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RESEARCH ARTICLE

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Post-release survival of shortfin mako (*Isurus oxyrinchus*) and silky (*Carcharhinus falciformis*) sharks released from pelagic tuna longlines in the Pacific Ocean

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Abstract

1. Substantial global population declines in pelagic sharks have led to the introduction of management and conservation measures, including gear restrictions and no-retention policies, to curb declines and encourage stock recovery. As the rate of discarding sharks increases, there is a growing need to understand prognostic factors that influence their post-release survival (PRS) outcomes.
2. PRS was measured with survival pop-up satellite archival tags attached to shortfin mako (*Isurus oxyrinchus*) and silky sharks (*Carcharhinus falciformis*) released or discarded from pelagic tuna longline fishing vessels operating in the Western and Central Pacific Fisheries Commission Convention Area. In total, 117 tags were deployed on 60 mako and 57 silky sharks captured as bycatch during commercial pelagic longline fishing trips in New Zealand ($n = 35$), Fiji ($n = 58$), New Caledonia ($n = 10$) and the Republic of the Marshall Islands ($n = 14$).
3. Mako engaged in long-distance movements between New Zealand, Australia, Fiji and New Caledonia, while silky sharks tagged in the Marshall Islands showed evidence of seasonal movements eastward.
4. PRS was determined for 110 sharks (57 mako, 53 silky sharks). Most tagged sharks of both species were uninjured (89%) at capture and most sharks (88%) survived post-release until tag loss or the programmed pop-up date (60 days). However, when considering a complete fishing interaction (haulback, handling,

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release), PRS estimates were markedly reduced to 48.6% and 52.3% for mako and silky sharks, respectively. For both species, survivorship was greater in large (>150 cm fork length) uninjured sharks and sharks released with low shark length to trailing branchline ratios.

5. While these findings suggest that retention bans offer sharks an increased chance of survival, continued efforts should be made to improve handling and release practices, reduce trailing gear and minimize pelagic shark bycatch.

KEYWORDS

bycatch, fisheries management, fishing mortality best practices, high seas, no retention policy, pelagic shark, RFMO

1 | INTRODUCTION

Sharks are susceptible to capture in commercial pelagic longline fisheries, and make up a large component of the bycatch (Oliver et al., 2015). The shark bycatch has typically been discarded at sea where observer coverage is low (<5%) and post-release survivorship (PRS) is unknown (Gilman et al., 2012; Peatman et al., 2018). Most commonly, discarded or released bycatch are not enumerated, and if they are, there is often no record of their condition (i.e. life status, Oliver et al., 2015; Tremblay-Boyer & Brouwer, 2016). Recent work has shown that even when the condition of released sharks is recorded, these categorical data may not be a reliable predictor of their PRS (Clarke et al., 2014). Accurate reporting of bycatch is further confounded by insufficient or unrepresentative observer coverage on fishing fleets (Debski, Pierre & Knowles, 2016). As a result, there is considerable uncertainty about shark mortality through commercial fishing activities, leading to a lack of clarity in defining and refining shark conservation and management measures (Campana et al., 2016; Davidson, Krawchuk & Dulvy, 2016).

Since 1970, pelagic sharks are estimated to have undergone a 71% decline in global abundance due to an 18-fold increase in relative global fishing pressure (Pacoureau et al., 2021). To curb declines and encourage stock recovery, management bodies have introduced no retention policies, among other conservation and management measures, which are designed to increase the magnitude of discarding (Gilman et al., 2015). Thus, to monitor the efficiency to achieve the management objectives of no retention policies, understanding PRS is becoming increasingly important. There are three main factors generally accepted by the scientific community that affect shark post-release survival rates in pelagic longline fisheries: (i) time spent struggling on the line; (ii) handling methods used to release/remove sharks from fishing gear; and (iii) species-specific resilience as some species are more physiologically sensitive to capture stress than others (Ellis, McCully & Poisson, 2017; Musyl & Gilman, 2019). Studies have identified species most sensitive to capture stress through physiological investigations and quantifying at-vessel mortality rates (for a review of studies see Ellis, McCully & Poisson, 2017). However, the effects of shark handling release methods on survival rates have only recently been explored for commercial longline vessels during typical fishing operations (Musyl & Gilman, 2018; Schaefer et al., 2021).

Here, PRS was measured for shortfin mako (*Isurus oxyrinchus*, herein referred to as mako) and silky sharks (*Carcharhinus falciformis*) released or discarded from select pelagic longline fishery vessels targeting tunas and operating in the Western and Central Pacific Fisheries Commission (WCPFC) Convention Area in the western central Pacific Ocean (WCPO). Sharks were tagged in a manner by which vessels routinely handled sharks during normal fishing operations to reflect realistic outcomes from fishing activities. The effects of handling and release on survival rates were evaluated, with the intention of identifying methods that maximize PRS. Rates of PRS will assist in evaluating the efficacy of currently existing regional conservation and management measures established to reverse pelagic shark declines and encourage stock recovery.

