Scott *et al. Animal Biotelemetry (2023) 11:34*
https://doi.org/10.1186/s40317-023-00346-x

Animal Biotelemetry

CASE REPORT

Open Access

Time of death: behavioral responses of an oceanic whitetip shark, *Carcharhinus longimanus*, to capture by a longline fishing vessel

Molly Scott[1,2,4*], Mark Royer[1] and Melanie Hutchinson[1,3,4]

Abstract

Background Bycatch mortality in longline fisheries is a major contributor to global declines in shark populations. The duration of time that an animal is hooked and the impacts of hooking on behavior affect the likelihood of mortality. However, limited information exists on the behavior of sharks to longline capture because of difficulties observing hooking events. Using a fortuitous recovery of an archival satellite tag, we describe the movement of an oceanic whitetip shark (*Carcharhinus longimanus*) and examine the behavior prior to its mortality in response to hooking on a longline.

Results A 1.5 m (fork length) *C.longimanus* was tagged and released in good condition by a fisheries observer following initial capture on a US longline fishing vessel. After release, the shark resumed normal vertical behavior within 5 h. Over 198 days, the shark undertook wide-ranging movements throughout the Pacific between Samoa, Niue, and Tonga. The shark was hooked by a second longline vessel while conducting routine yo-yo diving between 0 and 120 m depth. For the first hour after being hooked the shark exhibited high swimming activity with rapid vertical movements between 20 and 40 m indicative of an initial struggle against the line. After this, the shark struggled at the surface for approximately 5 h, until it succumbed to exhaustion and died on the line.

Conclusion Fight time has a strong influence on the mortality rates of sharks captured in commercial longline fishing operations. Data obtained from this shark offers further understanding of capture behavior and time to mortality on a longline for *C.longimanus* which may assist managers as they work on options to reduce mortality rates for this threatened species.

*Correspondence:
Molly Scott
mscott23@hawaii.edu
[1] Hawai'i Institute of Marine Biology, University of Hawai'i, 46-007 Lilipuna Rd, Kaneohe, Hawaii 96744, USA
[2] International Business Services and Sales, 1110 Bonifant St, Suite 501, Silver Spring, Maryland 20910, USA
[3] Present Address: Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, La Jolla, California 92037, USA
[4] Cooperative Institute for Marine and Atmospheric Research, Pacific Islands Fisheries Science Center NOAA-IRC, 1845 Wasp Blvd. Bldg 176, Honolulu, Hawaii 96818, USA

Background

Understanding the behavioral and physiological responses of threatened species (e.g., elasmobranchs) to fisheries capture is crucial for reducing fishing related mortality. Mounting evidence indicates that resilience to injury and mortality following capture is species-specific, and dependent upon capture method, capture duration, capture behavior, and the underlying physiology of the species [1–3]. Nevertheless, our capacity to develop measures to reduce fishing-related mortality is hampered by difficulties of monitoring changes in animal behavior and physiology while captured, and a limited understanding of the specific timepoints at which detrimental changes occur during the fishing process [4].

The oceanic whitetip shark (*Carcharhinus longimanus*, hereafter OCS) is an epipelagic, highly migratory species distributed throughout the world's tropical and subtropical waters. Once thought to be the most numerically abundant shark species in tropical waters [5, 6], OCS populations have experienced significant declines throughout their range over the last several decades due to increased fishing pressure and high demand in the international shark fin trade [7–9]. OCS are commonly caught in tropical tuna purse seine fisheries, hook and line fisheries, troll fisheries and pelagic and bottom trawls [10], yet the largest source of mortality of OCS is bycatch-related mortality in commercial longline fisheries [8, 11]. Following precipitous population declines, OCS was listed as 'Threatened' under the United States Endangered Species Act (ESA) [12] in 2018, as 'Critically Endangered' globally by the International Union for the Conservation of Nature (IUCN) also in 2018 [7], and under appendix II of the Conventions on the Conservation of Highly Migratory Species and on the International Trade of Endangered Species (CITES) in 2013.

Reducing fishing-related mortality to OCS continues to be a major goal of conservation and fisheries management organizations. Studies show increased survival of OCS with changes to operational and gear configurations and better fisher handling practices [2]. For example, leaving sharks in the water and removing as much trailing gear as possible (i.e. < 2.5 m; [2]), removing shallower hooks in longline sets [14, 15] and reducing soak time of hooks [16] has been shown to substantially increase the likelihood of survival for OCS and other species that are more sensitive to the lethal physiological changes of capture related stress [13]. Observable capture behavior can be used to make inferences on the internal physiology of caught species and provide additional information on methods to reduce mortality for longline caught sharks [16, 17]. However, collection of such data for threatened species is difficult, as is directly observing the sequence of events that determines the likelihood of survival after capture.

Using a recapture of an OCS tagged with an accelerometer, we describe the movements, behavior and body activity prior to its mortality after hooking by a longline fishing vessel in the Pacific Ocean. Specifically, we investigate (i) the overall movements between tagging and recapture, (ii) the fine-scale behavior of an OCS post-hooking, and (iii) the time taken for an OCS to fight against longline fishing gear prior to mortality. This data can be used to inform managers regarding options to reduce hooking mortality.

