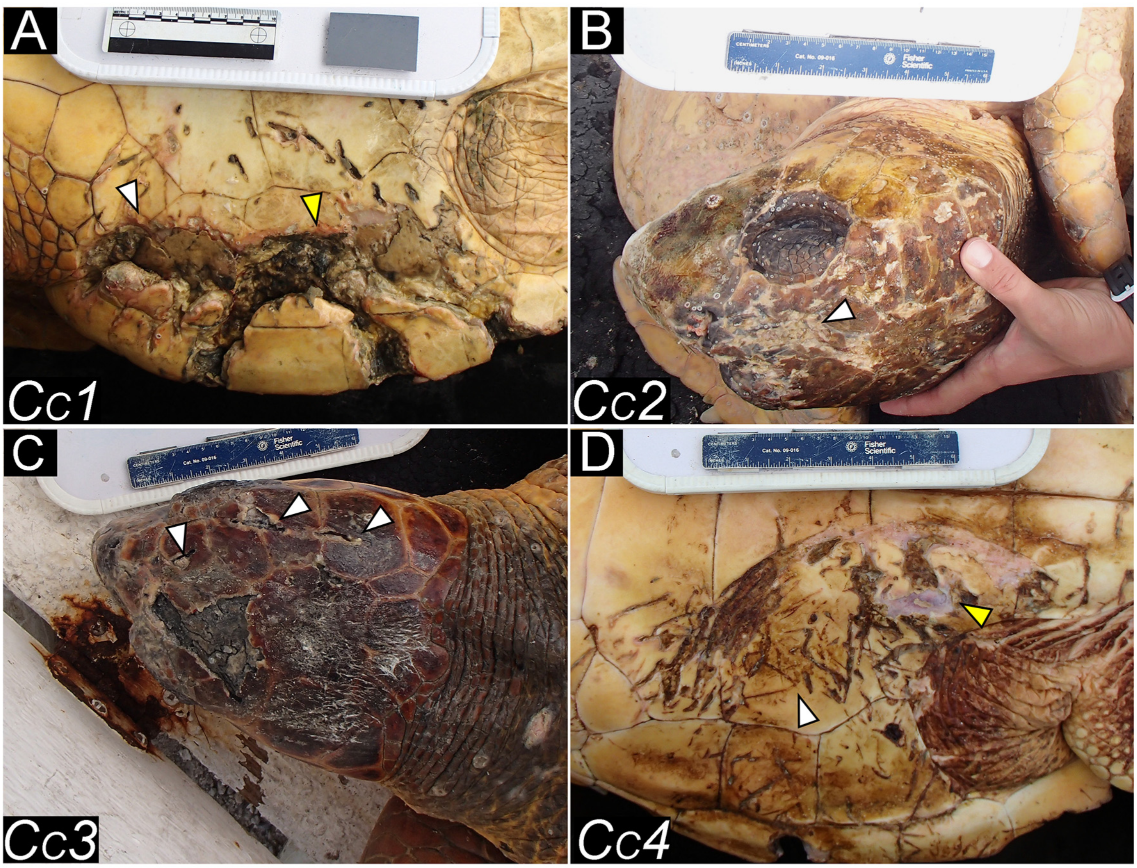

Fig. 3. Loggerhead sea turtles *Caretta caretta* used in the forensic analysis. Bite wound patterns displayed in each case were (A) overlapping semi-circular shark bites (white and yellow arrowheads); (B) rake marks on the turtle's head (white arrowheads); (C) healing puncture wounds (white arrowheads); and (D) numerous rake marks (white arrowhead) and a healing bite wound (yellow arrowhead). Photos from Inwater Research Group

semi-circular shark bite wound (Fig. 3A, yellow arrowhead) on the right lateral plastron. The narrow semi-circular arc suggests several overlapping bites in the same area. This turtle also had a partially amputated (~20 %) right hind limb (not pictured), a large periarticular protrusion from a dislocated or broken bone on the right front flipper (not pictured), and healing bite wounds around the tail (not pictured). A mean IDD of 20 mm and a BC of 412 mm suggest a 2.3–2.4 m white shark inflicted these wounds, while a 2.3–2.4 m tiger shark was also considered.

