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RESEARCH COMMUNICATION

Observations of fin injury closure in Great Hammerheads and implications for the use of fin-mounted geolocators

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Abstract

Objective: Sharks face a high risk of injuries throughout all life stages and are therefore expected to show a good wound closure capacity.

Methods: Here, the wound closure of one major injury and one minor injury to the first dorsal fins of two free-ranging, mature female Great Hammerheads *Sphyrna mokarran* is described macroscopically.

Result: The sharks showed complete wound closure of single, clean-cut lacerations measuring 24.2 and 11.6 cm in length after an estimated 323 and 138 days. These estimates were based on the observed closure rate and visual confirmation of a complete wound closure upon multiple resightings of the same individuals. Additionally, the posterior lateral displacement of fin-mounted geolocators within the fin and outside of the fin without causing external damage was documented in three additional Great Hammerheads.

Conclusion: These observations supplement findings about wound closure capabilities in elasmobranchs. The documented geolocator displacement furthers the discussion about the safe use of these geolocators to track shark movements but also has implications for future tagging studies.

KEYWORDS

ecology, Great Hammerhead, *Sphyrna mokarran*, tags and tagging, threatened and endangered species

INTRODUCTION

Healing from external trauma is a crucial ability for vertebrate survival (Belacortu and Paricio 2011). The risk of attaining an injury due to predation (e.g., van den Hoff and Morrice 2008), mating (e.g., Schulte et al. 2021), or human actions (e.g., Jakes et al. 2018) is prevalent throughout all life stages. In marine habitats, members of Chondrichthyes in the subclass Elasmobranchii (i.e., sharks and rays) seem to withstand trauma (e.g., Borucinska et al. 2020; Gardiner and Wiley 2020) and recover from severe, life-threatening injuries (Towner et al. 2012; Womersley et al. 2021). Bird (1978) documented extensive tissue healing of three carcharhinid sharks that suffered from deep wounds caused by plastic straps. Blacktip Reef Sharks *Carcharhinus melanopterus* showed complete recovery after being bitten by conspecifics, having a transmitter implanted into the body cavity through a ventral incision, or suffering from wounds that were likely caused by a boat propeller (Chin et al. 2015). In addition to the recovery from external trauma, sharks have also been shown to recover from grave internal damage. Kessel et al. (2017) documented a 435-day “transcoelomic expulsion” of a sharp object through the body wall of a Lemon Shark *Negaprion brevirostris* at a dive site in Florida. Further, it was demonstrated that shark genomes encode for a large number of genes suggested to provide a high tolerance of injuries: a study of the White Shark *Carcharodon carcharias* genome found that loci associated with wound healing were under positive selection, indicating that under natural conditions the function of polymorphisms at these loci are relevant for the fitness of the sharks (Marra et al. 2019).

Injuries can be detrimental at the individual level as well as at the population level and can have a negative impact on the recovery potential of threatened populations (Bansemer and Bennett 2010). Many shark species are threatened with extinction and have experienced substantial population declines (Dulvy et al. 2021); therefore, understanding how individuals recover from or withstand severe injuries becomes imperative. However, overall there are limited macroscopic and microscopic observations of wound healing and closure processes in elasmobranchs. The number of reports suggesting a high capacity for wound closure is still small and patchy, and only a few species are represented in the literature.

Great Hammerheads *Sphyrna mokarran* are listed as critically endangered by the International Union for Conservation of Nature's Red List (Rigby et al. 2019), and long-term data about their movements can help to define efficient conservation strategies. Shark tagging and movement studies are numerous in the published literature (Hussey et al. 2015). However, the use of new technologies (heavier, potentially less hydrodynamic multi-sensor tags; Andrzejaczek et al. 2019) or new attachment methods (e.g., clamps; Chapple et al. 2015) warrants more observations on the fate of such tags and geolocators after long periods. Little is known about how the constant forward motion of some shark species might alter potential attachments on the fin, and the highly migratory behavior of some shark species that are the focus of tracking studies makes it challenging to document how different tags and geolocators behave on the fins after long time periods. However, satellite-linked geolocators offer an opportunity to remotely collect shark movement data (Hammerschlag et al. 2011), which can help to design efficient conservation measures (e.g., White et al. 2017). A thorough understanding of the movement behavior of Great Hammerheads is needed for efficient conservation of this species (Gallagher and Klimley 2018).

Here, wound closure was opportunistically documented for dorsal fin injuries incurred by two mature female Great Hammerheads (hereafter, sharks 1 and 2) in Bimini, The Bahamas. In-water images and videos obtained during recreational or commercial free-diving and scuba diving activities between November 2019 and 2020 were assessed. To our knowledge, this is the first time that macroscopic wound closure processes have been documented for a species of the family Sphyrnidae other than the closure of the umbilical wound (Duncan and Holland 2006). We also present observations of the posterior lateral displacement of fin-mounted satellite-linked geolocators within and outside of the dorsal fin in three Great Hammerheads over time periods of 335 days (shark 3), 432 days (shark 4), and 671 days (shark 5). We discuss potential implications for the safety of the sharks and some considerations regarding new geolocator designs and long-term tracking studies.

Impact statement

Given their risk of injuries, understanding wound closure capabilities in sharks is important and is directly relevant to research methods such as the deployment of fin-mounted transmitters in movement studies. Here, we document the complete closure of first dorsal fin injuries in Great Hammerheads. The recorded shedding pattern of fin-mounted transmitters without causing external damage furthers the discussion about their safe use and yields implications for future tagging studies.