2 | METHODS

2.1 | Tag deployment

Between May 2017 and March 2019, mako and silky sharks were tagged in a phased design across the Exclusive Economic Zones of New Zealand, Fiji, New Caledonia and the Republic of the Marshall Islands (RMI) by trained national fisheries observers and vessel captains aboard commercial pelagic tuna longline fishing vessels operating in the WCPFC Convention Area (Figure 1). Tagging effort for mako was targeted at New Zealand, Fiji and New Caledonia, with Fiji and RMI were targeted for silky shark. The study design aimed to sample the targeted fishing sectors equally for each species (SPC, 2017). Tagging operations occurred between 8.5°N–39.6°S latitude and 161.3°E–179.9°W longitude. Tags were deployed in all months of the year for both species, although peak deployment periods were June–August for mako and July–September for silky sharks (see Supporting Information for full details of tagged sharks and deployment outcomes).

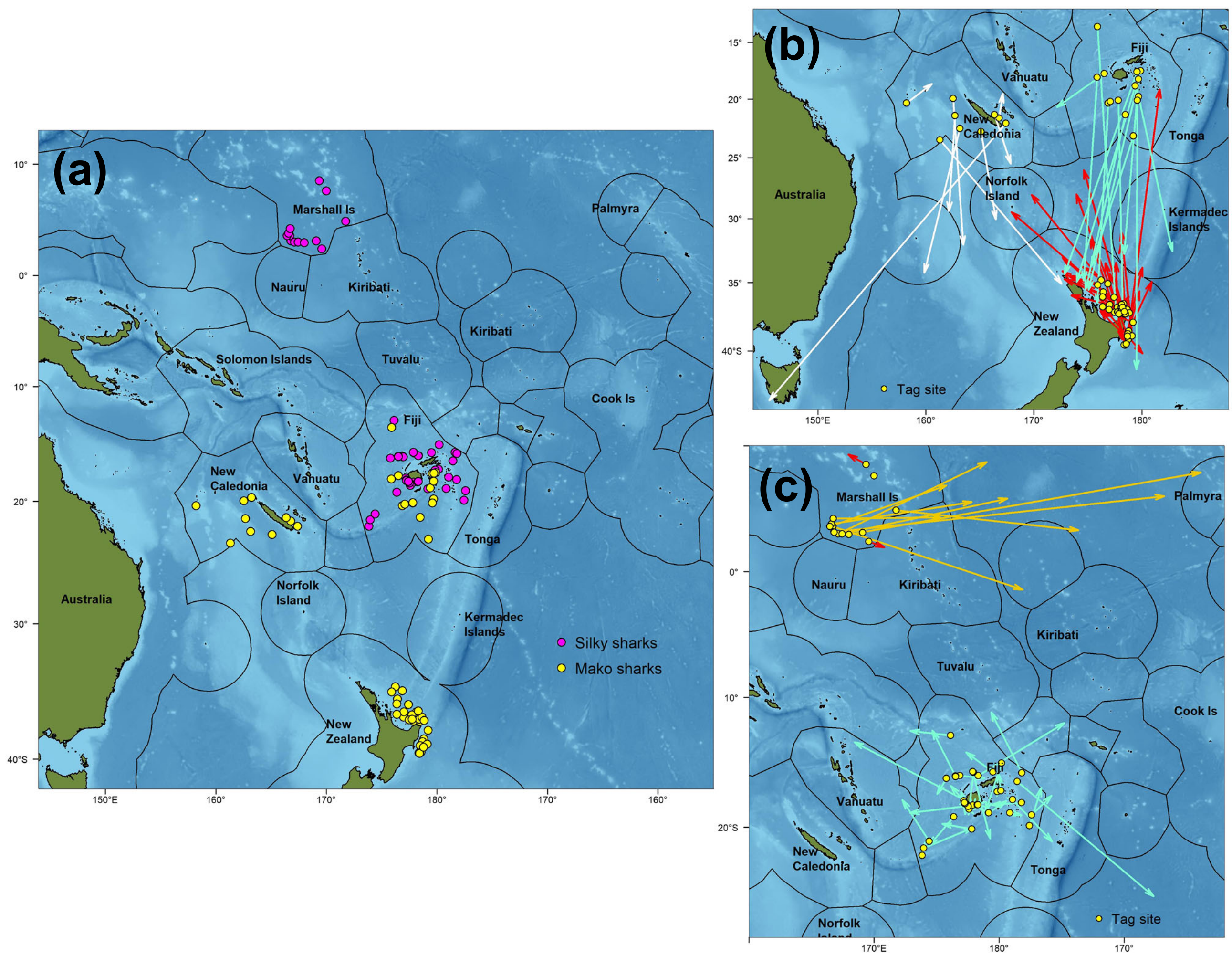

FIGURE 1 (a) Tagging locations of sharks in the Western and Central Pacific Fisheries Commission (WCPFC) Convention Area post-release survival study. Black lines indicate national Exclusive Economic Zone boundaries. (b) Mako movements between tag deployment (circles) and tag pop up (arrow heads). Movements for tags attached in New Zealand (red), Fiji (blue) and New Caledonia (white) are shown. (c) Silky shark movements between tag deployment (circles) and tag pop up (arrow heads). Movements for tags attached in Fiji (blue) and Marshall Islands (orange) are shown.

