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First Evidence of Individual Sharks Involved in Multiple Predatory Bites on People

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ABSTRACT

It is widely accepted that populations of terrestrial predators sometimes contain "problem individuals" that repeatedly attack humans, yet this phenomenon has never been demonstrated in sharks. Here, we present photographic and genetic evidence of individuals in populations of tiger *Galeocerdo cuvier* and oceanic whitetip *Carcharhinus longimanus* sharks that (1) demonstrated atypical behavior compared to the rest of the population, (2) engaged in repeated agonistic behavior directed toward humans, and (3) bit, or attempted to bite humans in probable foraging attempts. These case studies provide some of the first evidence for the existence of "problem individuals" among sharks. The percentage of fatalities due to the same shark individual are not known, so we recommend systematic swabbing of shark bite victims wounds to better understand the importance of this phenomenon and the possibility of identifying these animals. Environmentally conscientious management options for problem individuals range from prohibiting ocean activities (e.g., swimming and surfing) in their habitats to selectively removing the individual, although the latter would be challenging in the marine environment.

1 | Introduction

Sharks are a perennial source of fear and fascination for humans, yet shark bites are actually very rare events with only approximately 100 incidents reported per year worldwide and less than 15% proving fatal (Midway, Wagner, and Burgess 2019). A slight increase in fatalities in recent decades is attributed to concomitant significant increases in the number of ocean users (Ferretti et al. 2015; West 2011) combined with the emergence of new sports such as kite surfing that have extended human marine recreational activities into new, previously unused, and potentially dangerous areas (Clua, Bescond, and Reid 2014). Although rare, these human fatalities receive disproportionate media attention, with considerable psychological and economic repercussions, especially on island economies on the basis of beach tourism (Chapman and McPhee 2016).

The concept of a "rogue" shark "developing a taste for humans" resulting in multiple attacks first emerged in Australia in the early 1950s as a potential explanation for apparent clusters of fatal shark attacks (Coppleson 1950). However, this concept has subsequently been widely criticized as anthropomorphic and improbable (Pepin-Neff and Wynter 2019). The wildlife management response to fatal shark bites varies among geographic locations but is broadly divisible into culling or non-culling approaches. In locations where culling is still utilized either in response to fatal bites, or as an ongoing risk mitigation strategy, the practice is typically very unselective with many individuals of multiple species being intentionally or unintentionally killed (Sumpton et al. 2011). Wetherbee, Lowe, and Crow (1994) showed that mass culling of thousands of sharks in Hawaii (Pacific Ocean) during the 1960s did not reduce the frequency of shark bites, and recent mass culling around La Réunion island (Indian ocean) has proven similarly ineffective. Culling over 500 sharks in response to 5 fatal bites between 2011 and 2013 in La Reunion waters failed to prevent the occurrence of 6 fatal bites between 2015 and 2019 (EC, Pers. Obs.). After beach nets were deployed in New South Wales Australia in 1937, the annual number of shark bites decreased by ~90% (Dudley 1997) yet since 2000, there have been periods of more shark–human interactions at netted beaches than non-netted ones (Huveneers et al. 2024). Although shark culling campaigns still remain a politically attractive response to shark bites in some locations, there is no convincing evidence that they actually reduce risk (Ferretti et al. 2015) and the tide of public opinion is turning against them (Simmons and Mehmet 2018; Simmons et al. 2021) as the public learns more about the ecological importance of sharks and the conservation plight that they currently face from overfishing (Dulvy et al. 2017; Meeuwig and Ferreira 2014; Queiroz et al. 2019).

The original concept of "rogue" individuals among predator species has been superseded in recent decades by the concept of "problem individuals." Although widely accepted as valid in terrestrial predators such as big cats (Linnell et al. 1999; Packer et al. 2019), there is greater reluctance to accept that this phenomenon may also exist among large shark species (Pepin-Neff 2019). In this study, we provide empirical evidence of individuals from two species of shark repeatedly targeting humans and thereby meeting the definition of "problem individuals" as recognized in terrestrial predators.