METHODS

The Great Hammerhead is a large-bodied shark with a circumtropical distribution occurring in coastal waters and over continental shelves (Compagno 1984). All individuals included in this study were observed in the western North Atlantic region. To assess the wound closure process and the potential displacement of fin-mounted geolocators, we reviewed 28 images (shark 1: $n = 14$; shark 2: $n = 9$; shark 3: $n = 2$; shark 4: $n = 1$; shark 5: $n = 2$) in which sharks 1, 2, and 3 were identified based on external body characteristics (such as the occurrence of notches in the trailing edge of fins or ventral pigmentation patterns; Guttridge et al. 2017) and sharks 4 and 5 were identified based on the external National Marine Fisheries Service dart tag number. Sharks 1 and 2 were observed in Bimini, where Great Hammerheads are frequently fed as part of dive tourism activities (Heim et al. 2021) during their seasonal residency that occurs in the winter months (Guttridge et al. 2017). Length measurements for shark 1 (female; total length [TL] = 333 cm) and shark 2 (female;

TL = 305 cm) were available from unrelated captures of the animals during tagging efforts of the Bimini Biological Field Station Foundation. Shark 3 (female; precaudal length = 225 cm) was measured and tagged on February 2, 2019, in Bimini, receiving a fin-mounted satellite-linked geolocator similar to shark 4 (female; stretched TL = 220 cm), which was measured and tagged on January 19, 2020, in the Florida Keys. Shark 4 was later caught and landed by a commercial fishing vessel in the Florida Keys on March 25, 2021 (432 days posttagging), and the landing was reported through the National Oceanic and Atmospheric Administration's observer program. Shark 5 (female; precaudal length = 210 cm) was initially caught on January 21, 2021, in Andros, The Bahamas, and was tagged with the same geolocator type used for sharks 3 and 4. Shark 5 was resighted on November 22, 2022, within 1 km of its original capture location.

For an image to be included in the analysis, it needed to show the lateral side of the dorsal fin of an individual as close as possible to a 90° angle relative to the observer. Slight differences in the angle of the images existed. As a result, measurements of wound closure should be considered estimations to be interpreted with caution. For each suitable image, measurements were made using the segmented line tool in ImageJ version 1.53e (Schneider et al. 2012) and were standardized to centimeters based on scaling to the known length of each individual shark. Measurements of the total length of the wound and the closed section were rounded to one digit after the decimal point. The total length of the wound was measured as the distance between the origin (at the edge of the fin) and the end (within the fin) of the wound, irrespective of whether parts of the wound were closed or not. The closed part of the wound was measured as the distance between the end of the wound (within the fin) and the start of the still-open portion toward the origin of the wound. The origin of the wound was always measured to the wound's lower edge to avoid inaccurate measurements, as in some cases the upper part of the dorsal fin above the wound showed folding or bending. To classify the wounds in sharks 1 and 2, we used criteria described by Womersley et al. (2021): wounds that were longer than 25% of the total height of the dorsal fin were classified as "major," whereas wounds that were shorter than 25% of the total height of the dorsal fin were classified as "minor." The total height of the dorsal fin for both sharks was measured in photos taken before the wound was observed for the first time; this was done to account for potential deformities after the closure of the wound. Photos and screenshots of videos of sharks 1 and 2 were categorized by individual shark and date (Figure 1). The closed portion of the wound was plotted over time using R version 4.1.2 (R Core Team 2021).

To calculate the closure rate and to model the wound closure process, we followed the steps outlined by McGregor et al. (2019) and Womersley et al. (2021). First, we used a linear regression (response variable: closed wound portion, cm; explanatory variable: number of days since the first observation of the wound) to calculate the closure rate per day. A linear regression was chosen because only a portion of the entire closure process could be visually observed, and it explained the variance of the obtained data well for observations of shark 1 ($R^2 = 0.853$) and shark 2 ($R^2 = 0.943$). In this analysis, observations of full wound closure after the sharks returned to Bimini from their summer migrations (Guttridge et al. 2017) were removed to account for their wounds being fully closed before their return. Using the closure rate (in days), we estimated the theoretical date when the wounds were attained (hereafter, "wounding date") as well as the theoretical date of full wound closure. However, wound closure rates in elasmobranchs have been shown to follow a pattern in which the closure rate is fast in the beginning and then slows toward the completion of the closure (McGregor et al. 2019; Womersley et al. 2021). We therefore used the coefficients obtained from the linear regression and the estimated dates of attaining the injury and full closure of the wound to fit a nonlinear least-squares (NLS) regression. We checked the goodness of fit by calculating pseudo-R^2 values using the R package aomisc (Onofri 2020). All calculations were performed for each shark separately using R version 4.1.2 (R Core Team 2021).

Observations of the fate of fin-mounted satellite-linked geolocators (Smart Position and Temperature [SPOT] tags; Wildlife Computers) within the fin tissue were recorded in three female Great Hammerheads that were tagged as part of a regional movement study (Heim et al. 2023) and were resighted (shark 3) or landed by a commercial fishing vessel (shark 4). Shark 5 was caught during local research efforts (Guttridge et al. 2023) in Andros and was resighted 671 days later. All three sharks were tagged with a geolocator of the type SPOT-380 (Wildlife Computers), which contains two urethane bolts that are used to attach the geolocator through the fin tissue by using two different washers and a stainless-steel screw on the opposite side of the first dorsal fin. The geolocators measured 87 × 37 × 23 mm (length × width × height; Wildlife Computers). Via an antenna at the top of the geolocator, the device sends a transmission to satellites every time it breaks the water surface, and this information can be used to estimate the geographical position. The wet–dry sensors on the front of the geolocator register whether the fin of the shark (i.e., the antenna of the geolocator) is out of the water and then initiate the transmissions. Therefore, the geolocator was mounted as high and as vertically as possible onto the shark's fin to increase transmission rates.