Case *Cc2* was a female turtle with extensive rake marks over a 30 × 70 mm area of her head (Fig. 3B, white arrowhead). A mean IDD of 25 mm and lack of evidence of sawing or cutting was consistent with a 2.6 m mako shark. Other possible predators include 3.6 m tiger shark or a 3.0 m white shark. The head wounds likely came from a 'hit and run' attempt by the shark and were made with minimal sawing or cutting. This behavior is more consistent with mako sharks than tiger or white sharks.

Case *Cc3* showed healing puncture wounds (Fig. 3C, white arrowheads) on the turtle's head. Bite marks had a mean IDD of 52 mm and a BC estimate could not be determined. A lack of cutting and tearing indicate a 6.3–6.4 m white shark as the most probable predator. A 7.0 m tiger shark was also considered, but due to the lack of cutting and tearing evidence on the head, a white shark is more likely.

Case *Cc4* exhibited numerous rake marks (Fig. 3D, white arrowhead) and a 170 mm healing bite wound (Fig. 3D, yellow arrowhead) on the right lateral portion of its plastron. These wounds had a mean IDD of 19 mm and BC of 294 mm, suggesting predation by a 2.8 m tiger shark.

3.3. Kemp's ridley sea turtles *Lepidochelys kempii*

Two adult Kemp's ridley turtles were found deceased in the Gulf of Mexico (Fig. 1) in 2011 and 2015. Case *Lk1* was found stranded on Dauphin Island, Alabama, and was moderately decomposed with semi-circular bite wound patterns on the carapace (Fig. 4A, yellow arrowheads). A mean IDD of 15 mm, BC of 317 mm, and evidence of sawing suggest scavenging by either a 2.3–2.5 m bull shark or a 1.8–1.9 m white shark. The shark made clear attempts to saw at the turtle, which is consistent with bull, tiger, and white shark feeding tendencies; however, the scrapes on the right lateral carapace were more consistent with a bull or white shark, since tiger shark teeth tend to penetrate and then tear at the carapace.

Case *Lk2* was found stranded in Panama City, Florida, with arced bite marks on its plastron, a 125 × 50 mm notch missing from the left lateral carapace, a portion of the marginal scutes missing (not pictured), visible teeth marks on the posterior plastron, and amputation of the left and right front flippers and neck (not pictured) (Fig. 4B, yellow arrowheads). A mean IDD of 11 mm and BC of 212 mm suggest a smaller scavenger, likely a 1.4–1.7 m bull shark or a 1.6–2.0 m sandbar shark *Carcharhinus plumbeus*. This was an unusual bite to analyze, as the image suggests that the turtle's entire head was in the shark's mouth and only the anterior edge of the shark's jaws contacted the turtle. Because of the narrow arc of the bite, we suggest a bull shark or a sandbar shark as possible scavengers.