Methods

A 1.5 m (5ft, fork length) OCS was captured incidentally by a U.S.flagged, American Samoa (AS) permitted tuna longline vessel on 1 May 2018 (Fig. 1). AS permitted tuna vessels target albacore tuna (*Thunnus alalunga*) using deep-set longline fishing gear which includes; ~ 30 hooks per float; ~ 20 m long float lines; ~ 20 m long monofilament branchlines; and stainless steel circle hooks. A trained fisheries observer was onboard the vessel tagging sharks for a post release survival study. The shark was determined to be alive and in good condition, so the observer deployed a Pop-off Archival Tag (miniPAT, Wildlife Computers, Redmond, WA, USA) externally, anchoring the tether of the tag under the shark's dorsal musculature using a telescoping tagging pole. The miniPAT collected and stored temperature, depth, irradiance and tri-axial acceleration (*x*-axis, *y*-axis, *z*-axis, ranging from −2 to 2 G at 0.05 G resolution) time series data at a sampling rate of 5 s (0.2 Hz). The shark was released after tagging by cutting the branchline and it swam away in 'good' condition (see Hutchinson et al. [2] for condition descriptions) with a circle hook and approximately 1 m of monofilament trailing gear. Tagging took approximately 3 min from the shark being brought alongside the vessel to release.

The same shark was recaptured south of Tonga by a Tongan commercial longliner, 198 days after initial tagging and release on 12 November 2018 (Fig. 1). The vessel was targeting bigeye tuna with a configuration including; 10 hooks set between floats; 20 m long float lines; 20 m long monofilament branchlines with lightsticks; and stainless steel circle hooks (Fig. 2). The mainline was set at 22:10 UTC for a targeted soak time of 12 h. The shark was reported to be dead on the line when the gear was retrieved and it was brought to the vessel where the tag was removed from the shark and stowed on board.

Data analysis

Location estimates were generated using the tag manufacturer's geolocation processing software WC-GPE3 (Wildlife Computers). GPE3 uses a gridded hidden Markov model with 0.25° by 0.25° grid spacing and the maximum likelihood location estimates are interpolated to a 0.025 by 0.025 grid spacing and smoothed with a cubic spline. The resultant maximum likelihood locations and probability surfaces were analyzed and visualized via the RchivalTag package in R [19]. Additionally, depth time series data were used to identify and analyze characteristic dive patterns to assess; (i) time to recovery after the initial capture and tagging event, and (ii) the shark's vertical profile and hooking behavior.

The acceleration sampling interval (0.2 Hz) was too low to filter the static (tag orientation) and dynamic

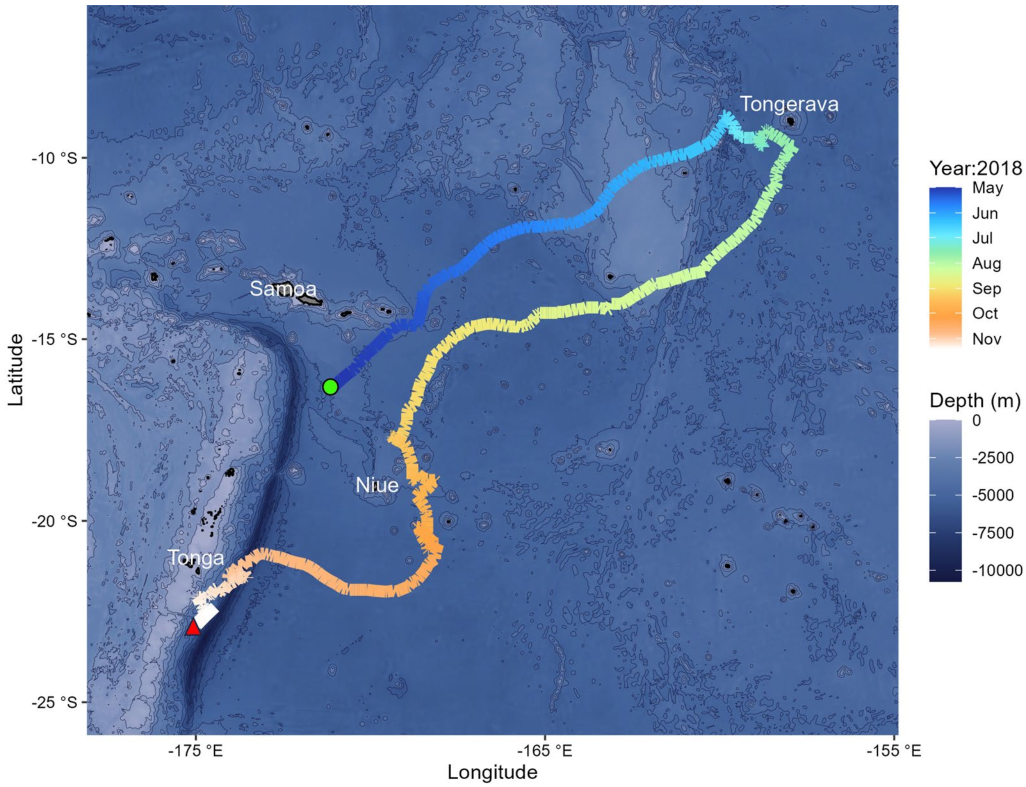

Fig. 1 A bathymetric map showing the maximum likelihood locations of the tagged OCS across the deployment period May–November 2018. Green circle indicates where the tag was deployed on 1 May 2018 and the red triangle indicates where the individual was re-captured and subsequently died on 12 November 2018