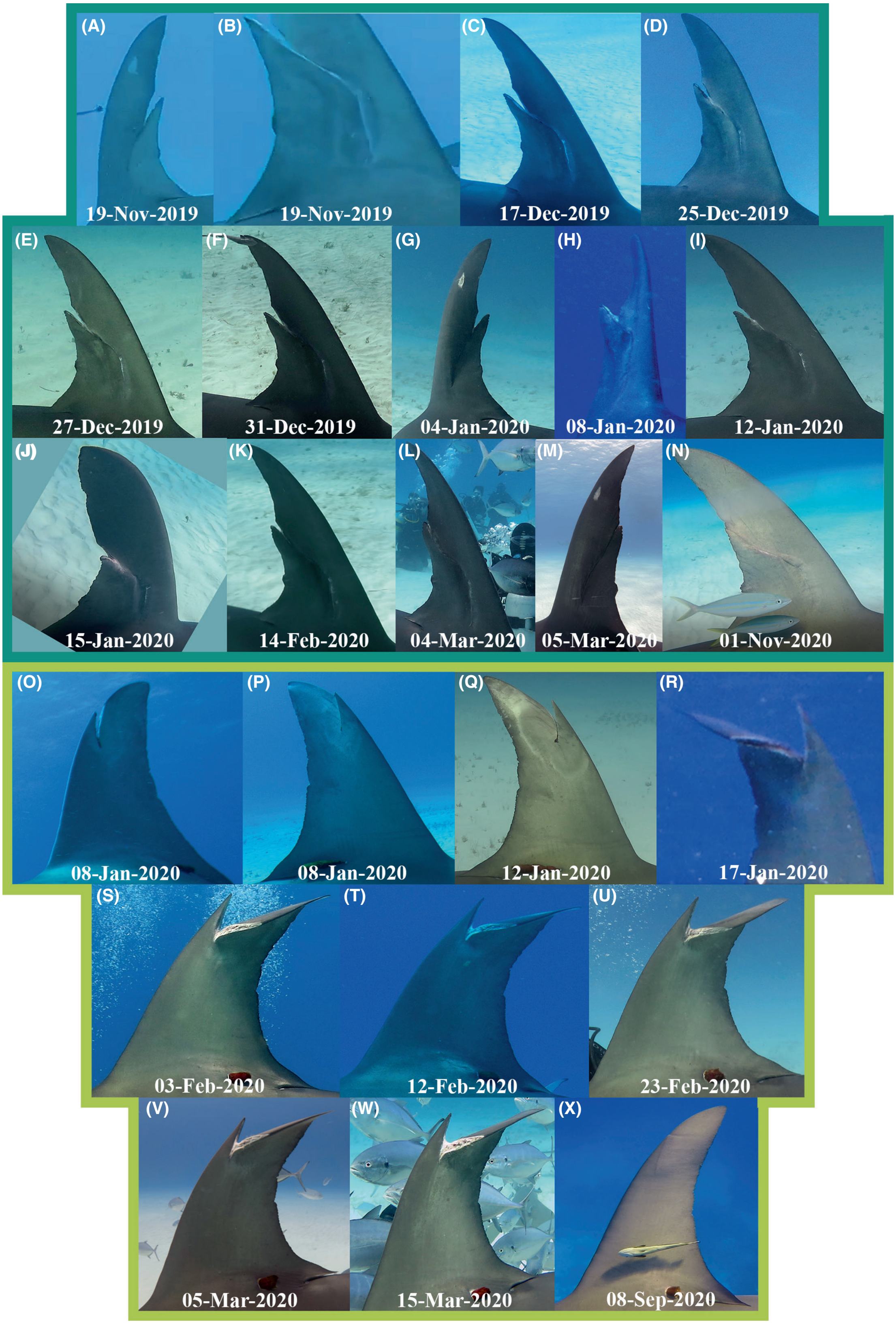

FIGURE 1 All documented stages of the wound closure process in the first dorsal fin of two female Great Hammerheads: (A–N) shark 1 and (O–X) shark 2. The date of the observation is shown at the base of each image. The first two images for each shark show the same day per individual but present a left and right lateral view of the wound. Due to the low quality of the image from shark 2 on January 17, 2020 (panel R), this image was not used for the calculations. Images A and B were provided by Sam Hawke; images H, M, O, S, and U were provided by Sean Williams; and image R was provided by Roberta Larosa and Alexandre de Sarazzin.

Changes in the geolocator's orientation and subsequent changes in the location of the wet–dry sensors and the antenna could impact the geolocator's transmission rates. The wet–dry sensors and the antenna are in line with the bolts; thus, a change in the angle of the bolts would also result in changes in the angle of the wet–dry sensors and the antenna. Available images upon resighting or recapture of the sharks were therefore used to document the orientation of the geolocator, including the angle of the bolts, wet–dry sensors, and antenna over time. The fins in the images were visually examined for macroscopic changes. For shark 3, images just after the release from the initial tagging were available (Figure 3A,B), allowing an assessment of the geolocator's orientation upon release. No release images were available for shark 4. Pictures of the initial capture and resighting of shark 5 were available, which allowed the state of the fin after geolocator deployment to be assessed.

RESULTS

The fin injuries differed in their magnitude and location but were similar in that they presented as single, clean-cut lacerations with smooth edges that partially severed the first dorsal fin. Shark 1 showed a diagonal wound of 24.2 cm between the trailing edge and the base of the first dorsal fin (Figure 1A,B). The first dorsal fin of shark 2 showed a vertical wound of 11.6 cm close to the top of the fin's leading edge (Figure 1O,P). The length of the wound in shark 1 was 49% of the total height of the first dorsal fin (49.2 cm) and was therefore classified as a major wound, whereas the length of the wound in shark 2 was 24% of the total height of the dorsal fin (49.2 cm) and was thus classified as minor (Womersley et al. 2021). Although the source of the wounds in both sharks was unknown and the discussion about their origin involves speculation, the clean-cut nature suggests that they may not have been natural injuries. A wide variety of scenarios could have led to the wounds, including but not limited to entanglement in fishing line, a cut by a foreign sharp object, or a previously embedded or attached item being ripped out of the fin. However, without witnessing the events that led to the injuries, these scenarios remain as hypotheses.

The first image of shark 1's wound was taken on November 19, 2019. Comparing the reddish-white, likely fibrotic tissue to the portion of the wound that was not yet healed (10.8 cm) showed that at this point in time, the wound was approximately 56% (i.e., measured closed length/total wound length) closed (13.4 cm; Figures 1A,B and 2). The wound was 96% closed (23.4 cm) on March 4, 2020 (107 days since first sighting), and complete closure (24.2 cm) was documented upon the shark's return to Bimini on November 1, 2020 (349 days since first sighting). The closure rate was estimated at 0.07 cm/day. This allowed for estimation of a wounding date of May 22, 2019 (i.e., 181 days prior to the wound being observed for the first time). Based on the estimated closure rate and the total wound length, the wound would have been fully closed