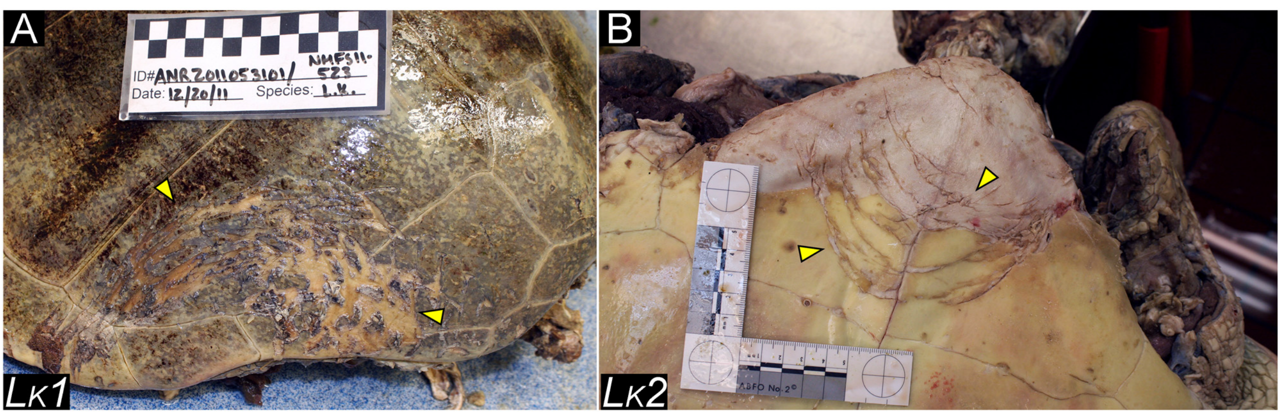

Fig. 4. Shark bite wounds on Kemp's ridley sea turtles *Lepidochelys kempii* including (A) semi-circular bite wounds (yellow arrowheads) and (B) bite marks on the turtle's plastron (yellow arrowheads). Photos from National Oceanic and Atmospheric Administration

3.4. Leatherback sea turtles *Dermochelys coriacea*

Two cases were adult leatherbacks encountered nesting on Juno Beach, Florida, in 2019 and 2020 whose bite wounds did not prevent them from crawling up the beach or completing their nesting fixed action pattern (Bacon 1970, Keinath & Musick 1993, Dutton & McDonald 1994, Dutton 1996, Perrault et al. 2012). Head wounds for case *Dc1* showed visible healing rake marks (Fig. 5A, yellow arrowheads), consistent with a shark's upper jaw. A mean IDD of 29 mm and BC of 250–280 mm indicate that the wounds were inflicted by a 4.2 m tiger shark, which also likely caused the puncture wounds on the turtle's left front flipper (Fig. 5B, yellow arrowheads) based on similar IDD and BC estimates. Other candidates include a 3.1 m mako shark (longfin: *I. paucus* or shortfin: *I. oxyrinchus*) or 3.5 m white shark. The tooth spacing indicates a mako shark; however, this size is not large enough to prey on an adult leatherback turtle. Therefore, a nearshore bite from a tiger shark was deemed most likely.

Case *Dc2* showed healing rake marks with 29–33 mm IDD on the right side of the turtle's head, presumably created by the upper jaw of either a 3.3 m longfin mako shark or a 3.8 m white shark (Fig. 5C, yellow arrowheads). The large gap size of the teeth makes longfin mako or white shark the most likely predators; a 4.4 m tiger shark was also considered, but that size shark is beyond the bounds of the regression generated in Lowry et al. (2009) (i.e. a specimen that large could not be obtained for use in generating the regression). The turtle also had multiple sets of bite scars (Fig. 5D, yellow arrowheads) on its carapace with a mean 28 mm IDD that were likely caused by either a 3.0 m longfin mako, a 3.0 m shortfin mako, or a 3.4 m white shark, assuming that the shark's upper jaw contacted the turtle. A 4.1 m tiger

