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NOTE

Kit-Based Sampling by Trained Fishers Yields Successful DNA Identification of Depredating Shark Species in the Marianas

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Abstract

Shark depredation is a worldwide yet not well understood problem that is responsible for economic losses in both commercial and recreational fisheries. We collaborated with fishers from the Mariana Islands in the western Pacific to identify depredating shark species via mitochondrial DNA (mtDNA) barcoding of partially consumed fish from real-world depredation events. Trained fishers collected swabs from 29 shark depredation events in a line fishery targeting snappers, emperors, and jacks. Results showed that an assemblage of coral reef- and shelf-associated shark species was responsible for catch depredation in this fishery. The successful collection of transfer DNA from depredated fish by trained fishers and a 90% success rate in identifying the depredating shark species via mtDNA barcoding confirm that this approach is a practical tool for improving our understanding of depredation in a wide variety of fisheries. Although identifying the depredating shark species does not solve the problem of shark depredation in fisheries, it is a critical step in better understanding the phenomenon so that potential solutions can be identified.

Shark depredation, in which a shark partially or completely consumes an animal caught by fishing gear before it can be retrieved, is a global issue plaguing both commercial and recreational fisheries (Mitchell et al. 2018). Depredation can result in loss of commercially valuable catch and fishing gear, increased mortality of target fish species, and potential injury or mortality of the depredating species (Gilman et al. 2007; Mitchell et al. 2018). Despite the multiple negative consequences for both small- and large-scale fisheries, studies that specifically identify depredating species, whether sharks or other large predators, are uncommon. From 1955 to 2018, 61 studies highlighted the complexity of the depredation issue, revealing a complex array of causes and consequences of depredation by sharks and other large predators, but few studies characterized the composition of culprit species. These studies found that depredation rates were influenced by spatial, temporal, and environmental factors as well as fishing method (Mitchell et al. 2018). As depredation rates alter across environmental gradients, solutions must be tailored to the specific species that are responsible for shark depredation in a given area. This makes the identification of culprit species in shark depredation essential for developing strategic solutions.

Shark depredation is more prevalent in tropical zones than in subtropical or temperate zones (Sivasubramaniam 1964; IOTC 2007; Romanov et al. 2013) and is a persistent problem in the Mariana Islands (including Guam and the Commonwealth of the Northern Mariana Islands [CNMI]) in the western Pacific Ocean, but to date there has been no formal study of the phenomenon in this region. Trolling and bottom fishing are the two most popular small-boat fisheries in the Mariana Islands (Myers 1993; Dalzell et al. 1996; Ayers 2018). These fisheries are important to the local communities as a source of fresh food and basic income, and they play an integral part in the islands' traditional and modern cultures (Amesbury et al. 1986; Ayers 2018; Chan and Pan 2019). The average profit margin per fishing trip in the Mariana Islands ranges from US$17 to $220 (Chan and Pan 2019), so even

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a small number of depredation losses is economically significant to fishers. Shark depredation has been a concern for both fishing methods in the area since 2004 (WPRFMC 2004). In 2006, some fishers reported losing up to 60% of their catch to shark depredation, and by 2013, reports cited a significant increase in fish loss due to depredation and more aggressive shark behavior during fishing activities (WPRFMC 2006, 2013). The occurrences of these depredation events only increased, and in 2015, 55% of fishers interviewed by the Western Pacific Regional Fishery Management Council reported shark interactions (WPRFMC 2016).

Anecdotal observations and reported shark landings in the Mariana Islands suggest that depredation in troll fisheries targeting pelagic fishes may be due to the Silky Shark *Carcharhinus falciformis*, Galapagos Shark *C. galapagensis*, and Oceanic Whitetip Shark *C. longimanus*. The culprit shark species responsible for depredation in fisheries targeting bottom fish are thought to include the Tiger Shark *Galeocerdo cuvier*, Blacktip Shark *C. limbatus*, and Whitetip Reef Shark *Triaenodon obesus* (Langseth et al. 2019). Despite these anecdotal reports, considerable uncertainty remains about the shark species involved in depredation, as most events occur at depth and are not directly observed. Even when witnessed, sharks can be difficult to visually identify due to the relatively subtle differences in morphological characteristics among species (Campagno 1984).