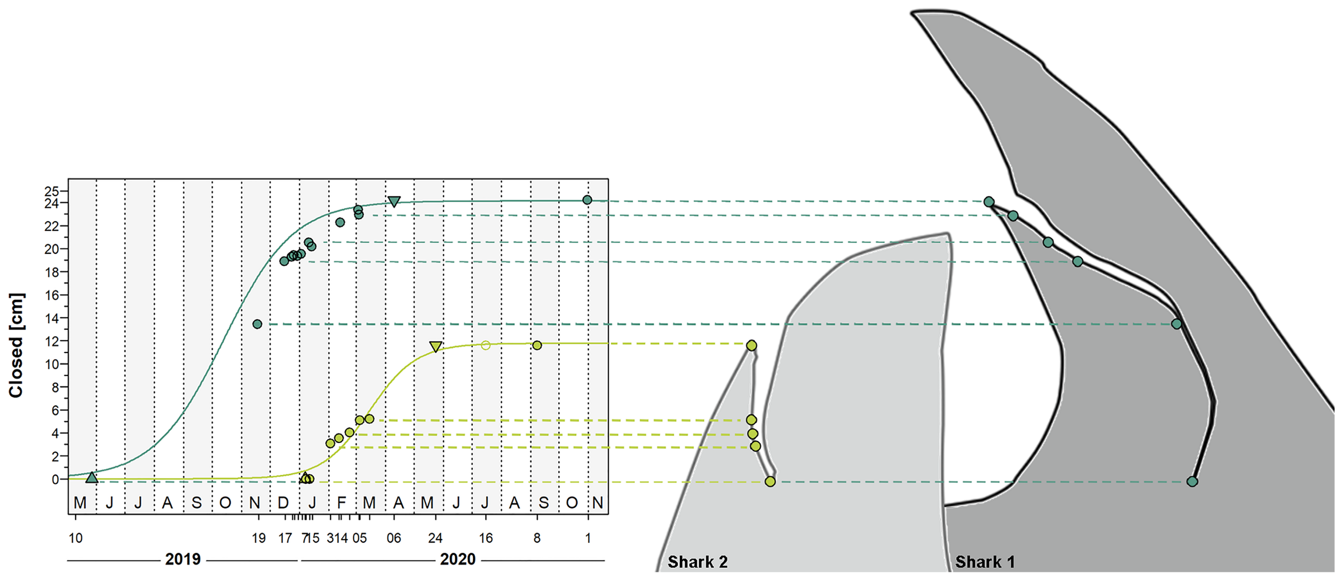

FIGURE 2 The wound closure process in two female Great Hammerheads (sharks 1 and 2) over time. Filled circles represent measurements derived from available images. Upright triangular symbols represent the estimated wounding dates (i.e., estimated dates on which the injuries were attained) for sharks 1 and 2 while upside down triangular symbols represent the approximate days when the wounds were estimated to be fully closed. The hollow circle represents an observation of shark 2 on July 16, 2020, with a fully closed wound but without photo documentation. The lines represent the nonlinear least-squares regression curves for each shark.