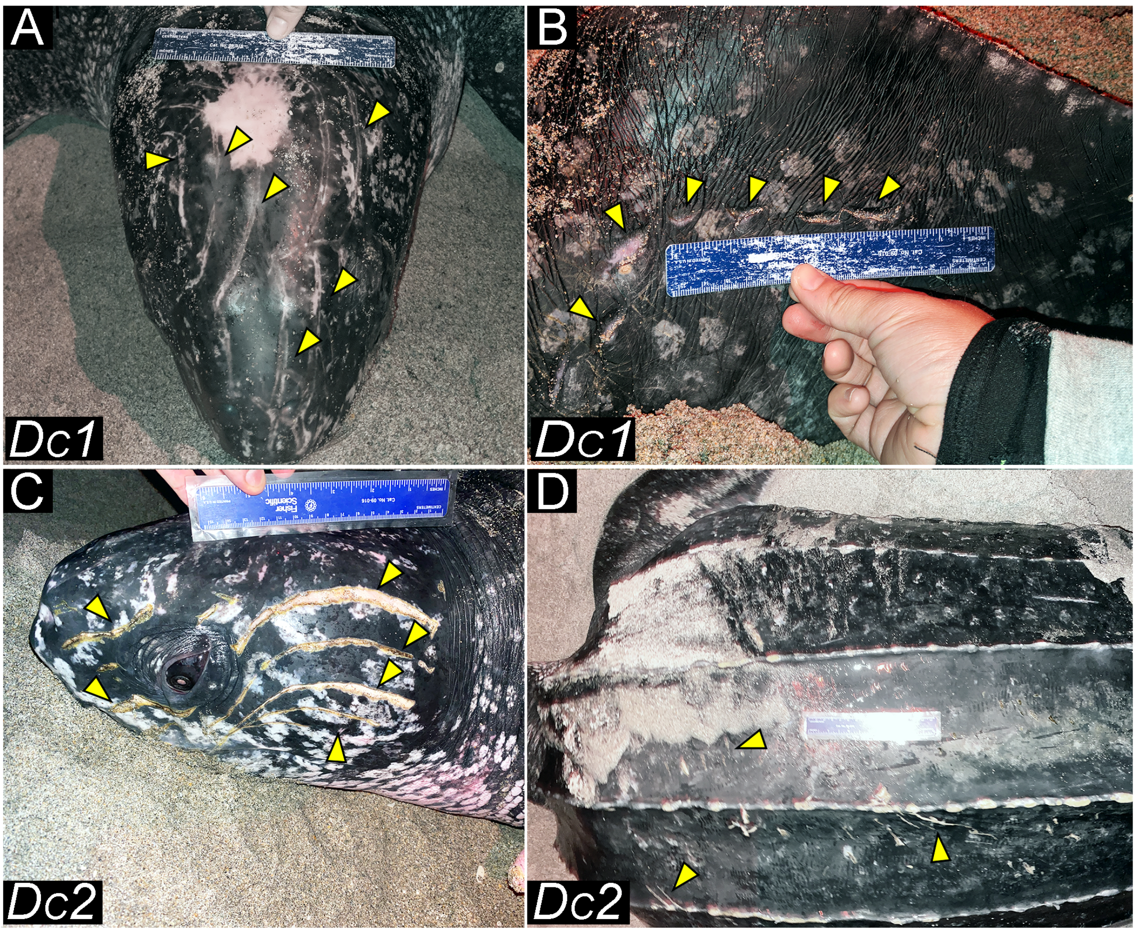

Fig. 5. Shark bite wounds on nesting leatherback sea turtles *Dermochelys coriacea* including (A,C) healing rake marks (yellow arrowheads), (B) puncture wounds (yellow arrowheads), and (D) multiple sets of bite scars (yellow arrowheads). Photos from Loggerhead Marinelife Center

shark was also considered, but was beyond the bounds of the regression generated in Lowry et al. (2009). While the teeth of mako sharks and white sharks differ markedly regarding width, curvature, and presence/absence of serrations, the hallmarks of these differences are not apparent from gross photographic examination, and ranges of IDD overlap substantially among species. Presence/absence of microstriations left by serrations on the teeth of white sharks, but not makos, are often only distinguishable from photographs that show a cross-section of wounded flesh. Measurement of bite wound metrics and assignment to likely shark species was further complicated by partial healing in this latter case and by the fact that all 3 species capable of generating the observed damage patterns share similar pelagic habitat distributions.

4. DISCUSSION

4.1. Forensic analysis

Forensic analysis of bite wounds on sea turtles improves our understanding of predator–prey interactions that are often difficult to observe in the wild (Heithaus et al. 2002). The methods applied here have been used previously to better understand shark bites on humans (Ritter & Levine 2004, 2005, Lowry et al. 2009, Clua & Séret 2010, Clua & Reid 2017), and are increasingly being applied to address questions on the ecology of predator–prey dynamics (van den Hoff & Morrice 2008, Bornatowski et al. 2012, Serres et al. 2022). Combining forensic analysis with knowledge of shark anatomy and behavior allowed us to suggest 1 or 2 predators for 10 of the 13 cases (77%) examined here. This demonstrates the utility of forensic analysis in determining a specific predator that can be applied to other prey species (e.g. marine mammals, elasmobranchs) to further analyze bite wound patterns.