(tag movement) components from the raw acceleration. Therefore, standard acceleration metrics for body activity (overall dynamic body acceleration (ODBA) and tailbeat acceleration or cycle) could not be estimated. Rather, we conducted a qualitative examination of the tri-axial acceleration coupled with the depth recordings to estimate the hooking and mortality events. The z-axis measured acceleration along the vertical axis of the tag (from the antenna to the base pin attached to the tether) and was used as a general indicator of the shark's body orientation where recorded z-axis values of −1 G indicate the tag was static and in a vertical orientation with the antenna pointing towards the surface. All dates and times are reported in UTC for consistency because of the location of the tag deployment and recovery which crossed the international date line (Fig. 1).

Results

The OCS of unknown sex was tagged and released by an American Samoa permitted longline vessel due south of Samoa (Fig. 1) on May 1st, 2018 at 07:43 UTC. Immediately after tagging, the shark gradually swam down from the surface to 110 m over 41 min and began conducting narrow, irregular vertical movements between 110 and 140 m (Fig. 3). This erratic 'recovery' behavior lasted approximately 5 h (until 12:43 UTC), before the shark transitioned to normal "yo–yo" diving, moving from the top 20 m to 120 −140 m in an oscillatory manner (Fig. 3). Once normal swimming behavior resumed, the shark headed northeast towards Tongareva and remained within this region between June and July (Fig. 1). In August 2018, it began moving back in the direction it came and followed the bathymetry of underwater seamounts towards Niue (Fig. 1). In October 2018, the shark headed southwest towards Tonga where it was recaptured by a Tongan longline fishing vessel and died on 12 November 2018 south of Tonga (Figs. 1, 4).

The vertical profile and body acceleration of the shark was quantified across an 18-h period during capture on 12–13 November 2018 (Fig. 4). Just prior to capture, the shark was undertaking routine 'yo-yo' swimming behavior between 10 and 120 m (time A, Fig. 4) and had normal acceleration amplitude (lower panel, Fig. 4). At approximately 22:50 UTC on 12 November, the ascent phase of the last dive ended abruptly around 40 m where the shark presumably first experienced the tension from the line, (time C, Fig. 4). Based on the configuration of the longline gear (Fig. 2) and the depth records from the

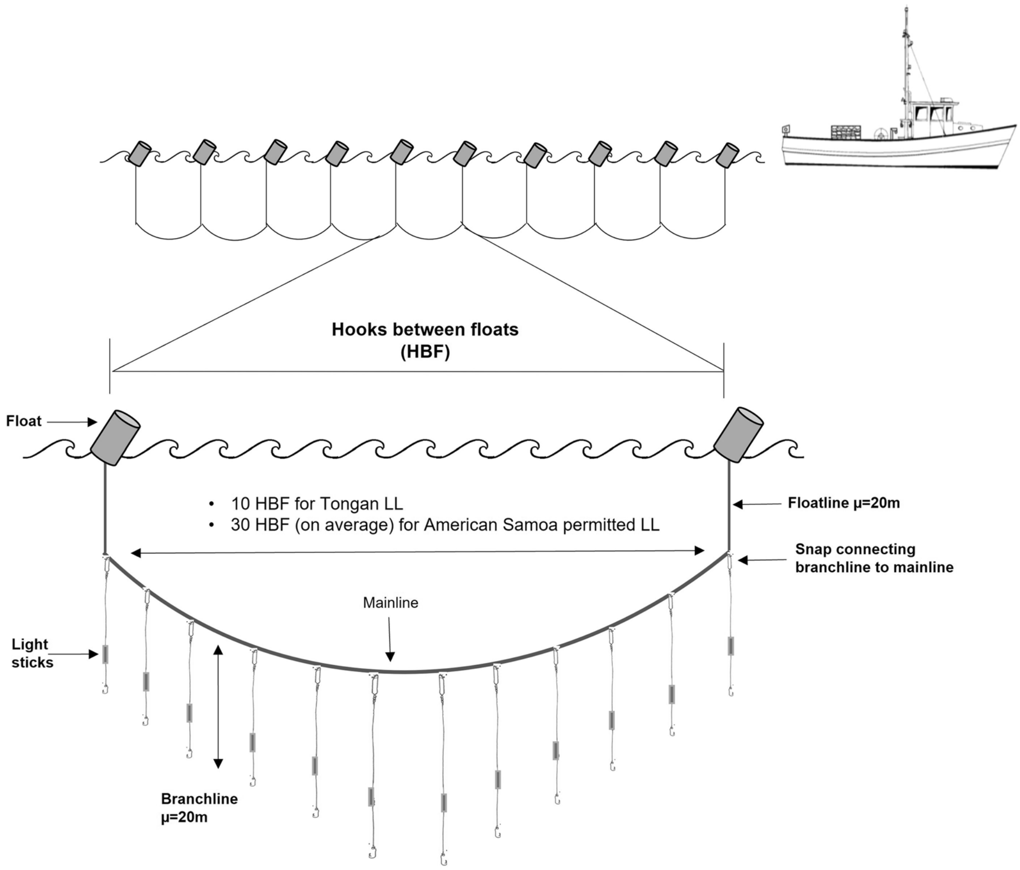

Fig. 2 Schematic representation (not to scale, adapted from [18]) of tropical tuna longline fishing gear configuration. The image shows; length of the floatline; length of the branchline; mainline; hook position; hooks between floats (HBF). Fishers use a set speed and specific distance between hooks that will allow hooks between floats with 20 m lines to fish at depths of ~ 200 m on average [18]