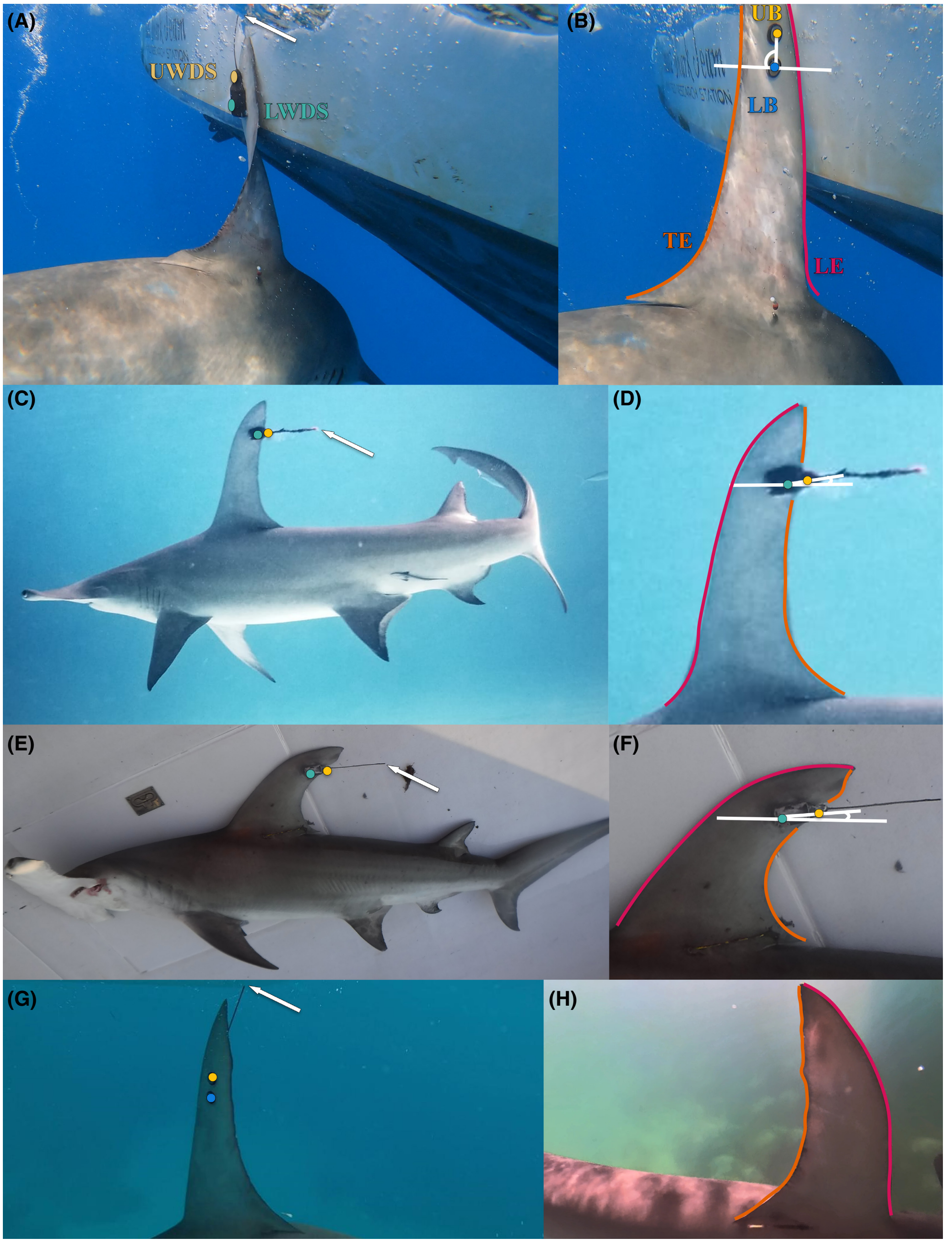

FIGURE 3 (A, B) Initial placement of a fin-mounted geolocator on shark 3; (C, D) position of the geolocator after 335 days in shark 3; (E, F) position of the geolocator after 432 days in shark 4; (G) position of the geolocator on the first dorsal fin of shark 5 when released after the initial capture; and (H) image of the first dorsal fin of shark 5 upon resighting 671 days later. All three individuals are female Great Hammerheads. In sharks 3 and 4, the fin-mounted geolocator showed a lateral posterior displacement away from the leading edge (LE) toward the trailing edge (TE). The different displacement rate of the upper bolt (UB) relative to the lower bolt (LB) caused a change in the approximately 90° angle of the bolts upon release (B; i.e., the geolocator position), indicated by the white lines in panels B, D, and F. Locations of the upper wet–dry sensor (UWDS) and the lower wet–dry sensor (LWDS) are shown in panels A and C–F. The tip of the antenna is indicated by the white arrow in panels A, C, E, and G. For visual reasons, abbreviations are only displayed once, but their color coding and corresponding symbols are maintained throughout all panels. Images C and D were taken by Deano Cook, images E and F were taken by Michele Barger (National Oceanic and Atmospheric Administration), image G was taken by Gabby Lozada, and image H was taken by Leila Molle.

after approximately 323 days, on April 9, 2020 (143 days after first sighting; Figure 2). However, while there was full wound closure with re-epithelialization, the fin of shark 1 showed a deformity after full closure of the wound (Figures 1N and S1B,D [available in the Supplementary Material in the online version of this article]). The closure process followed a pattern of a logistic curve, with a fast closure rate once the wound closure started but then a slower rate toward the completion of the closure process (NLS regression; $y[x] = 24.14/\{1 + e^{[-(-4.46 + 0.03x)]}\}$; pseudo-$R^2 = 0.995$).

The wound in the first dorsal fin of shark 2 was first documented on January 8, 2020 (Figure 1O,P). At first, the wound showed external structural deterioration—that is, bending of the posterior part of the wound and subsequently an increase in the distance between the wound edges (Figure 1Q–W). However, while this bending may have complicated the closure process, the wound was completely closed (11.6 cm) with re-epithelialization upon resighting on September 8, 2020 (245 days after first sighting; Figure 1X). The closure rate based on the linear regression was 0.08 cm/day. This resulted in an estimated wounding date of January 7, 2020 (1 day before first sighting), and full closure of the wound was estimated to have occurred on May 24, 2020 (137 days since first sighting). Full wound closure was therefore expected to have taken place over a period of approximately 138 days. We did not observe any deformity of the fin after complete wound closure in shark 2 (Figure S1E,F). Based on the NLS regression, the wound closure followed the same pattern as described for shark 1 ($y[x] = 11.76/\{1+e^{[-(-2.66+0.04x)]}\}$; pseudo-$R^2 = 0.976$), but the closure progression plateaued faster.

Shark 3 was resighted and photographed by a recreational scuba diver on January 2, 2020 (335 days posttagging), in Bimini, close to where it was originally tagged. The images allowed successful identification of the individual based on notch patterns in the fins recorded in an identification sheet prior to its capture in 2019 (Heim et al. 2023). At this point in time, the upper and lower bolts of the geolocator showed lateral posterior displacement compared to their original location during tagging (Figure 3A–D). The upper bolt was displaced far enough that it was completely outside of the fin, such that the geolocator was only attached by the lower bolt (Figure 3C,D). Shark 4 was landed by a commercial fishing boat on March 25, 2021 (432 days posttagging), in the Florida Keys. The same geolocator displacement pattern was observed in shark 4 (Figure 3E,F), with the primary difference being that both bolts were still embedded in the fin tissue of this individual. In both sharks, the upper bolts were displaced at a seemingly faster rate than the lower bolts, causing an additional downward displacement of the upper bolt, which resulted in the geolocators "laying down" (i.e., a decrease in the angle of the bolts relative to the horizontal axis of the shark; Figure 3D,F). Consequently, the upper wet–dry sensor on the front of the geolocator was now lower than where it was originally positioned during the deployment and was nearly at the same level as the lower wet–dry sensor (Figure 3C,E). Additionally, this change in the orientation caused the antenna to be lowered so that in both sharks, the antenna was trailing behind the trailing edge of the fin rather than towering above it (Figure 3C,E). During its capture (Figure 3G) on January 21, 2021, shark 5 was tagged with a fin-mounted satellite-linked geolocator that was missing during the shark's resighting 671 days later on November 22, 2022 (Figure 3H). Although the geolocator was completely shed, there was no sign of external damage or macroscopic changes to the first dorsal fin of the shark (Figure 3H).

DISCUSSION

We documented the complete closure of single, clean-cut lacerations, which severed parts of the first dorsal fin of Great Hammerheads, as well as documenting the posterior lateral displacement of fin-mounted geolocators through the fin tissue. While the minor wound (shark 2) closed without showing any sign of deformity, the complete closure of the major wound (shark 1) resulted in a slight deformity of the fin.

Great Hammerheads are only seasonal residents in Bimini; at the end of spring, they leave the islands for long-distance return migrations (Guttridge et al. 2017). Therefore, the sharks could not have been monitored year-round, but they returned to Bimini the following winter. Using macroscopic observations and measurements taken on a series of images of the dorsal fins and supporting these with statistical analysis, the estimated time period until complete closure of the wounds was approximately 323 days for the major wound (shark 1) and 138 days for the minor wound (shark 2). The estimates of the duration until completion of the closure process solely based on the visual confirmation would therefore likely be an overestimation, and the closure might have been completed earlier. For example, shark 1 showed a progression in closure from 56% to 96% within 107 days (Figure 2), and it is likely that the last 4% closed at some point during the summer (before the 323-day maximum). This closure progression is comparable with that described for first dorsal fins in Whale Sharks *Rhincodon typus*, for which approximately 57% of the fin wounds were closed by day 125 (Womersley et al. 2021). Shark 2 was seen at another Bahamian dive site on July 16, 2020, and the dive instructor of the boat observed that the wound was fully closed at that point (Neal Watson Jr., Neal Watson's Bimini Scuba Center, personal communication). This confirms that the estimation of an earlier closure on May 24, 2020, is realistic. The closure rate in shark 2 was slightly faster than that in shark 1. Faster closure rates in minor wounds compared to major wounds were also observed in Whale Sharks (Womersley et al. 2021). However, this difference could be due to the observation of shark 2 during an earlier stage of the closure process, when the closure rate was faster, compared to shark 1, which was observed at a later stage of the closure process. Given that (1) measurements made from images at slightly different angles were used and (2) these measurements were standardized using length measurements from the capture of the sharks, this minor difference in rates might also be explained by the measuring process itself. Because the sample size presented here was low ($n = 2$ individuals; $n = 23$ images), more observations will be needed to understand the full wound closure capacity from dorsal fin lacerations in Great Hammerheads. However, to our knowledge, this is the first time that the closure of single, clean-cut lacerations in Great Hammerhead fins has been described, and hopefully the reported observations will supplement future studies about wound closure processes in hammerheads and sharks in general.