Recent proof-of-concept studies have used transfer DNA to definitively identify depredating shark species via mitochondrial DNA (mtDNA) bar coding (Drymon et al. 2019; Fotedar et al. 2019). The epithelium of sharks is covered by a thin mucous layer known to contain their DNA (Lieber et al. 2013). When sharks bite their prey, some of this mucus is transferred to the prey and can be collected by swabbing the damaged catch for DNA analysis and identification. Previous studies that identified depredating species via transfer DNA used recreational fishing methods (Drymon et al. 2019) or utilized experienced scientific staff to collect samples (Fotedar et al. 2019). Using the baseline methodologies provided by these studies, we developed easy-to-use swab kits for collection of transfer DNA from shark-damaged fish. We trained volunteer fishers in Guam and Saipan to use these kits in order to characterize shark depredation interactions with the local fisheries. Our goals were to (1) provide the first insight into the shark species responsible for catch depredation in the Mariana Islands and (2) demonstrate that kit-based field sampling of shark transfer DNA from depredated catches can be successfully accomplished by fishers with minimal training.

METHODS

Sample collection.— Volunteer fishers were recruited and trained to use DNA swab kits at workshops held in Guam and Saipan during January 2020. The DNA swab kits included sterile swabs, nitrile gloves, storage vials containing DNA extraction buffer (which doubles as a preservative; see next section), scissors, written instructions, a data sheet for recording depredation metadata, and a link to a YouTube training video (Figure 1). The bitten fish were recovered, and the bite margins were thoroughly swabbed with sterile swabs to collect shark transfer DNA (three replicates per fish; Fotedar et al. 2019). The tips of the swabs were carefully cut off and stored in vials containing DNA lysis buffer (Qiagen ATL Buffer; Kraft et al. 2021). Between February and August 2020, volunteer fishers collected swab samples from depredated fish. Sample vials were placed on ice for the remainder of fishing trips and were then stored frozen until they were shipped to the Hawai'i Institute of Marine Biology (University of Hawai'i at Mānoa) for analysis. The DNA swab sampling activities were conducted under the University of Hawai'i Institutional Animal Care and Use Committee Protocol 19-3168 and CNMI Scientific Research License SRC21-05-RE.

Extraction and sequencing of DNA.— Extraction and amplification of DNA was carried out at the Hawai'i Institute of Marine Biology. Extraction of DNA used the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Mississauga, Ontario), with some minor changes to the manufacturer's protocol for tissue specimens. One-third of the swab tip along with 360 µL of the associated lysis buffer from the collection tube (Buffer ATL) and 40 µL of proteinase K (enzyme number 3.4.21.64; IUBMB 1992) were used in an initial digestion of 2 h (rather than overnight as specified by the Qiagen protocol). Double volumes of each

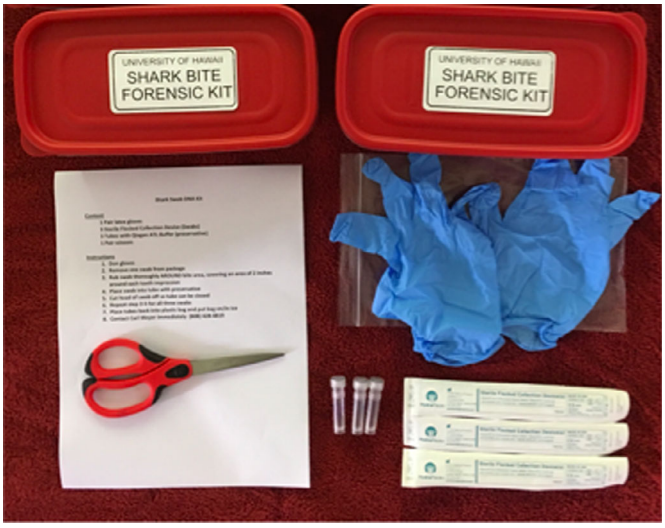

FIGURE 1. Kits that were prepared and delivered to fishers for DNA collection from depredation events.

reagent were used until all of the digested sample was transferred through the filter column.