The dual role played by sharks as both predators (i.e. antemortem tissue consumption) and scavengers (i.e. postmortem tissue consumption) of sea turtles has previously complicated accurate determination of the timing of shark-inflicted wounds (Bornatowski et al. 2012). Scavenging interactions can have strong impacts on food webs, and in marine systems, little is known about the role of facultative scavenging in the behavioral ecology of predators (McShea 2000, DeVault et al. 2003, Hammerschlag et al. 2016). Gross necropsy and histopathological examination of wound margins can reveal whether bite wounds result from predation or scavenging. This is an important distinction when estimating the relative severity of threats to sea turtle populations because postmortem bite wounds indicate that sharks are likely not the primary cause of death and can mask other direct causes of sea turtle mortality (Stacy et al. 2021). In a recent study on stranded Kemp's ridley (n = 46), loggerhead (n = 8), and green (n = 16) sea turtles in the southeastern USA, 80% of shark bite wounds were determined to have occurred postmortem, while only 10% occurred antemortem and 10% occurred peri-mortem (i.e. wounds inflicted at or near the time of death) (Stacy et al. 2021). Most shark bite wounds that resulted in amputation, decapitation, or major tissue loss on turtles without evident intravital responses were determined to be the result of scavenging; thus, the deaths of most turtles in that study were attributed to other factors, such as interactions with fishing gear or vessel strikes, not shark predation (Stacy et al. 2021).

Sources of uncertainty exist with forensic methods, as injury size varies with body sizes of predator and prey (Heithaus 2001a,b). Additionally, the origin and timing of the initial injury and behavioral pattern causing the injury can be difficult to determine (Witzell 2007). The presence or absence of a reference scale adjacent to the wound in gross photos can affect the accuracy of measurements made using computer software, and IDD and BC values can only be calculated if the wounds exhibit clearly distinguishable bite mark; however, in turtles that survive a shark attack, bite wounds become less distinct over time as wounds heal due to individual healing patterns (i.e. age and location of wound) and environmental factors that accelerate or delay decomposition (Mutsaers et al. 1997, Lowry et al. 2009, Stacy et al. 2021), limiting the accuracy and confidence of forensic analysis. Furthermore, knowledge of regional shark biology and feeding behavior is necessary to accurately conduct this analysis, since there can be significant overlap between IDD and BC among different shark species. For prey species that migrate long distances, non-lethal bite wounds may also be acquired in a variety of habitats and locations, making fresh wounds on live animals of greatest utility for correlation with local predatory fauna. In this study, there were 3 cases in which distinguishing a single shark species was not possible because the IDD and/or BC were similar among more than one species; however, we were able to infer 1 or 2 likely candidates using their individual tooth structure and general predicted behavioral patterns. For instance, forensic evaluation suggested that the predator in case *Dc1* could be a mako, tiger, or white shark. The IDD and BC suggested a 3.1 m mako shark; however, large turtles such as leatherbacks are not known to be included in the diet of sharks this size, and mako sharks do not typically inhabit the nearshore waters in south Florida (Heithaus 2013, Vaudo et al. 2016, 2017). Thus, we posit a tiger shark was the most likely predator because adult tiger sharks are strong enough to prey on a large turtle and tend to inhabit shallow coastal waters that overlap with turtle habitats during leatherback nesting season in Florida. Because the wound was healed and the timing of infliction not known, however, we were unable to fully ascertain if this predatory event occurred near nesting grounds or elsewhere (Eckert et al. 2006, Bornatowski et al. 2012, Aines et al. 2018). We also discerned that during the attack, both the shark and the leatherback were orientated in a natural swimming position (dorsal side up) and the shark's upper jaw contacted the leatherback's skin, lending insight into the in-water positioning and movement of both species during a predation event (Ritter & Levine 2005). The rake marks evident on the turtle's head (Fig. 5A) could also have resulted from mating behavior, as male leatherbacks have been seen biting females during mating interactions; however, mating wounds are often irregular and found on the dorsal side of the turtle's head, and marks in our study were found on the lateral side of the turtle's head and neck in a defined parallel pattern, leading us to posit the wounds were inflicted by a shark (Reina et al. 2005, Archibald & James 2018). Had high-resolution, close-up images of wound tracts been available, it may have been possible to distinguish microstriations left by serrations on the teeth of the shark, further limiting the list of candidate species. To facilitate robust examinations of bite wounds on animals and bite damage in the future, it is recommended that researchers photograph both gross and fine-scale aspects of the damage (i.e. close-up photographs depicting the entire bite wound, excised tissue, and photos of individual tooth marks).