The observed deformity in the first dorsal fin of shark 1 could potentially change the fin's hydrodynamic properties. Longer and "sharper" dorsal fins are suggested to allow faster swimming speeds in fish (Zhong et al. 2019). A normally functioning, uninjured dorsal fin creates vortices, which are important for an efficient thrust created by the caudal fin. Additionally, the first dorsal fin in Great Hammerheads helps to reduce the energetic costs of transport when the sharks swim at an angle (Payne et al. 2016). Therefore, the energy expenditure of shark 1 while swimming might be increased due to the deformity of its dorsal fin. However, sharks with deformed or injured dorsal fins are caught and encountered frequently, and despite their abnormal fins they appear to be healthy and in good body condition (R. D. Grubbs, personal observation). It is therefore likely that the deformity documented here will not result in long-term negative consequences for this shark. The resighting of shark 1 during the following winter in Bimini further supports this scenario.

Fin-mounted geolocators are frequently used in studies investigating the horizontal movement patterns of sharks (Hussey et al. 2015), and their deployment protocol often requires drilling holes in the fin to accommodate bolts that are used to attach the geolocators (Hammerschlag et al. 2011). Although some studies have found little impact of bolted, satellite-linked geolocators mounted on the first dorsal fins of White Sharks (Nasby-Lucas and Domeier 2020), others have documented that these geolocators can damage the fins (e.g., bending, degradation, or scarring) of the sharks if they do not detach after long time periods (Jewell et al. 2011). Here, the fate of geolocators attached to the first dorsal fin in three female Great Hammerheads observed 335, 432, and 671 days (sharks 3, 4, and 5, respectively) after initial deployment was documented.

All three sharks presented externally undamaged fins when they were resighted or recaptured. In sharks 3 and 4, the geolocators showed a lateral posterior displacement, most likely a result of the constant drag caused by the water pressure against the geolocator during forward swimming of the animals. No open wounds or deformities were observed. Shark 3 showed a more progressed geolocator displacement, with the upper bolt completely exiting the fin, whereas both of the geolocator's bolts in shark 4 were still embedded in the fin tissue. Based on the observed geolocator displacements, it is likely that both bolts would have eventually left the fin at the trailing edge, resulting in the shedding of the geolocator similar to what was observed in shark 5. These apparently minimal impacts of fin-mounted geolocators on the fins are similar to findings in White Sharks (Nasby-Lucas and Domeier 2020). However, the displacements documented here seem to have happened over a shorter time period compared to those observed by Nasby-Lucas and Domeier (2020); in that study, geolocator detachments after 2.2–3.7 years were documented, but multiple White Sharks with fully attached geolocators up to 11 years after tagging were also recorded. Kessel et al. (2017) documented an active expulsion of a foreign object through the coelom and the body wall of a shark. The geolocator displacements we documented likely do not represent expulsions but instead reflect a passive displacement caused by the constant pressure against the geolocator when the shark is moving. Additionally, the expulsion detailed by Kessel et al. (2017) was documented in a Lemon Shark with an ingested object that was expelled through the stomach lining and the body wall. The underlying processes of the expulsion described by Kessel et al. (2017) and the geolocator displacements described in the present study are therefore likely different based on the different tissues involved as well as the anatomy and the location of the structures through which the objects passed.

Sharks 3, 4, and 5 were adults. Therefore, the fin growth in these sharks was likely slower than it would have been in smaller juvenile individuals, and it is unclear how the geolocator displacement would have affected the fins of smaller individuals. However, fin-mounted satellite-linked geolocators affected the fins of juvenile and immature White Sharks to a greater extent (Jewell et al. 2011) than adult White Sharks, which displayed minimal impacts (Nasby-Lucas and Domeier 2020). The geolocators used here had two urethane bolts, which were secured on the other side of the fin by a combination of a rubber and stainless-steel washer and a stainless-steel screw inserted into each hollow bolt. It is unknown how geolocator displacements would have differed with different materials (e.g., stainless-steel bolts), attachment methods (e.g., hex bolts and nuts), or geolocator sizes or shapes.

The rate of bolt displacement differed between the upper and lower bolts, with the upper bolt seemingly exhibiting a faster rate of displacement compared to the lower bolt. Additionally, there was a downward movement of the upper bolt as well that caused a change in the orientation of the geolocator. Clearly, this study is limited by the very small sample size of only three individuals in which geolocator displacement was demonstrated. More observations of geolocator positions on the fin over time are required to draw conclusions about the displacement potential of these devices, but the risk for long-term trauma caused by these geolocators in mature Great Hammerheads seems to be relatively low.