Polymerase chain reactions were used to amplify DNA via shark-specific primers targeting the cytochrome c oxidase subunit 1 (COI) region of the mitochondrial genome. The shark-specific primers COIshark25F (5'-AGC AGG TAT AGT TGG AAC AGC CC-3') and COIshark315R (5'-GCT CCA GCT TCT ACT CCA GC-3'; Fotedar et al. 2019) amplified shark DNA from a wide variety of shark species without coamplifying the contaminating DNA from depredated fish. Polymerase chain reactions included 8.6 μL of ultrapure water, 10 μL of GoTaq Green Master Mix (Promega Corporation, Madison, Wisconsin), 0.2 μL of each primer (10 μM), and 1 μL of template DNA for a total reaction volume of 20 μL. Amplification used a T100 Thermal Cycler (Bio-Rad Laboratories, Inc., Hercules, California) with an initial denaturation at 95°C for 3 min, followed by 35 cycles of 95°C for 30 s, annealing at 62°C for 45 s, and 72°C for 1 min and a final extension at 72°C for 5 min. The PCR products were examined using 1% agarose gel stained with GelRed, and samples that failed to amplify were retested. Samples that appeared in gel images with distinct bands were purified using ExoFap (exonuclease I, FastAP; Life Technologies, Carlsbad, California). For sequencing preparations, 5 μL of ExoFap product were mixed with 1 μL of either forward or reverse primer (3.2 μM). These purified PCR products were shipped to Genewiz, Inc. (South Plainfield, New Jersey) for sequencing using Applied Biosystems BigDye version 3.1 and an Applied Biosystems 3730xl DNA Analyzer (Applied Biosystems, Foster City, California).

Sequence data were processed in Geneious version 10.0.9 (Kearse et al. 2012). Sequences were trimmed at an error rate probability of 0.05, and forward and reverse sequences were assembled and edited by eye. Sequences from replicate DNA swabs were also aligned to parse out the outlier replicates that may have been contaminated. Assembled sequences were exported as a fasta file and sent through the Basic Local Alignment Search Tool (BLASTn) from GenBank (Altschul et al. 1990).

RESULTS

Swab samples were collected from a total of 29 shark depredation events in waters of Guam and Saipan. Metadata were only supplied for 22 of these events as one fisher's data sheet was lost in shipping, but we include these samples because they still inform the species composition of depredating sharks even without knowledge of the depredated catch species. All samples for which metadata were provided were collected during bottom fish fishing trips, with 17 samples collected by two Guam-based fishers and the remaining 5 samples collected by one Saipan-based fisher. Depredated fishes included Dogtooth Tuna *Gymnosarda unicolor* and several snapper and jack species. Barcoding analyses successfully identified the shark species involved in 26 of the 29 depredation events (~90%). Five depredating shark species were identified from DNA swabs: Silvertip Shark *Carcharhinus albimarginatus*, Silky Shark, Grey Reef Shark *C. amblyrhynchos*, Whitetip Reef Shark, and Tiger Shark (Table 1).

DISCUSSION

We obtained the first definitive identification of the unseen shark species that were responsible for depredating bottom fish catches off Guam and Saipan, and we confirmed that kit-based swab sampling is a viable collection method for downstream mtDNA barcoding analysis. The depredating shark species identified are representative of the coastal shark assemblage in the Marianas Archipelago (Compagno 1984; Compagno and Niem 1998). Three of the five species identified (Silvertip, Grey Reef, and Whitetip Reef sharks) are strongly reef associated (Last and Stevens 1994), while the remaining two species (Silky and Tiger sharks) are found in shelf habitats and drop-off zones (Compagno 1984; Compagno and Niem 1998; Meyer et al. 2018). Both groups (reef and drop-off shark assemblages) are likely to co-occur with fishery target species in the same habitats.

Sharks are known to be particularly attracted to erratic low-frequency sounds of the kind produced by struggling fish (Nelson and Gruber 1963; Nelson 1967; Myrberg et al. 1969, 1972; Nelson and Johnson 1972; Corwin 1981; Myrberg 2001; Chapuis 2017) and will opportunistically prey on injured fish. As hooked fish often mimic the behavior of injured prey, it is logical that sharks will similarly prey on hooked fish (Mitchell et al. 2018). Reef-associated sharks also often exhibit site fidelity (e.g., Bond et al. 2012; Vianna et al. 2013; Pillans et al. 2021), so if fishers repeatedly fish the same locations, resident sharks may learn to associate fishing vessels with foraging opportunities through positive reinforcement from depredating catches (Nelson and Johnson 1972; Lieberman 1990; Labinjoh 2014). This pattern could explain the increase in depredation incidents and shark boldness over time, as reported by the Mariana Islands' fishers.