tag, the animal could have become hooked anywhere between 40 and 100 m depth between 22:50 UTC and 22:57 UTC (times B–C, Fig. 4). The animal was able to make its way to the surface post-hooking (across 42 min) and at ~ 30 m, it performed a series of rapid vertical movements between 20 and 60 m (time C, Fig. 4) for an hour. This erratic behavior is also reflected in the wider acceleration amplitude values (lower panel, Fig. 4). The shark moved gradually shallower (times C–D, Fig. 4), and body activity remained high (compared to its normal swimming behavior) while the shark was holding near the surface at 00:12 suggesting that it was likely trying to stay near the surface while struggling against the line and with the weight of the fishing gear (time D, Fig. 4). The shark remained near the surface for approximately 4 h until 04:00 UTC, at which point the vertical profile showed the individual sank to 120 m (times E–F, Fig. 4). The associated low levels of acceleration amplitude between 04:05 and 04:19 (lower panel, Fig. 4) suggests the shark likely died at this point, weighing down the branch line and changing the orientation of the tag, as the shark's negatively buoyant body was hanging vertically from the line while the positively buoyant tag was attempting to orient with the antennae pointing towards the surface (z-axis (red), lower panel, Fig. 4).

At 04:38 (UTC) the shark was hauled towards the surface as the vessel began to retrieve the longline (time F, Fig. 4). At this point, tension from the mainline during the haul kept the shark's body near the surface for a period of 5 h (times G–H, Fig. 4). At 09:44 UTC, the shark was brought onboard where the tag was removed and stored on the vessel (time H, Fig. 4). From these observations, we can infer that the shark struggled against the gear for just under 5 h before dying on the line.

Discussion

Reducing fishing mortality for bycatch species that are subject to no retention measures, such as OCS requires improved knowledge of direct behavioral and physiological responses to capture. In this study, we use body acceleration and depth data to describe the response of an OCS to hooking in longline fishing gear. We show

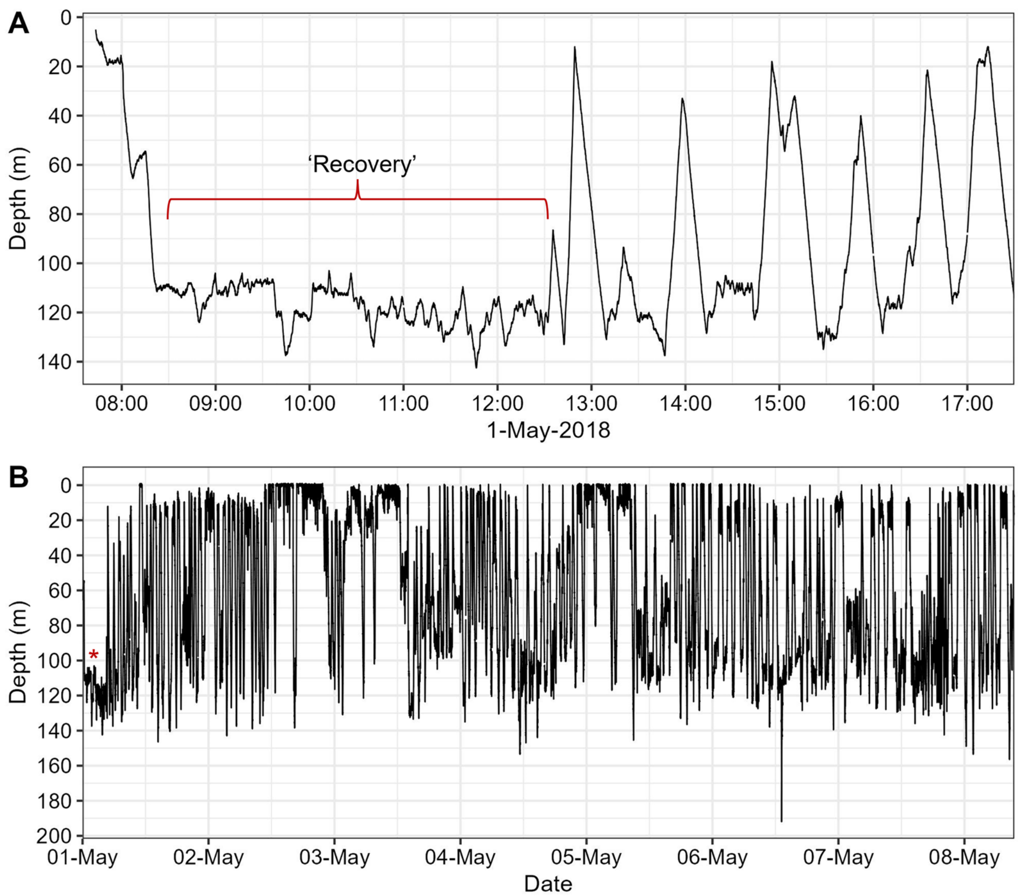

Fig. 3 **A** The depth and recovery profile of the OCS after being tagged and released by a US commercial longline vessel on 1 May 2018. **B** shows the return to regular dive behavior across the first week (1–8 May) after the tagging and recovery event (designated by the red asterisk)