Although the risk of permanent damage to the fins of the sharks might be low, there are other factors that should be taken into consideration in relation to geolocator position on the fin over time. The transmission rates of fin-mounted satellite-linked geolocators depend on, among other factors, the orientation of the device—that is, the position of the wet–dry sensors and the antenna. The change in angle of the geolocators during displacement as observed here might therefore change the position of the wet–dry sensors as well as the antenna and negatively impact the transmission rate. The geolocators used in the corresponding study that included sharks 3 and 4 had a relatively short battery life of about 180 days. Both sharks transmitted locations after 180 days (Heim et al. 2023). The displacement rate might therefore have been slow enough to minimize the risk of data loss due to the location change of sensors and antenna. The geolocator on shark 5 transmitted location estimates for 199 days (Guttridge et al. 2023); therefore, it cannot be concluded with certainty whether the battery or shedding of the tag caused the cessation of data transmission. As such, the displacement is desirable because it means that geolocators that are no longer transmitting will leave the animal without having a long-lasting impact on the fin. However, the displacement rate compared to the battery life could have implications for future tagging studies, where multiyear geolocators are used to create long-term data sets. The displacement could have negative consequences for geolocator deployments if the geolocator orientation changes significantly or if the geolocator is displaced far enough to exit the fin before the battery life is exhausted. Depending on the desired battery life (i.e., monitoring duration), geolocator shapes that further reduce drag (e.g., with a leading edge) might need to be explored.

In conclusion, we found that the Great Hammerhead with the major wound (shark 1) that progressed further into the fin tissue and toward the base of the fin showed full wound closure with re-epithelialization and deformity of the dorsal fin. The fin was bent and showed an external indentation along the laceration site (Figure S1B,D). The Great Hammerhead with the minor wound closer to the anterior edge of the fin (shark 2) showed full wound closure with re-epithelialization but without deformity of the dorsal fin. The wound closure patterns observed in sharks 1 and 2 likely enabled the closure of fin tissue during the observed lateral posterior displacement of geolocators through the fins in sharks 3 and 4 and during the shedding of the geolocator by shark 5. This might make the closure of fin wounds realistic, even when wounds are caused by unexpected geolocator removal, for example during entangling and forceful removal of the geolocator. The geolocators used here, which contain urethane bolts, apparently yield the potential to eventually leave the fin without causing fin deformity and therefore enable a relatively safe use while providing crucial results to advance our knowledge about the movement patterns of sharks to develop adequate conservation management strategies (Hammerschlag et al. 2011). However, the displacement of the geolocators could negatively impact transmission rates over time, and the use of different geolocator shapes based on the planned monitoring duration should be discussed.

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CONFLICT OF INTEREST STATEMENT

The authors herewith declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw data on which calculations were performed and conclusions were drawn will be made available by the authors upon request.

ETHICS STATEMENT

The documentation of the wound closure of the injuries of the Great Hammerheads in Bimini, Bahamas was completed using noninvasive research methods and the protocols were approved under permit MA&MR/FIS/17B issued to the Bimini Biological Field Station Foundation by the Department of Marine Resources (DMR), Bahamas. The tagging of Great Hammerheads was completed as part of research efforts by Heim et al. (2023) and Guttridge et al. (2023) and all capture and tagging protocols were approved under the corresponding permits: The shark in Andros was caught and tagged under the permits MAMR/FIS/17 and MAMR/FIS/2/12A/17 issued to T. L. Guttridge by the DMR, Bahamas. All fieldwork in Bimini was conducted under the permit MA&MR/FIS/17B issued to the Bimini Biological Field Station Foundation by the DMR, Bahamas. The shark in the Florida Keys was caught and tagged under permits FKNMS-2018-062 and SAL-19-1345 issued to R. D. Grubbs. All field work protocols were optimized towards reducing stress for the target individuals.

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REFERENCES

Andrzejaczek, S., Gleiss, A. C., Lear, K. O., Pattiaratchi, C. B., Chapple, T. K., & Meekan, M. G. (2019). Biologging tags reveal links between fine-scale horizontal and vertical movement behaviors in Tiger Sharks (*Galeocerdo cuvier*). *Frontiers in Marine Science*, *6*, Article 229. https://doi.org/10.3389/fmars.2019.00229

Bansemer, C. S., & Bennett, M. B. (2010). Retained fishing gear and associated injuries in the east Australian grey nurse sharks (*Carcharias taurus*): Implications for population recovery. *Marine and Freshwater Research*, *61*(1), 97–103. https://doi.org/10.1071/MF08362

Belacortu, Y., & Paricio, N. (2011). *Drosophila* as a model of wound healing and tissue regeneration in vertebrates. *Developmental Dynamics*, *240*(11), 2379–2404. https://doi.org/10.1002/dvdy.22753

Bird, P. M. (1978). Tissue regeneration in three Carcharhinid sharks encircled by embedded straps. *Copeia*, *1978*(2), 345–349. https://doi.org/10.2307/1443580

Borucinska, J., Adams, D. H., & Frazier, B. S. (2020). Histologic observations of dermal wound healing in a free-ranging Blacktip Shark from the southeastern U.S. Atlantic Coast: A case report. *Journal of Aquatic Animal Health*, *32*(4), 141–148. https://doi.org/10.1002/aah.10113

Chapple, T. K., Gleiss, A. C., Jewell, O. J. D., Wikelski, M., & Block, B. A. (2015). Tracking sharks without teeth: A non-invasive rigid tag attachment for large predatory sharks. *Animal Biotelemetry*, *3*, Article 14. https://doi.org/10.1186/s40317-015-0044-9

Chin, A., Mourier, J., & Rummer, J. L. (2015). Blacktip Reef Sharks (*Carcharhinus melanopterus*) show high capacity for wound healing and recovery following injury. *Conservation Physiology*, *3*(1), Article cov062. https://doi.org/10.1093/conphys/cov062

Compagno, L. J. V. (1984). *FAO species catalogue. v. 4: (2) Sharks of the world. An annotated and illustrated catalogue of shark species known to date, pt. 2: Carcharhiniformes*. Food and Agriculture Organization of the United Nations.

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*(21), 4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

Duncan, K., & Holland, K. (2006). Habitat use, growth rates and dispersal patterns of juvenile Scalloped Hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series*, *312*, 211–221. https://doi.org/10.3354/meps312211

Gallagher, A. J., & Klimley, A. P. (2018). The biology and conservation status of the large hammerhead shark complex: The Great, Scalloped, and Smooth hammerheads. *Reviews in Fish Biology and Fisheries*, *28*(4), 777–794. https://doi.org/10.1007/s11160-018-9530-5

Gardiner, J. M., & Wiley, T. R. (2020). Escaped bait: Bull Shark *Carcharhinus leucas* with an intentionally attached harness rig. *Journal of Fish Biology*, *98*(3), 891–894. https://doi.org/10.1111/jfb.14623

Guttridge, T. L., Matich, P., & Guttridge, A. E. (2023). Elasmobranch movement ecology [Unpublished raw data]. Saving the Blue.