4.2. Predator–prey dynamics of sharks and sea turtles

The most frequently identified probable predator in this study is the white shark, with 3 definitive cases and 2 possible cases ascribed to this species. White sharks are known to opportunistically target sea turtles while seeking more desirable prey, such as other elasmobranchs and teleosts, but more in-depth information on these interactions is limited because turtles typically constitute only a small portion of white sharks' diet (Fergusson et al. 2000). Both white sharks and sea turtles, particularly loggerheads, greens, and Kemp's ridleys, inhabit coastal habitats in Florida year-round (Curtis et al. 2014, Bovery & Wyneken 2015), which could lead to a higher probability that a white shark would attack a sea turtle. In northern California in the 1990s, 2 stranded leatherback turtles had wounds attributed to predation by white sharks, with both turtles missing large portions of their carapace and hind limbs, but it was unclear whether the sharks were directly responsible for the turtles' deaths or if the wounds occurred postmortem (Long 1996). Our results show a higher attack rate from white sharks than previous studies (Bornatowski et al. 2012); however, this could be attributed to the fact that white sharks may be attacking and wounding sea turtles, but not severely enough to result in death (i.e. investigating potential prey). Two of the 3 definitive cases attributed to white sharks (*Cc1* and *Cc3*) were of live, healthy loggerheads. Since most information on sea turtle predators comes from stomach content analyses (Heithaus et al. 2008b), it is likely that attacks from white sharks are underreported, especially if the sea turtle survives the attack.

Tiger sharks were identified as the primary predator in 3 cases. Tiger sharks are opportunistic foragers and exhibit ontogenetic shifts in their diets as they age (Motta & Wilga 2001). In a comprehensive dietary analysis of tiger sharks in the northwest Atlantic Ocean and Gulf of Mexico, when juvenile and adult tiger sharks preyed on sea turtles, they predominantly attacked green turtles, followed by Kemp's ridley and loggerhead turtles (Aines et al. 2018). Tiger sharks >3 m TL are most likely to target larger prey such as other elasmobranchs, seabirds, and marine mammals (Estupiñán-Montaño et al. 2017), which may explain why smaller adult tiger sharks (~2.3–2.4 m TL) were found to have targeted juvenile turtles in this study. Forensic analysis of shark predation and scavenging in Brazil showed that the estimated size of tiger sharks that attacked sea turtles ranged from 2.2–3.3 m TL (Bornatowski et al. 2012), similar to the estimated tiger shark size ranges presented here. One case in our study was a nesting leatherback with bite wounds ascribed to a large (4.2 m TL) tiger shark. This is not uncommon for larger tiger sharks, since leatherbacks nesting on St. Croix, US Virgin Islands are often seen with partial flipper/limb amputations and fresh and healed bite scars, including at least one case that was attributed to a tiger shark of unknown size (Eckert et al. 1986, Keinath & Musick 1993, Asada et al. 2021).