2 | Methods

2.1 | Identification of a "Problem Shark" Through Genetics (Case Study 1)

When sharks bite, they deposit mucus on the bite margins, allowing for swabbing to recover DNA residues suitable for genetic analysis (Fotedar et al. 2019; Kraft et al. 2021; Martin et al. 2024; Webb et al. 2022). In two recent shark bite incidents in the Caribbean (Case study 1), medical personnel swabbed the bite wounds (n = 6 swabs) to collect shark mucus transfer before disinfecting the wounds. These swabs were then preserved in 90% alcohol and subsequently analyzed to determine the individual genetic profile (fingerprinting) of the biting shark, utilizing microsatellite markers (Clua et al. 2020). Single source and mixed forensic samples are prone to PCR inhibition and DNA degradation resulting in poor amplification and allele dropout (McCord et al. 2011). To account for possible transfer DNA washout and degradation at bite wound sites, we performed two separate and independent fingerprinting runs for each of the two sets of samples (see technical details in the Supporting Information Appendix S1). Genetic analyses (extraction, PCR) were conducted in the CRIOBE lab in Perpignan (France). Sequencing was performed by an external company. As a quality control process, reading and analysis of the allele matching were performed independently by two different experts co-authoring this study. In order to increase the reliability of our analysis, an allelic reference database was constructed from at least 40 DNA samples from individuals of the shark species identified as responsible for the bites and captured within 50 km of bite incidents. This number of samples has the potential to allow the calculation of allelic frequencies in a reliable and accurate manner, as 25–30 individuals are usually sufficient for this type of study (Hale, Burg, and Steeves 2012).

2.2 | Identification of "Problem Sharks" Through Photo-Identification (Case Studies 2 and 3)

Photo-identification is a reliable method for distinguishing individual sharks in species with distinctive body or fin patterns, such as tiger sharks *Galeocerdo cuvier* (Bègue et al. 2020) and oceanic whitetip shark (OWT) *Carcharhinus longimanus* (Myrberg 1991). The ubiquity of low-cost digital cameras among recreational divers has resulted in a large and growing database of shark images useful for photo-identification studies (e.g., Séguigne et al. 2023). We used photos and videos collected by recreational divers to identify individual sharks responsible for human fatalities in the Eastern Pacific (tiger shark) and Red Sea (OWT shark).

Case study 2: Following two bites on divers in November 2017 and the injury of another diver in April 2018, the first author was invited by the Costa Rican government to visit Cocos Island in September 2018 to officially interview witnesses, examine photographic evidence, and explore the incident locations. On the basis of several converging testimonies of local diving experts, tiger sharks were sometimes curious but never aggressive toward scuba divers until 2014 when one particular individual began to behave more aggressively. Interviews (n = 7 corresponding to 1 h 42 min of testimony) were conducted with two boat captains, two diving supervisors and two dive masters from the two main dive companies working in the area as well as the Cocos Island National Park ranger diver directly involved in shark-related issues. The first author E.E.G.C. carried out 18 exploratory dives at both ecotourism (n = 15) and non-ecotourism (n = 3) locations. E.E.G.C. also examined photographs and videos documenting sightings of tiger sharks displaying agonistic behaviors toward humans (n = 18) and injuries from the two shark bite incidents (n = 11). Finally, he was provided with another testimony of an agonistic encounter in November 2018 and photographs (n = 2) from a recreational diver who experienced several close encounters with an agonistic shark in September 2019. The evidence collected was used to evaluate the hypothesis that a single "problem individual" was responsible for both bite incidents and other aggressive interactions with divers.

Case study 3: The coauthor S.S., a dive master in Egypt for the past 20 years (permit ref# (435) 21-5-2013), conducted over 5000 dives with recreational divers on live-aboard trips covering all major diving sites in the Egyptian Red Sea. He collected detailed voluntary interviews, photos, and videos documenting agonistic behaviors by OWT sharks toward divers, including himself. These data were analyzed to identify "problem sharks."