that the individual struggled against the gear for approximately 5 h prior to dying on the line. Although from a single event, this dataset fills important knowledge gaps regarding the resilience of OCS to capture stress which can inform conservation management decisions for mortality mitigation of protected species. While many of the drivers of at-vessel mortality are difficult for fishers to control [16], knowledge of the effects of fishery characteristics (i.e., soak times and gear composition) can help inform the decision making process when accounting for trade-offs in catch versus mortality mitigation of endangered species [20, 21].

OCS populations have undergone precipitous declines globally, and Western Central Pacific Ocean stock assessments have shown the stock is overfished with overfishing still occurring [8, 22]. Because fishing has been identified as the largest source of mortality for OCS, a series of conservation and management measures within all major tuna Regional Fisheries Management Organizations have been adopted. These include measures prohibiting retention of OCS in tropical tuna fisheries world-wide [23–26], and gear modifications such as banning shark lines [27, 28] and a compulsory switch to monofilament (rather than wire) leader material to allow sharks to 'bite-through' the line [26, 29]. While these measures may be effective in reducing overall bycatch mortality [2, 30, 31], many caught individuals may be dead or dying by the time fishing gear is retrieved [15]. At-vessel mortality rates for OCS in US fisheries are relatively high (21.5–32.7%, [2]). Thus, simple fishery modifications such as banning wire leaders to allow bite-offs [2, 18, 29, 31], reducing time spent on a hook [16, 20], and hook depth [14, 15] may be tangible options for reducing fishing mortality rates for OCS and other important bycatch species [16, 32].

Observing the sequence of behaviors before and during longline capture can provide key information on best practices to increase post-release survival rates for bycaught sharks [17]. When it was first hooked on the line, the OCS observed here exhibited initial increases in overall body activity coupled with erratic narrow vertical movements. The capture behavior of this OCS was

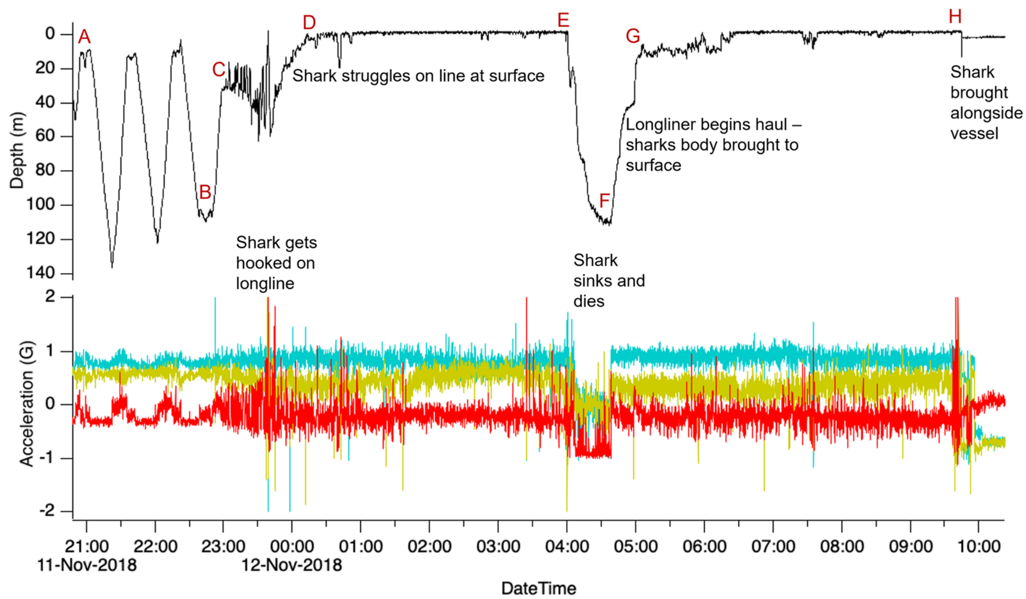

Fig. 4 **A** visual depiction of depth use (upper panel) and tri-axial acceleration (lower panel; teal; *x*-axis, gold; *y*-axis, red; *z*-axis) for the OCS across an 18 h period between 12-Nov-2018 12:10 and 13-Nov-2018 01:30 UTC pre and post hooking. Each letter represents a change in shark behavior across the capture process. Points **A**–**B** show normal yo-yo diving behavior. Near point C the shark likely gets hooked or first experiences tension from the line if it was hooked during the ascent between points (**B**) and (**C**). Between points **C** and **D,** the shark fights actively against the gear and brings it towards the surface. Between points **D** and **E,** the shark struggles on the line at the surface, then gradually sinks (times **E**–**F**) while on the line. The negative value of the *z*-axis acceleration (red) indicates the tag was in an upright orientation, pointed towards the surface. The shark is brought to the surface between points (**F**) and (**G**) due to the tension from the haul of the longliner. Point **H** depicts the shark being handled near the vessel where it was recorded as dead on the line