Previous proof-of-concept studies evaluating DNA bar coding of depredated fishes relied on researchers to swab the depredated target species (Drymon et al. 2019; Fotedar et al. 2019), whereas we demonstrate that volunteer fishers with minimal training can collect viable transfer DNA from depredated fishes. Our success suggests that a kit-based approach could be easily used in other fisheries where shark depredation occurs (e.g., high-seas longline fisheries) to more fully characterize depredating species and improve understanding of indirect and unaccounted mortality resulting from predation associated with

TABLE 1. Summary of shark depredation events and depredating shark species that were successfully identified through DNA bar coding. Superscript numbers next to shark species names indicate the number of swab replicates per bite (3 for events 1–22; 1 replicate for events 23–29 due to lost metadata) that yielded viable transfer DNA and an over 98% homologous match with GenBank species references.

Event	Date	Damaged species	Depredating species
1	Apr 19, 2020	Redgill Emperor *Lethrinus rubrioperculatus*	Inconclusive
2	Apr 19, 2020	Redgill Emperor	Silvertip Shark[3]
3	Apr 19, 2020	Redgill Emperor	Grey Reef Shark[3]
4	Aug 15, 2020	Dogtooth Tuna	Silvertip Shark[3]
5	Aug 15, 2020	Dogtooth Tuna	Silvertip Shark[3]
6	Aug 15, 2020	Amberjack *Seriola* sp.	Grey Reef Shark[1]
7	Apr 13, 2020	Onaga *Etelis coruscans*	Silvertip Shark[1]
8	May 28, 2020	Common Bluestripe Snapper *Lutjanus kasmira*	Whitetip Reef Shark[3]
9	Jun 18, 2020	Onaga	Whitetip Reef Shark[3]
10	Apr 8, 2020	Onaga	Inconclusive
11	Mar 9, 2020	Trevally *Caranx* sp.	Silvertip Shark[1]
12	Jun 6, 2020	Onaga	Silvertip Shark[2]
13	Jun 6, 2020	Onaga	Silvertip Shark[1]
14	May 23, 2020	Onaga	Silvertip Shark[1]
15	May 9, 2020	Onaga	Silvertip Shark[3]
16	May 16, 2020	Onaga	Silvertip Shark[3]
17	Feb 8, 2020	Onaga	Silvertip Shark[2]
18	Apr 11, 2020	Deepwater Red Snapper *Etelis carbunculus*	Silvertip Shark[1]
19	Jul 21, 2020	Pale Snapper *Etelis radiosus*	Silvertip Shark[1]
20	Jul 25, 2020	Chum bag	Tiger Shark[1]
21	Aug 15, 2020	Dogtooth Tuna	Silky Shark[2]
22	Aug 29, 2020	Onaga	Silky Shark[2]
23	N/A	N/A	Inconclusive
24	N/A	N/A	Tiger Shark[1]
25	N/A	N/A	Tiger Shark[1]
26	N/A	N/A	Tiger Shark[1]
27	N/A	N/A	Silky Shark[1]
28	N/A	N/A	Silky Shark[1]
29	N/A	N/A	Silky Shark[1]

commercial and recreational fishers. Although sequencing costs remain, the kit-based approach reduces the field sampling costs by removing the need for specialized personnel to collect samples. By partnering with fishers from local communities and on-the-ground stakeholders, we can broaden our scope of understanding of the issue and build relationships with fishery communities, likely leading to more equitable and viable solutions for dealing with shark depredation.

Future work should focus on expanding the use of this kit-based DNA bar coding approach to increase our baseline understanding of depredating species across a wider range of fisheries. Identifying the species responsible for depredation is an important step toward developing potential solutions to reduce depredation. For example, known depredating species can be targeted for telemetry studies to understand their use of fishing grounds. These types of studies can reveal the times, locations, or environmental triggers that predict low or high catch depredation rates, which may then be exploited by fishers to passively reduce depredation (Mitchell et al. 2018). A more ambitious goal is to develop devices that actively deter sharks from depredating catches. Devices that target sharks' highly sensitive electroreceptive system could be used to deter sharks but with no impact on fishery target species, as the latter (e.g., teleost fishes) lack this sensory system. Because the sensitivity of electroreceptive systems varies among shark species (Mitchell et al. 2018), identification of the depredating species will be important for developing effective active deterrents.