3 | Results

3.1 | Case Study 1: Genetic Identification of a "Problem Tiger Shark" in the Caribbean (Atlantic Ocean)

In December 2020, a female swimmer was fatally wounded by the removal of her entire left thigh by a shark in Orient Bay on the French Caribbean island of St. Martin. One month later, another snorkeler survived having her left leg entirely severed by a shark in the coastal waters of St. Kitts and Nevis, 85 km away. In both cases, witnesses identified a tiger shark of approximately 3 m in total length (TL) as the biter. In both cases, wound swabs were collected from victims to collect transfer DNA from the biting shark (see details in the Supporting Information Appendix S1). Although degraded, sufficient nuclear DNA was recovered to permit fingerprinting through a single-tandem repeats (STRs) comparison (see the Supporting Information Appendix S2/Table S1) to test the hypothesis that a single shark was responsible for both incidents. This comparison was validated by calculating the allelic frequencies in the reference sample of 49 tiger sharks captured in the waters of Saint Martin and St. Barth ($n = 35$) and St. Kitts and Nevis ($n = 14$). Of the 26 STRs examined, 2 could not be amplified, 3 were monomorphic (the Supporting Information Appendix S2/Table S1), and 21 STRs were classified as identical in samples from both incidents, including nine STRSs that were very polymorphic (the Supporting Information Appendix S3/Tables S2 and S3), resulting in an extremely low probability (8.15×10^{-11}) that two different individuals were responsible for these bites.

3.2 | Case Study 2: Photo-Identification of a "Problem Tiger Shark" in Cocos Island (Costa Rica)

A 3-m female tiger shark with distinctive markings (named "Lagertha" by local divers, Figure 1) began to show atypical curiosity toward divers as early as 2014 (see the Supporting Information Appendix S4/Table S4). This shark was easily identifiable through a permanent white spot on its dorsal fin (Figure 1B). Although other tiger sharks always remained at a distance of several meters from divers, Lagertha would approach closely (sometimes <1 m), while closing the nictitating membranes (to protect its eyes during an agonistic interaction—see the Supporting Information Appendix S5/Video 1) and pseudo-biting expressed by the jaw opening and closing with sometimes simultaneous sideways movement of the head (Ritter and Godknecht 2000) (see Figure 1 and see the Supporting Information Appendix S5/Video 1). Other visual evidence of aggressiveness also included flank displaying (see the Supporting Information Appendix S5/Video 2, Video 3, and Video 6: a sustained [>5 s] perpendicular bodily orientation of a signaler's body [the shark] toward a receiver [the diver], displaying its lateral surface) and pectoral fin depression (see the Supporting Information Appendix S5/Video 4) a sustained (>5 s), bilateral lowering of the pectoral fins from their usual position during swimming (Martin 2007). Lagertha also consistently approached divers while they were in the water column (several meters above the bottom), on their way to the surface at the end of the dive (see the Supporting Information Appendix S4/Table S4). In November 2017, a tourist scuba diver and dive-master, ascending from a dive in the Manuelita Canal (Figure S1B in the Supporting Information Appendix S4), were approached by the female tiger shark during their decompression safety stop. The shark was initially pushed away by the dive master but it managed to injure him. The captain rescued the diver master, whose foot was bleeding heavily, by hauling him aboard while the shark headed toward the other diver who had curled up on the surface. The boat rammed the shark on the surface as it was biting the remaining diver, allowing the captain to clearly identify the shark as Lagertha on the basis of the white spot on the dorsal fin. The second diver died within a minute of her retrieval due to blood loss following the entire removal of the left thigh (see the Supporting Information Appendix S4/Table S4). In April 2018, an experienced underwater photographer diving on the outskirts of Manuelita Island (Figure S1B in the Supporting Information Appendix S4) became separated from his group at the end of the dive. He was swimming at a few meters depth when he was struck from behind by what he identified as a large shark that grabbed the SCUBA tank and buoyancy compensator in its mouth (see the Supporting Information Appendix S4/Table S4). The diver abandoned his diving equipment (that the shark kept in its mouth while swimming away), surfaced, and took refuge on a rock, where he was able to observe and identify the shark as Lagertha patrolling at the surface while a boat was coming to pick him up (see additional details in the Supporting Information Appendix S4). In September 2019, after no sightings for several months, Lagertha repeatedly approached a recreational diver who had separated from his group. During his ascent from 20 m depth, the diver had to repel the shark three times by hitting its snout with his camera gear before being hauled aboard a boat. This diver photographed the shark enabling its identity to be confirmed (Figure 1F).