In Florida, bull sharks are common and typically inhabit shallow, inshore waters (Snelson et al. 1984). Both juvenile bull sharks and juvenile green turtles use the Indian River Lagoon in eastern coastal Florida as a developmental and foraging habitat (Zug & Glor 1998, Simpfendorfer et al. 2005, Curtis et al. 2013). Smaller bull sharks (≤1.4 m TL) prey mainly on teleosts, while bull sharks ≥1.8 m typically prey on larger animals including marine mammals, birds, and sea turtles (Cliff & Dudley 1991). Combining forensic analysis with our knowledge of bull shark habitat, distribution, and behavior in this region allows us to confidently identify large (1.9–2.2 m TL) bull sharks as the primary predator of 2 juvenile green turtles that stranded along the Indian River Lagoon and probable scavengers for both Kemp's ridley turtles that stranded in the Gulf of Mexico.

In at least one case each, we attributed wounds to attacks by mako and dusky sharks. Mako sharks are a surprising inclusion in this study, as they are infrequent predators of sea turtles, and only a few instances of predations have been reported on hard-shelled sea turtles through stomach content analysis and pop-up satellite archival transmitter tags (Carranza et al. 2006, Biton Porsmoguer et al. 2015, Hall & James 2021). Similarly, dusky sharks are not common predators of sea turtles, but remains have been found in stomach content studies (Gelsleichter et al. 1999). Our finding of a sandbar shark as the likely scavenger of case *Lk2* was also surprising since this species is not reported to prey on large sea turtles (Ellis 2003, McElroy et al. 2006). Thus, more research is needed to determine whether sandbar sharks are more common predators of sea turtles in the waters of the southeastern USA than previously thought, or whether they are largely opportunistic scavengers of diverse marine organisms.

In the last decade, various studies have addressed the predator–prey relationships between sharks and sea turtles in the Atlantic Ocean, but information gaps remain (Foley et al. 2015). In Juno Beach, Florida, an important nesting beach for sea turtles (Stewart et al. 2011, Ceriani et al. 2017), shark bite wounds were observed on 9 of 450 nesting loggerhead turtles during 2019–2020 (Ataman et al. 2021) and 4 of 142 nesting leatherback turtles during 2019–2021 (Klingshirn 2021). In temperate waters off Nova Scotia, Canada, and on Matura Beach, Trinidad, West Indies, during 2012–2015, 36 of 228 leatherbacks had predation injuries; however, probable predators for each injury were not determined (Archibald & James 2018). Previous studies point out that shark predation on adult sea turtles is likely underreported because shark stomach content analysis would likely miss these rare events, and sharks are less likely to consume a whole adult turtle. Thus, we can deduce that sub-adult and adult sea turtles (particularly leatherbacks) are susceptible to non-lethal predatory shark interactions in the northwestern Atlantic Ocean (Heithaus et al. 2008b, Bornatowski et al. 2012, Klingshirn 2021). Further studies, such as stable isotope analyses of shark species to identify the contributions of different sea turtle species in dietary compositions, could also be performed to report shark predation attempts on sea turtles. Observation of nesting sea turtles and physical examination of stranded turtles represent optimal opportunities to evaluate the frequency of shark-inflicted predation wounds for a given population since there is usually significant overlap between coastal sea turtle habitats and the habitats of various shark species. Understanding the predator–prey dynamics of these sharks and sea turtles at or near sea turtle nesting beaches is crucial to understand the frequency of shark–sea turtle interactions and how shark attacks influence sea turtle behavior.

This study demonstrates that forensic analysis is a useful approach for analyzing shark–sea turtle interactions. Successful determination of the timing of an attack and assignment of a shark species based on bite wound characteristics depends on numerous factors, including the quality and freshness of the wound(s), image detail and sharpness, and the observers' knowledge of shark behavior and ecology. When these factors are accounted for, an estimated TL and shark species can be derived from 2 measurements that are easily obtainable through direct measurements and photographs. While this method does not always provide definitive documentation regarding the species and size of a potential predator, it introduces a reproducible scientific method that can support other forms of injury assessments. Application of these methods in future studies will continue to enhance our understanding of rarely witnessed sea turtle–shark interactions and improve the accuracy of the forensic analysis.

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