Conclusion

Shark depredation in fisheries is a widespread problem, and identifying the depredating shark species is a major knowledge gap that hinders mitigation of the issue. The successful collection of transfer DNA from depredated fishes

by trained fishers in tandem with our 90% positive identification rate of culprit species demonstrates that our approach can be a practical tool for better understanding depredation in a wide variety of fisheries. Although the identification of depredating species does not automatically solve the problem, it is a critical step to better understanding the phenomenon so that potential solutions can be found. Working with local stakeholders shows great promise as an inclusive and productive means for gathering data to improve our knowledge of depredation in local fisheries.

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REFERENCES

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. Basic local alignment search tool. Journal of Molecular Biology 215:403–410.

Amesbury, S. S., F. A. Cushing, and R. K. Sakamoto. 1986. Guide to the coastal resources of Guam: fishing on Guam, volume 3. University of Guam Press, Mangilao.

Ayers, A. L. 2018. The Commonwealth of the Northern Mariana Islands fishing community profile: 2017 update. NOAA Technical Memorandum NMFS-PIFSC-66.

Bond, M. E., E. A. Babcock, E. K. Pikitch, D. L. Abercrombie, N. F. Lamb, and D. D. Chapman. 2012. Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. PLOS (Public Library of Science) ONE [online serial] 7(3):e32983.

Chan, H., and M. Pan. 2019. Tracking economic performance indicators for small boat fisheries in American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands. NOAA Technical Memorandum NMFS-PIFSC-79.

Chapuis, L. 2017. The acoustic world of sharks. Doctoral dissertation. University of Western Australia, Perth.

Compagno, L. J. V. 1984. Sharks of the world: an annotated and illustrated catalogue of shark species known to date, part 2: Carcharhiniformes. FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 125.

Compagno, L. J. V., and V. H. Niem. 1998. Requiem sharks. Pages 1312–1360 *in* K. E. Carpenter and V. H. Niem, editors. The living marine resources of the western central Pacific, volume 2: cephalopods, crustaceans, holothurians and sharks. Food and Agriculture Organization of the United Nations, Rome.

Corwin, J. T. 1981. Audition in elasmobranchs. Pages 81–105 *in* W. N. Tavolga, A. N. Popper, and R. R. Fay, editors. Hearing and sound communication in fishes. Springer, New York.

Dalzell, P., T. J. H. Adams, and N. V. C. Polunin. 1996. Coastal fisheries in the Pacific Islands. Oceanography and Marine Biology: an Annual Review 33:395–531.

Drymon, J. M., P. T. Cooper, S. P. Powers, M. M. Miller, S. Magnuson, E. Krell, and C. Bird. 2019. Genetic identification of species responsible for depredation in commercial and recreational fisheries. North American Journal of Fisheries Management 39:524–534.

Fotedar, S., S. Lukehurst, G. Jackson, and M. Snow. 2019. Molecular tools for identification of shark species involved in depredation incidents in Western Australian fisheries. PLOS (Public Library of Science) ONE [online serial] 14:e0210500.

Gilman, E., S. Clarke, N. Brothers, J. Alfaro-Shigueto, J. Mandelman, J. Mangel, S. Petersen, S. Piovano, N. Thomson, P. Dalzell, M. Donoso, M. Goren, and T. Werner. 2007. Shark depredation and unwanted bycatch in pelagic longline fisheries: industry practices and attitudes, and shark avoidance strategies. Western Pacific Regional Fishery Management Council, Honolulu, Hawaii.

IOTC (Indian Ocean Tuna Commission). 2007. Workshop on the depredation in the tuna longline fisheries in the Indian Ocean. IOTC, Victoria, Seychelles.

IUBMB (International Union of Biochemistry and Molecular Biology). 1992. Enzyme nomenclature 1992. Academic Press, San Diego, California.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647–1649.

Kraft, D. W., M. K. Webb, L. Meyer, K. Scidmore-Rossing, E. Clua, C. Huveneers, and C. Meyer. 2021. Development and successful real-world use of transfer DNA techniques to identify species involved in shark bite incidents. Journal of Forensic Science 66:2438–2443.

Labinjoh, L. 2014. Rates of shark depredation of line-caught fish on the Protea Banks, KwaZulu-Natal. Master's thesis. University of Cape Town, Cape Town, South Africa.