3.3 | Case Study 3: Photo-Identification of a "Problem Oceanic Whitetip Shark" in Egypt (Red Sea)

On June 1, 2009, a 47-year-old female swimmer died following the loss of her right leg after several bites from an individual >3 m female OWT in Gota Kebir (St Johns Reef) at 09:00 a.m. On this day, only three OWT sharks were present at the diving spot, including two small individuals and the large female that was photographed (Figure 2A) and clearly identified as the bite perpetrator (the Supporting Information Appendix S6/T01). The day after on June 2, 2009, at 10:10 a.m. in Gota Soraya, 1.5 km from the previous location, this same shark (Figure 2B) attempted to bite the shoulder of a 36-year dive-master (the Supporting Information Appendix S6/T02). On the third day, 3 km away in Habili Gafar, the same shark was again involved in a bite attempt at 10:30 a.m. on the fins and calf of a 21-year-old dive-master (co-author of this study) (Figure 2C, the Supporting Information Appendix S6/T03 and Table S5). This individual was clearly

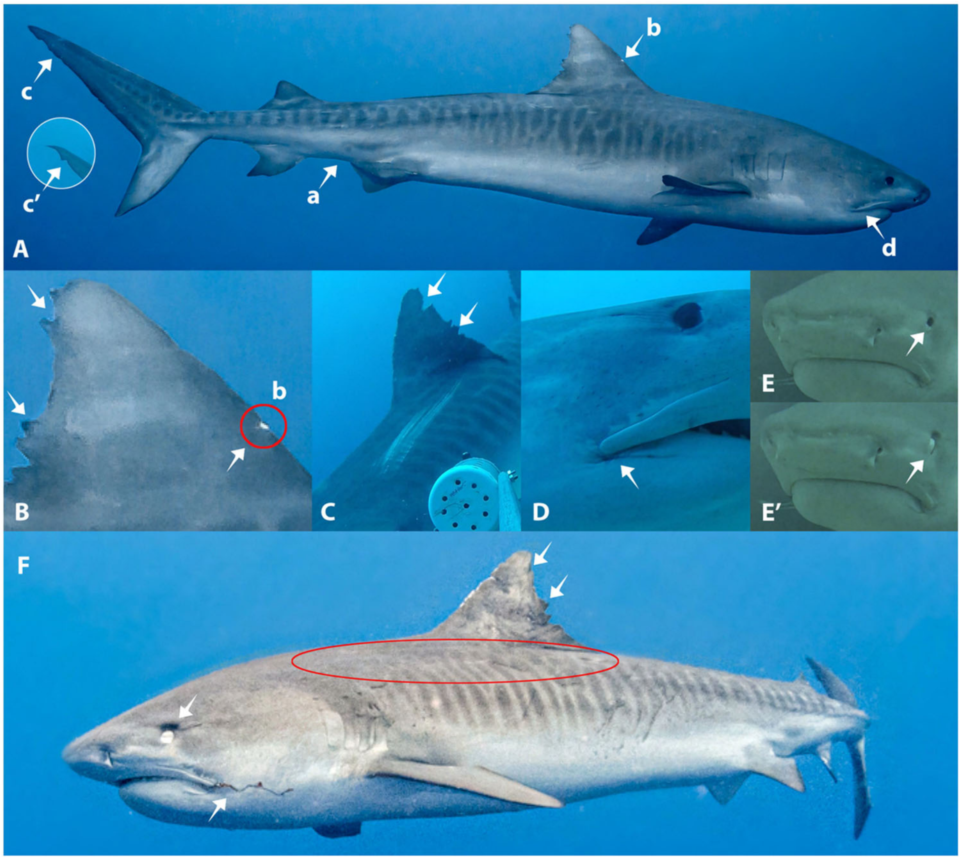

FIGURE 1 | Photo-identification of the “problem” female tiger shark “Lagertha.” This individual was individually identified on the basis of specific distinguishing marks such as (A and B): (a) absence of claspers, (b) presence of a white spot on the right front edge of the dorsal fin, (c) absence of the subterminal notch on the back edge of the caudal fin (as in c′ for another shark), and (d) a down-curving shape of the mouth. (B) Close up on the dorsal fin (right side) that shows the several specific cuts (probably mating wounds that have healed; see white arrows) and the very specific white dot (red circle on the front edge) that allows any diver (with no specific skills) to easily recognize this shark. (C and D) Close-up allowing the observation of the dorsal fin notches and healed wounds on the corner of the mouth (see white arrow), probably linked to fishing hooks that have disappeared. (E) Chronological display of the shark head before a contact with a diver showing an open eye (E) before the closure (E′) of the nictitating membrane for protecting the eyes during a bite. (F) Left flank displaying of Lagertha in September 2019 showing the closing of the nictitating membrane before a close encounter with a diver and the presence of an embedded hook on the left corner of the mouth (see white arrows) as well as a poor general condition. *Source*: (A and B) Photo courtesy of M. Hunkel. (C and D) Photos courtesy of J. Spaet through the use of a video recorded at a bait site on September 26, 2018. (E) Photo courtesy of C. De la Cruz. (F) Photo courtesy of S. Boaz.