similar to that documented by [17] that showed hooking and capture initiates an immediate stress response and depending on condition, individuals may respond with high intensity burst swimming to escape and/or force oxygenated water over their gills to maintain ram ventilation [1, 17]. This prolonged exhaustive activity, over the course of 5 h, likely caused irreparable physiological damage leading to the death of the shark [1]. Improved methodologies to reduce capture stress coupled with safe handling and release practices could provide important opportunities to increase post-release survivorship [2]. Additionally, the depth of the hook on which the individual was caught may have influenced its susceptibility to capture. In this study, the OCS was caught on a hook between 40 and 100 m, confirming previous studies of increased catch rates of OCS on shallower hooks < 100 m [14, 33] and on longline vessels targeting swordfish that operate to 100 m [34]. We echo previous studies suggesting that the removal of shallow hooks on longline gear may be an effective mitigation option to reduce OCS bycatch [14, 15, 34].

The 5-hour time to mortality in this study suggests that shorter hook soak times may assist in reducing OCS mortality. However, further sampling is crucial to understand variability in time to mortality across individuals and species (see Additional file 2: Table S1 [4, 35, 36] for more information variability to capture stress across species). In general, OCS are thought to be relatively resilient to capture. OCS caught in pelagic longline gear have demonstrated post-release survival rates of up to 85% (provided they are in good condition at the vessel and trailing gear is minimized [2]), and 23.5% of hooked individuals can survive more than 8 h, with some surviving up to 14 h on the line (Additional file 2: Table S1, [20]. The comparatively short time to mortality in this study may have been influenced by a relatively small body size of 150 cm FL [32, 37], its condition at capture [2, 36], and/ or its recent diving behavior [38, 39]. Although there was no evidence of external injuries, the individual had survived a previous hooking event on a longline 198 days earlier. Further, in the preceding 10 h before capture, the individual made deep-dives to 800 m (5 °C water temperature, Additional file 1:Figure S1) and was captured at 24.5 °C (the lower end of its preferred thermal range [15]). Quick movements into colder waters below the mixed layer are thought to be an important foraging strategy for OCS [32, 40, 41], yet can lead to high energy expenditure [42] and require rapid returns to shallow waters to prevent heat loss [43]. Therefore, the relatively quick mortality in this case may have potentially been induced by a low-energy, and poor or weaker condition state of the hooked individual.

This dataset has identified the 'fight time' to mortality for an individual from a population that has been assessed as overfished with overfishing still occurring [8]. Accurate and effective management to reduce fishing mortality to OCS will require a deeper understanding of the biotic and abiotic drivers of fishery interactions and animal behavior prior to and during capture. The combination of a reduction in hook soak times with the implementation of safe handling and release practices, such as minimizing trailing gear could improve the efficacy of current no-retention measures and thus, assist in the recovery of OCS populations [2, 44].

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-023-00346-x.

Additional file 1: Figure S1. Deep diving behavior and temperature profile of the OCS down to 800 m and approximately 5 ℃ 10 h prior to capture (represented by the black circle).

Additional file 2: Table S1. Comparison of studies carried out under explicit longline fisheries settings that investigate the impact of soak time (as primary variable of interest, defined as the length of time the gear was in the water in hours) and other fishery characteristics on mortality and survival in epipelagic sharks. *Only studies that have been conducted under explicit longline fisheries settings and that have reported a significant effect of soak time have been included. Acronyms: PRM = post-release mortality.

Acknowledgements

The authors would like to thank the NOAA American Samoa Observer Program and Dan Landry for the assistance with the tagging and support for the post release survival research program. We also thank the captain and crew of the American Samoa fishing vessel, America for facilitating the research. We are very grateful to Rosemarie Palu from Atlantis Fisheries and Pacific Sunrise Fishing in the Kingdom of Tonga, and the captain and crew of the fishing vessel Pacific Sunrise for pulling the tag and returning it to us. This work would not have been possible without their help.

Author contributions

MR analyzed the data and MS, MR, MH interpreted the data. MS was a major contributor in writing the manuscript. MH devised, funded and executed the field study. All authors edited, read and approved the final manuscript.

Funding

This project was funded through the 2018 NOAA Bycatch Reduction Engineering Program award number NA18NMF4720282.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from MH following the publication of the larger post release survival study on reasonable request.