Guttridge, T. L., Van Zinnicq Bergmann, M. P. M., Bolte, C., Howey, L. A., Finger, J. S., Kessel, S. T., Brooks, J. L., Winram, W., Bond, M. E., Jordan, L. K. B., Cashman, R. C., Tolentino, E. R., Grubbs, R. D., & Gruber, S. H. (2017). Philopatry and regional connectivity of the Great Hammerhead shark, *Sphyrna mokarran* in the U.S. and Bahamas. *Frontiers in Marine Science*, *4*, Article 3. https://doi.org/10.3389/fmars.2017.00003

Hammerschlag, N., Gallagher, A. J., & Lazarre, D. M. (2011). A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, *398*(1–2), 1–8. https://doi.org/10.1016/j.jembe.2010.12.012

Heim, V., Dhellemmes, F., Smukall, M. J., Gruber, S. H., & Guttridge, T. L. (2021). Effects of food provisioning on the daily ration and dive site use of Great Hammerhead sharks, *Sphyrna mokarran*. *Frontiers in Marine Science*, *8*, Article 628469. https://doi.org/10.3389/fmars.2021.628469

Heim, V., Grubbs, R. D., Frazier, B. S., Carlson, J. K., Smukall, M. J., & Guttridge, T. L. (2023). Large-scale movements of Great and Scalloped hammerheads, *Sphyrna mokarran* and *S. lewini*, between the US Atlantic and the Gulf of Mexico [Unpublished raw data]. University of Basel.

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Mills Flemming, J. E., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, *348*(6240), Article 1255642. https://doi.org/10.1126/science.1255642

Jakes, A. F., Jones, P. F., Paige, L. C., Seidler, R. G., & Huijser, M. P. (2018). A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. *Biological Conservation*, *227*, 310–318. https://doi.org/10.1016/j.biocon.2018.09.026

Jewell, O. J. D., Wcisel, M. A., Gennari, E., Towner, A. V., Bester, M. N., Johnson, R. L., & Singh, S. (2011). Effects of smart position only (SPOT) tag deployment on White Sharks *Carcharodon carcharias* in South Africa. *PLoS One*, *6*(11), Article e27242. https://doi.org/10.1371/journal.pone.0027242

Kessel, S. T., Fraser, J., Van Bonn, W. G., Brooks, J. L., Guttridge, T. L., Hussey, N. E., & Gruber, S. H. (2017). Transcoelomic expulsion of an ingested foreign object by a carcharhinid shark. *Marine and Freshwater Research*, *68*(11), 2173–2177. https://doi.org/10.1071/MF17022

Marra, N. J., Stanhope, M. J., Jue, N. K., Wang, M., Sun, Q., Pavinski Bitar, P., Richards, V. P., Komissarov, A., Rayko, M., Kliver, S., Stanhope, B. J., Winkler, C., O'Brien, S. J., Antunes, A., Jorgensen, S., & Shivji, M. S. (2019). White Shark genome reveals ancient elasmobranch adaptations associated with wound healing and the maintenance of genome stability. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(10), 4446–4455. https://doi.org/10.1073/pnas.1819778116

McGregor, F., Richardson, A. J., Armstrong, A. J., Armstrong, A. O., & Dudgeon, C. L. (2019). Rapid wound healing in a reef manta ray masks the extent of vessel strike. *PLoS One*, *14*(12), Article e0225681. https://doi.org/10.1371/journal.pone.0225681

Nasby-Lucas, N., & Domeier, M. L. (2020). Impact of satellite linked radio transmitting (SLRT) tags on the dorsal fin of subadult and adult White Sharks (*Carcharodon carcharias*). *Bulletin of Marine Science*, *96*(1), 23–30. https://doi.org/10.5343/bms.2019.0019

Onofri, A. (2020). *The broken bridge between biologists and statisticians: A blog and R package*. Statforbiology.

Payne, N. L., Iosilevskii, G., Barnett, A., Fischer, C., Graham, R. T., Gleiss, A. C., & Watanabe, Y. Y. (2016). Great Hammerhead sharks swim on their side to reduce transport costs. *Nature Communications*, *7*, Article 12289. https://doi.org/10.1038/ncomms12289

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R. W., Liu, K. M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2019). *Sphyrna mokarran*. The IUCN Red List of Threatened Species 2019:e.T39386A2920499. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39386A2920499.en

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schulte, L. M., Martel, A., Cruz-Elizalde, R., Ramírez-Bautista, A., & Bossuyt, F. (2021). Love bites: Male frogs (*Plectrohyla*, Hylidae) use teeth scratching to deliver sodefrin precursor-like factors to females during amplexus. *Frontiers in Zoology*, *18*(1), Article 59. https://doi.org/10.1186/s12983-021-00445-6

Towner, A., Smale, M. J., & Jewell, O. (2012). Boat strike wound healing in *Carcharodon carcharias*. In M. L. Domeier (Ed.), *Global perspectives on the biology and life history of the White shark* (pp. 77–84). CRC Press.

van den Hoff, J., & Morrice, M. G. (2008). Sleeper shark (*Somniosus antarcticus*) and other bite wounds observed on southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science*, *24*(1), 239–247. https://doi.org/10.1111/j.1748-7692.2007.00181.x

White, T. D., Carlisle, A. B., Kroodsma, D. A., Block, B. A., Casagrandi, R., De Leo, G. A., Gatto, M., Micheli, F., & McCauley, D. J. (2017). Assessing the effectiveness of a large marine protected area for reef shark conservation. *Biological Conservation*, *207*, 64–71. https://doi.org/10.1016/j.biocon.2017.01.009

Womersley, F., Hancock, J., Perry, C. T., & Rowat, D. (2021). Wound-healing capabilities of Whale Sharks (*Rhincodon typus*) and implications for conservation management. *Conservation Physiology*, *9*(1), Article coaa120. https://doi.org/10.1093/conphys/coaa120

Zhong, Q., Dong, H., & Quinn, D. B. (2019). How dorsal fin sharpness affects swimming speed and economy. *Journal of Fluid Mechanics*, *878*, 370–385. https://doi.org/10.1017/jfm.2019.612

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