identified through its size, gender, and specific pattern of the white tip of the dorsal fin as well as a skin excrescence at the end of the left pectoral fin (Figure 2A–C).

4 | Discussion

Between 2010 and 2020, there was an annual average of only eight fatal shark bites on humans worldwide (GSAF 2022), making these events extremely rare and effectively impossible to anticipate and document systematically. Although our sample size is small, we demonstrate that individuals of two traumatogenic shark species have repeatedly targeted humans in what appear to be foraging attempts on the basis of the removal of large amounts of tissue or even limbs from three victims (sharks sometimes bite humans for other reasons, such as self-defense, but the wounds tend to be relatively minor by comparison, see Klimley et al. 2023 for details).

To our knowledge, this is the first definitive evidence of individual sharks repeatedly targeting humans as potential prey. The Caribbean tiger shark and the easily distinguishable Pacific female tiger shark as well as the OWT meet all three of the criteria that define a “problem individual”: (1) atypical behavior compared to the rest of the population, (2) repeated agonistic behavior directed toward humans, and (3) feeding or attempting to feed on humans, including a human fatality attributed to each individual. Poor physical condition revealed by the depression in the dorsal musculature evident in Figure 1F may have been a motivation for atypical aggressive behavior by the tiger shark “Lagertha” at the Cocos Island (Figure 1A,F) as has been noted in some terrestrial predators involved in predatory interactions with humans (Patterson, Neiburger, and Kasiki 2003). However, the aggressive OWT shark, as well the tiger shark involved in the Caribbean attacks, appeared to be in normal physical condition, suggesting inherent personality traits such as boldness and risk-taking may be important drivers of agonistic encounters with humans. The presence of a subset of bold individuals in