Declarations

Ethics approval and consent to participation

All animal procedures were conducted in accordance with the ethical standards set forth by the Institutional Animal Care and Use Committee (IACUC) at University of Hawaii. The IACUC has reviewed and approved the animal protocols for this study (Protocol #15-1630-8, 'Fishing Impacts on Non-Target Species'), and all efforts were made to reduce the number of animals used and minimize animal suffering.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

Received: 12 April 2023 Accepted: 12 September 2023
Published online: 29 September 2023

References

1. Mandelman JW, Skomal GB. The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comp Biochem Physiol A: Mol Integr Physiol. 2012;162(2):146–55.
2. Hutchinson M, Siders Z, Stahl J, Bigelow K. Quantitative estimates of post-release survival rates of sharks captured in Pacific tuna longline fisheries reveal handling and discard practices that improve survivorship. NOAA PIFSC Data Report DR-21-001. 2021.
3. Talwar BS, Bouyoucos IA, Brooks EJ, Brownscombe JW, Suski CD, Cooke SJ, Grubbs RD, Mandelman JW. Variation in behavioural responses of subtropical marine fishes to experimental longline capture. ICES J Mar Sci. 2020;77:2763–75.
4. Ellis JR, McCully Phillips SR, Poisson F. A review of capture and post-release mortality of elasmobranchs. J Fish Biol. 2017;90(3):653–722.
5. Mather FJ, Day CG. Observations of pelagic fishes of the tropical Atlantic. Copeia. 1954;3:179–88.
6. Backus RH, Springer S, Arnold EL Jr. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Res. 1956;3(3):178–88.
7. Rigby CL, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Herman K, Jabado RW, Liu KM, Marshall A, Pacoureau N, Romanov E, Sherley RB, Winker H. *Carcharhinus longimanus*. The IUCN Red List of Threatened Species. 2019; e.T39374A2911619. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39374A2911619.en.
8. Tremblay-Boyer L, Carvalho F, Neubauer P, Pilling G. Stock assessment for oceanic whitetip shark in the Western and Central Pacific Ocean. WCPFC-SC15-2019/SA-WP-06. Report to the WCPFC Scientific Committee. Fifteenth regular session, Pohnpei, Federated States of Micronesia, 12–20 Aug 2018.
9. Young CN, Carlson JK. The biology and conservation status of the oceanic whitetip shark (*Carcharhinus longimanus*) and future directions for recovery. Rev Fish Biol Fisheries. 2020;30(2):293–312.
10. Compagno LJV. Food and Agriculture Organization: Species Catalogue Vol 4. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Parts 1 and 2. FAO Fisheries Synopsis No. 125. FAO, Rome, Italy, 1984; 4: 655.
11. Young CN, Carlson JK, Hutchinson M, Hutt C, Kobayashi D, McCandless CT, Wraith J. Status review report: oceanic whitetip shark (*Carcharhinus longimanus*). Final Report to the National Marine Fisheries Service, Office of Protected Resources. Dec 2017.
12. The Endangered Species Act of 1973 (ESA or "The Act"; 16 U.S.C. § 1531 et seq.)
13. Mandelman JW, Skomal GB. Differential sensitivity to capture stress assessed by blood acid–base status in five carcharhinid sharks. J Comp Physiol B. 2009;179:267–77.
14. Watson JT, Bigelow KA. Trade-offs among catch, bycatch, and landed value in the American Samoa longline fishery. Conserv Biol. 2014;28(4):1012–22.
15. Tolotti MT, Bach P, Hazin F, Travassos P, Dagorn L. Vulnerability of the oceanic whitetip shark to pelagic longline fisheries. PLoS ONE. 2015;10(10): e0141396.
16. Morgan A, Carlson JK. Capture time, size and hooking mortality of bottom longline-caught sharks. Fish Res. 2010;101(1–2):32–7.