Langseth, B., J. Syslo, A. Yau, and F. Carvalho. 2019. Stock assessments of the bottomfish management unit species of Guam, the Commonwealth of the Northern Mariana Islands, and American Samoa, 2019. NOAA Technical Memorandum NMFS-PIFSC-86.

Last, P., and J. Stevens. 1994. Sharks and rays of Australia, 2nd edition. Commonwealth Scientific and Industrial Research Organisation, East Melbourne, Victoria, Australia.

Lieber, L., S. Berrow, E. Johnston, G. Hall, J. Hall, C. Gubili, D. W. Sims, C. S. Jones, and L. R. Noble. 2013. Mucus: aiding elasmobranch conservation through non-invasive genetic sampling. Endangered Species Research 21:215–222.

Lieberman, D. 1990. Learning: behaviour and cognition. Wadsworth, Belmont, California.

Meyer, C. G., J. M. Anderson, D. M. Coffey, M. R. Hutchinson, M. A. Royer, and K. N. Holland. 2018. Habitat geography around Hawaii's oceanic islands influences Tiger Shark (*Galeocerdo cuvier*) spatial behaviour and shark bite risk at ocean recreation sites. Scientific Reports 8:article 4945.

Mitchell, J. D., D. L. McLean, S. P. Collin, and T. J. Langlois. 2018. Shark depredation in commercial and recreational fisheries. Reviews in Fish Biology and Fisheries 28:715–748.

Myers, R. F. 1993. Guam's small-boat-based fisheries. Marine Fisheries Review 55:117–128.

Myrberg, A. A. 2001. The acoustical biology of elasmobranchs. Pages 31–46 *in* T. C. Tricas and S. H. Gruber, editors. The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson. Springer, Dordrecht, The Netherlands.

Myrberg, A. A., A. Banner, and J. D. Richard. 1969. Shark attraction using a video-acoustic system. Marine Biology 2:264–276.

Myrberg, A., J. Ha, W. Alewski, and J. C. Banbury. 1972. Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bulletin of Marine Science 22:926–949.

Nelson, D. R. 1967. Hearing thresholds, frequency discrimination, and acoustic orientation in the Lemon Shark, *Negaprion brevirostris* (Poey). Bulletin of Marine Science 17:741–768.

Nelson, D. R., and S. H. Gruber. 1963. Sharks: attraction by low-frequency sounds. Science 142:975–977.

Nelson, D. R., and R. H. Johnson. 1972. Acoustic attraction of Pacific reef sharks: effect of pulse intermittency and variability. Comparative Biochemistry and Physiology Part A: Physiology 42:85–95.

Pillans, R. D., W. Rochester, R. C. Babcock, D. P. Thomson, M. D. E. Haywood, and M. A. Vanderklift. 2021. Long-term acoustic monitoring reveals site fidelity, reproductive migrations, and sex specific differences in habitat use and migratory timing in a large coastal shark (*Negaprion acutidens*). Frontiers in Marine Science 8:616633.

Romanov, E. V., P. S. Sabarros, L. L. Foulgoc, J.-P. Lamoureux, N. Rabearisoa, and P. Bach. 2013. Assessment of depredation level in Reunion Island pelagic longline fishery based on information from self-reporting data collection programme. Indian Ocean Tuna Commission, Victoria, Seychelles.

Sivasubramaniam, K. 1964. Predation of tuna longline catches in the Indian Ocean by killer-whales and sharks. Bulletin of the Fisheries Research Station, Ceylon 17:221–236.

Vianna, G. M. S., M. G. Meekan, J. J. Meeuwig, and C. W. Speed. 2013. Environmental influences on patterns of vertical movement and site fidelity of Grey Reef Sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. PLOS (Public Library of Science) ONE [online serial] 8:e60331.

WPRFMC (Western Pacific Regional Fishery Management Council). 2004. Minutes of the 123rd council meeting. WPRFMC, Honolulu, Hawaii.

WPRFMC (Western Pacific Regional Fishery Management Council). 2006. Minutes of the 135th council meeting. WPRFMC, Honolulu, Hawaii.

WPRFMC (Western Pacific Regional Fishery Management Council). 2013. Minutes of the 158th council meeting. WPRFMC, Honolulu, Hawaii.

WPRFMC (Western Pacific Regional Fishery Management Council). 2016. Minutes of the 166th council meeting. WPRFMC, Honolulu, Hawaii.