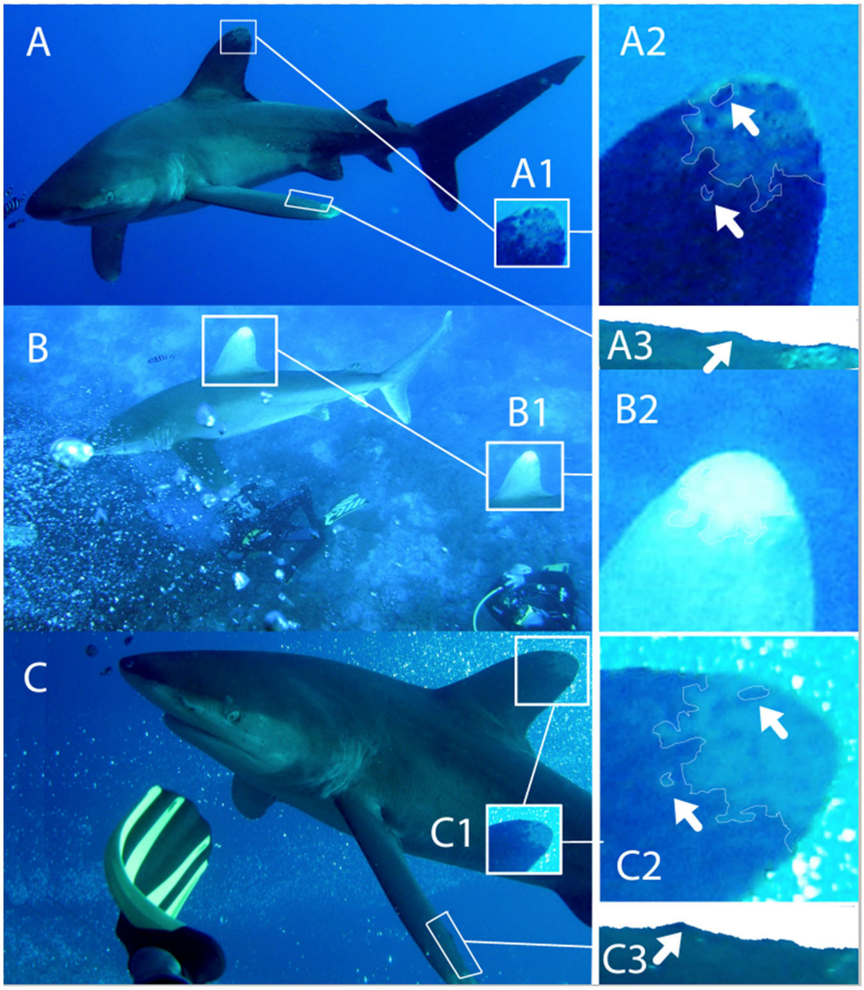

FIGURE 2 | Photo-identification of the "problem" female Oceanic Whitetip (OWT) shark from the Red Sea. Photographs of the large female OWT individual that was involved in agonistic behaviors toward humans. (A) Photo taken in the context of the fatal bites on a female swimmer on June 1, 2009 (see Case 1 in Table S5), then in (B), in the context of the non-fatal bite on a diver on June 2, 2009 at a distance of 1.5 km from the original incident (see Case 2 in Table S5), and finally in (C), again the same individual involved in an agonistic behavior 3 km away on June 3, 2009 (Case 3 in Table S5). (A1, B1, and C1) Close-up of the dorsal fin (left side) with contrast increased to better discriminate the margins of the terminal white spot. (A2, B2, and C2) Close-up of A1, B1, and C1 in order to better observe the similarities of the white margins, in particular (1) a small zone without a white coloration close to the proximal end (top arrow in A2 and C2) and (2) a small white spot, detached from the main white spot (lower white arrow in A2 and C2). In addition to the features of the white coloration of the dorsal fin, this shark has, in the last third of the posterior margin of its left pectoral fin, a skin excrescence (possibly a healed injury) that is clearly visible in close up A3 and C3. *Source*: (A) Photo courtesy of O. Rocchia. (B) Photo courtesy of D. Guillemet. (C) Photo courtesy of Y. Eekout.

predator populations may be an evolutionarily stable state where the heightened propensity to try novel prey sometimes confers fitness advantages (Clua and Linnell 2018). There is certainly a growing body of evidence of different "personalities" in large predatory sharks with some individuals being consistently bolder and more willing to investigate and bite unfamiliar objects that may be novel prey (Dhellemmes et al. 2021; Dingemanse 2021; Kim et al. 2012; Matich, Heithaus, and Layman 2011; Towner et al. 2015). Positive reinforcement to target humans could occur if investigative or direct predation bites are rewarded by the scent or taste of palatable tissue, thus encouraging naturally bold individuals to become "problem individuals" (such as the Caribbean tiger shark that struck in Saint Martin and St Kitts and the OWT shark from the Red Sea; see the Supporting Information Appendix S6/Table S5).