17. Knotek RJ, Brooks EJ, Howey LA, Gelsleichter JG, Talwar BS, Winchester MM, Mandelman JW. Merging technologies and supervised classification methods to quantify capture behavior on hook-and-line. J Exp Marine Biol and Ecol. 2022;555:151782. https://doi.org/10.1016/j.jembe.2022.151782.
18. Scott M, Cardona E, Scidmore-Rossing K, Royer M, Stahl J, Hutchinson M. What's the catch? Examining optimal longline fishing gear configurations to minimize negative impacts on non-target species. Mar Policy. 2022;1(143): 105186.
19. Bauer, RK. RchivalTag: Analyzing Archival Tagging Data. R package version 0.1.2 https://cran.r-project.org/web/packages/RchivalTag/RchivalTag.pdf. 2020
20. Poisson F, Gaertner JC, Taquet M, Durbec JP, Bigelow K. Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish. Fish Bull. 2010;108:268–81.
21. Morgan A, Burgess GH. At-vessel fishing mortality for six species of sharks caught in the Northwest Atlantic and Gulf of Mexico. Gulf and Caribbean Research. 2007;19(2):123–9.
22. Rice J, Harley S. Stock assessment of oceanic whitetip sharks in the western and central Pacific Ocean. WCPFC-SC8–2012/SA-WP-06 Rev 1. Report to the Western and Central Pacific Fisheries Commission Scientific Committee. Eighth Regular Session, Busan, Korea, 7–15 August 2012
23. Western and Central Pacific Fisheries Commission (WCPFC). CMM 2011-04; Conservation and management measure for oceanic whitetip shark. Tumon, Guam, USA, 26–30 March 2012.
24. Inter-American Tropical Tuna Commission (IATTC). Resolution C-11–10; Resolution on the conservation of oceanic whitetip sharks caught in association with fisheries in the Antigua convention area. 2011
25. Indian Ocean Tuna Commission (IOTC). Resolution 13/06; On a scientific and management framework on the conservation of shark species caught in association with IOTC managed fisheries. 2013
26. International Commission for the Conservation of Atlantic Tuna (ICCAT). Resolution 10–07; Recommendation by ICCAT in the conservation of oceanic whitetip shark caught in association with fisheries in the ICCAT convention area. 2010
27. Western and Central Pacific Fisheries Commission (WCPFC). CMM 2014-05; Conservation and management measures for sharks: (2) Measures for longline fisheries targeting sharks. Apia, Samoa, 1–5 December 2014.
28. Harley S, Caneco B, Donovan C, Tremblay-Boyer L, Brouwer S. Monte Carlo simulation modelling of possible measures to reduce impacts of longlining on oceanic whitetip and silky sharks. Oceanic Fisheries Programme, Secretariat of the Pacific Community and DMP Statistical Solutions UK Limited. 2015.
29. Western and Central Pacific Fisheries Commission (WCPFC). CMM 2022-04; Conservation and management measures for sharks. Da Nang City, Vietnam, 28 November - 3 December 2022.
30. Musyl MK, Brill R, Curran DS, Fragoso NM, McNaughton L, Nielsen A, Kikkawa BS, Moyes CD. Post-release survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish Bull. 2011;109(4):341.
31. Bigelow K, Carvalho F. Review of potential mitigation measures to reduce fishing-related mortality on silky and oceanic whitetip sharks (Project 101). WCPFC-SC17–2021/EB-WP-01. PIFSC Working Paper WP-22-002. Electronic meeting, 11–19 August 2021.
32. Massey Y, Sabarros PS, Bach P. Drivers of at-vessel mortality of the blue shark (Prionace glauca) and oceanic whitetip shark (*Carcharhinus longimanus*) assessed from monitored pelagic longline experiments. Can J Fish Aquat Sci. 2022;79(9):1407–19.
33. Nakano H, Okazaki M, Okamoto H. Analysis of catch depth by species for tuna longline fishery based on catch by branch lines. Bull Nat Res Inst Far Seas Fish. 1997;34:43–62.
34. Tolotti MT, Travassos P, Frédou FL, Wor C, Andrade HA, Hazin F. Size, distribution and catch rates of the oceanic whitetip shark caught by the Brazilian tuna longline fleet. Fish Res. 2013;143:136–42.
35. Hutchinson M, Lopez J, Wiley B, Pulvenis JF, Altamirano E, & Aires-da-Silva A. Knowledge and research gaps to the implementation of best handling and release practices for vulnerable species. Inter-American Tropical Tuna Commission, Working Group on Ecosystem and Bycatch. Document EB-01-01. 2023; 1–52
36. Musyl MK, Gilman EL. Meta-analysis of post-release fishing mortality in apex predatory pelagic sharks and white marlin. Fish Fish. 2019;20(3):466–500.
37. Diaz GA, Serafy JE. Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release. Fish Bull. 2005;103:720–4.
38. Sims DW. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. J Fish Biol. 2003;63:53–73.
39. Haesemeyer M. Thermoregulation in fish. Mol Cell Endocrinol. 2020;518: 110986.
40. Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LK, Brooks A, Williams S, Gospodarczyk E, Chapman DD. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the western North Atlantic. PLoS ONE. 2013;8(2):e56588.
41. Andrzejaczek S, Gleiss AC, Jordan LK, Pattiaratchi CB, Howey LA, Brooks EJ, Meekan MG. Temperature and the vertical movements of oceanic whitetip sharks, *Carcharhinus longimanus*. Sci Rep. 2018;8(1):8351.
42. Weihs D. Mechanically efficient swimming techniques for fish with negative buoyancy. J Mar Res. 1973;31:194–209.
43. Klimley PA, Beavers SC, Curtis TH, Jorgensen SJ. Movements and swimming behavior of three species of sharks in La Jolla Canyon. California Environ biol fishes. 2002;63:117–35.
44. Francis MP, Lyon WS, Clarke SC, Finucci B, Hutchinson MR, Campana SE, Musyl MK, Schaefer KM, Hoyle SD, Peatman T, Bernal D. Post-release survival of shortfin mako (*Isurus oxyrinchus*) and silky (*Carcharhinus falciformis*) sharks released from pelagic tuna longlines in the Pacific Ocean. Aquat Conserv Mar Freshw Ecosyst. 2023;33(4):366–78.
45. Campana SE, Joyce W, Manning MJ. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. Mar Ecol Prog Ser. 2009;387:241–53.
46. Campana SE, Joyce W, Fowler M, Showell M. Discards, hooking, and post-release mortality of porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), and blue shark (*Prionace glauca*) in the Canadian pelagic longline fishery. ICES J Mar Sci. 2016;73(2):520–8.
47. Gallagher AJ, Orbesen ES, Hammerschlag N, Serafy JE. Vulnerability of oceanic sharks as pelagic longline bycatch. Glob Ecol Conserv. 2014;1:50–9.
48. Gallagher AJ, Serafy JE, Cooke SJ, Hammerschlag N. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar Ecol Prog Ser. 2014;496:207–18.
49. Carruthers EH, Schneider DC, Neilson JD. Estimating the odds of survival and identifying mitigation opportunities for common bycatch in pelagic longline fisheries. Biol Cons. 2009;142(11):2620–30.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.