Other bite motivations than foraging could theoretically lead to the emergence of "problem individuals," but the absence of the central and complementary "feeding reward" trigger in association with personality traits, such as boldness and risk-taking, makes this possibility highly unlikely for sharks. These incidents involved two of the primary shark species known to be responsible for human fatalities (Midway, Wagner, and Burgess 2019). Additionally, previous spatiotemporal clusters of shark bites have been associated with the other two species, namely, the white shark *Carcharodon carcharias* and the bull shark *Carcharhinus leucas*, which account for a significant proportion of shark bite incidents overall. Although we lack definitive proof such as images or DNA evidence, these clusters are consistent with the presence of "problem individuals" (Clua and Linnell 2018) (Figure 3).

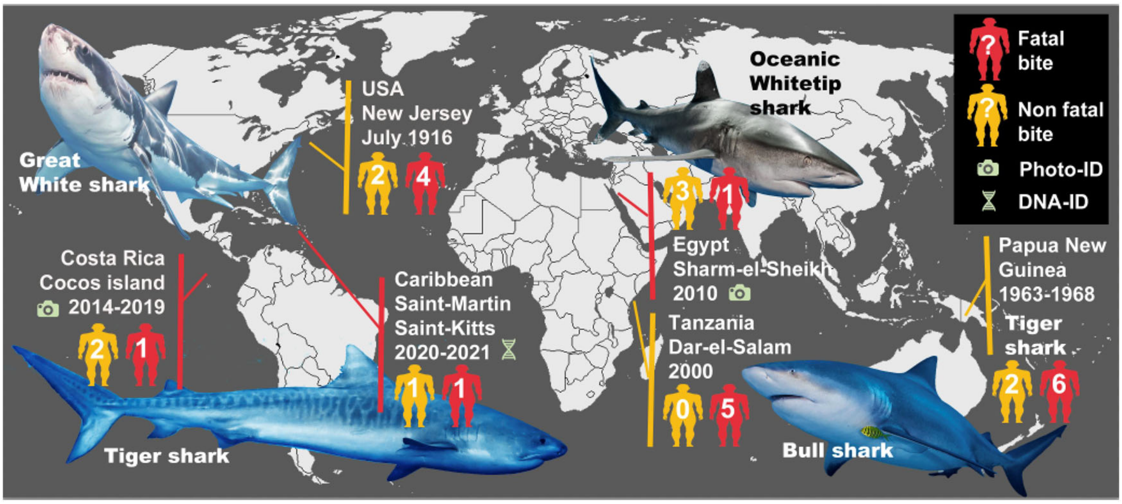

FIGURE 3 | Potential shark bite clusters involving the four most traumatogenic species. Examples of spatiotemporal clusters of shark bites on humans that are consistent with the activities of problem Individuals. Great white shark: the summer of 1916 in New Jersey (USA) experienced a highly unusual series of fatal bites that occurred on swimmers (Fernicola 1916). Bull shark: Tanzania experienced a fatal bite in May 1968 (unknown species), then no fatalities for more than 30 years until June 2000 when an initial fatality in Dar-es-Salam, was followed by four additional fatalities within the next 3 months in the same area, involving this same species and until swimming was forbidden after death number 5. Oceanic Whitetip shark: The northern Red Sea experienced a cluster of several bites around the site of Sharm-el-Sheikh from October to December 2010, with a high probability of the same individual being involved (Levine et al. 2014). Tiger shark: In addition to the Costa Rica case study (tiger shark "Lagertha"), Papua New Guinea experienced a total of 12 bites (possibly more), including 10 fatal, involving this species. Among these bites, 6 were believed to be perpetrated by a single individual nicknamed "Big fellow" (24). *Source*: The figure was developed with the technical assistance of S. Roddier.

In this study, we provide empirical evidence of individuals from two shark species repeatedly biting or showing aggression toward humans. In a terrestrial setting, predators exhibiting this pattern of behavior would be classified as "problem individuals" (Swan et al. 2017). Although this pattern is superficially similar to the original concept of a "rogue" shark, there are important distinctions between these two concepts. The term "rogue" implies an animal with savage or destructive tendencies' or "a person or thing that behaves in an aberrant, faulty, or unpredictable way." Thus, "rogue" anthropomorphizes the motivations of sharks that bite people in a way that "problem individual" does not imply that there is something "wrong" with the animal. However, a perfectly normal healthy individual exhibiting normal behavior could be a "problem individual." For example, the OWT observed biting humans in the Red Sea appeared to be in good physical condition. Some of the shark bites on humans may just be a natural consequence of the shark's natural dietary plasticity and natural tendency to explore potential prey by biting (Clua and Meyer 2023). If a shark receives positive reinforcement from one of these encounters, then they may be more likely to try it again and thus become a "problem individual" from a human perspective. There is nothing aberrant about this positive reinforcement mechanism, rather it is the normal process through which sharks learn to exploit prey, expand their prey repertoire, and hence there is nothing "rogue" about "problem individuals." Moreover, the "problem individual" hypothesis does not discount the potential role of environmental factors (e.g., water conditions, distribution/abundance of prey) in shark bites on humans (Chapman and McPhee 2016) because these are not mutually exclusive phenomena.

We do not yet know the proportion of all shark bites that are attributable to "problem individuals," but our results suggest that DNA fingerprinting samples obtained by taking swabs from bite wounds on people or equipment could answer this question. Research by Oury et al. (2021) has shown the feasibility of profiling individual sharks using mucus samples retrieved from human wounds. Specifically, they found that fatal shark bites on Reunion Island in 2015 and 2019 were caused by different individuals within the local bull shark population. However, this analysis has only been conducted on two out of the 11 fatalities recorded on the island between 2011 and 2019. Forensic analyses of eight bites occurring between April 2015 and February 2018 identified bull sharks as the species involved in four cases, with three individuals measuring around 2.5 m in TL (Clua et al. 2020). Given the prolonged duration (almost 10 years) and frequency (25 bites), it is possible that "problem individuals" were also involved in these incidents. We then suggest that the wounds of shark bite victims should be routinely swabbed to identify the biting species and individual (Clua et al. 2020; Martin et al. 2024). These samples should be collected without compromising medical care but before any wound cleaning chemicals that may hamper any molecular analysis are applied. Broader use of shark bite wound swabbing will help determine the proportion of bites caused by "problem individuals," enabling a clearer assessment of whether a combination of selective removal and non-lethal strategies, such as drone surveillance, could replace harmful, non-selective mass culling as a shark risk mitigation strategy.

Author Contributions

E.E.G.C. designed the study and implemented the acquisition, analysis and interpretation of data, and drafting of the article. A.H. suggested and designed the testing of fingerprinting on human wounds. M.V., H.B., and M.F. contributed to the field data (DNA) collection in the Caribbean case study. S.B., C.S., H.B., and S.P. conducted the genetic analysis as well as the interpretation of results. S.S. and T.V. provided data on potential problem individuals among other species than tiger sharks and revised the article. J.D.C.L. and C.G.M. made substantial contributions to refining the conceptual idea of problem individuals and revised the article. All authors approved the final version of the manuscript and agreed to be held accountable for its content.

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Ethics Statement

The study was approved by the ethics committee of "The Ecole Pratique des Hautes Etudes" (Paris Science et Lettres) Institutional Review Board—biomedical research protocol involving experimentation with humans referenced no. 980034BPC. All methods in the study were carried out in accordance with the Helsinki guidelines and declaration or any other relevant guidelines. Additional information regarding these case studies and fulfillment of ethics are provided in Supporting Information.

Consent

For the Cocos Island case studies, we received informed consent for the use of photographs and videos from C. De la Cruz (Dive director of Undersea hunters boat). Informed consent was obtained from all subjects and/or their legal guardian(s) for the publication of identifying information or images in an online open-access publication.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets generated and analyzed during the current study are available in The GENBANK, Bethesda, MD, USA repository at: SUB12912314. Accession number(s) for the six nucleotide sequences are: OQ569456, OQ569457, OQ569458, OQ569459, OQ569460, OQ569461. Other GENBANK reference numbers and primer sequences used for the fingerprinting are available in Table S1.

Conformity of Protocols and Respect for Guidelines

All experimental protocols were approved by Ad Hoc institutions and/or licensing committees (details provided in acknowledgements and Supplementary Information). All methods were carried out in accordance with relevant guidelines and regulations with ARRIVE guidelines (https://arriveguidelines.org), the only interaction with the animals being underwater photographs.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.