Sampling protocols replicated commercial fishing conditions for the targeted fishing sectors (e.g. soak time, gear specifications) and sharks were tagged in a manner by which the crew routinely handled sharks during normal longline operations (i.e. on deck if the vessel routinely hauled sharks onboard, or in the water if not). The following details were collected for each shark: length (cm fork length, FL); sex (male, female, unsexed); condition (alive uninjured, AU; alive injured, AI; dead); latitude and longitude at every hour of the set, and at the tagging location (where applicable); hook location (mouth, gills, gut, gullet, other); hook shape and manufacturer code for size; bait type (finfish, squid); leader and branchline material; branchline length (m); and, where applicable, tagging site (in-water or on deck). Sharks were randomly selected for tagging from those greater than ~100 cm natural total length, considered alive and without a clearly fatal injury (e.g. bleeding from a torn or severed gill arch, multiple fins missing, serious damage to eyes or head, broken jaw that will affect its ability to feed, deep wounds with internal organs visible, large amounts of blood loss). Details on the condition of the shark at capture and at release as well as any injuries were recorded (see Supporting Information for condition criteria).

Sharks were tagged with Wildlife Computers (WC) survival pop-up archival tags (sPATs, Survivorship PAT-355E Wildlife Computers, Redmond, WA, USA) or MiniPATs (MiniPAT-348) reprogrammed to report as sPATs. Tags were deployed with custom-made tagging poles (a 3-m telescopic pole for in-water tagging and a 1-m tagging pole for on-deck tagging), and tethered to the shark with a single WC small titanium anchor. Rigged tags (i.e. tag head, tether, crimps) were tested to ensure they were positively buoyant to discriminate a floating tag from a mortality (Musyl & Gilman, 2018). Tags were intended to be inserted into the dorsal musculature near the base of the first dorsal fin. Most sharks (80%, mako = 39, silky = 49) were tagged in the water, 18 mako and two silky sharks were tagged on deck, and the tagging sites of two silky sharks were unknown.

Each tag was programmed to record depth (±0.5 m), temperature (±0.1°C) and light intensity at 10-s intervals for New Zealand-tagged mako and for the last 5 days of deployment for all other sharks for interpretation of the tag/shark's fate, and to detach from the sharks after 60 days at liberty. Minimum and maximum daily depth and temperature values were available for all sharks throughout their deployments except for tags in which the depth sensor failed. Premature tag detachment was initiated in the event that a tag exceeded the critical depth threshold (1,400 m), or when the shark had been lying on the sea bed for 2 days, whichever came first. These events were considered to be post-release mortalities. Data with a premature release, and abrupt temperature increases followed by no contrast in either temperature at variable depths or light intensity through time were assumed to have been ingested by another animal, and were interpreted as indirect mortalities. Tags that detached prematurely, but not on account of exceeding the critical depth threshold or remaining motionless, were not regarded as mortalities because the sharks were alive at the time of detachment. Tags that recorded a continuous depth of 0 m for 48 hours were assumed to represent failure of the attachment system and excluded from survivorship analysis (Hutchinson et al., 2015; Musyl & Gilman, 2018).

2.2 | Post-release survival analysis

A minimum deployment period of 30 days was considered long enough to cover the period of acute (immediate) fishery mortality, determined by an expert workshop hosted at the National Institute of Water and Atmospheric Research (NIWA) in Wellington, New Zealand (SPC, 2017). This period has been shown to account for approximately 90% of pelagic shark mortality outcomes (Musyl & Gilman, 2019). The maximum tag deployment period was then extended to 60 days on behalf of a contribution by WC, and this allowed for assessment of delayed mortality events that may occur after the initial 30-day period (e.g. due to trailing gear, Hutchinson et al., 2021). PRS rates of tagged sharks were estimated by fitting Kaplan–Meier (K-M) survivorship curves (Campana, Joyce & Manning, 2009; Musyl & Gilman, 2018). K-M survivorship tracks the loss of sharks from the tagged population as they die or tags detach through time, and the fitted function can be used to predict the proportion of survivors in the population at any time. K-M models involve two components, a survival component (the time between tagging and the death of each shark known to have died) and a condition component (whether the shark was alive at the last observation of the tag immediately before pop up or tag shedding). The latter component is coded in a 'censor' variable for which live sharks (i.e. right censored) are represented by a zero and dead sharks are represented by a one.

2.3 | Joint regional analysis of PRS

To assess PRS across regions, results from this study were compared with studies using similar methods for the same species (Table 1). For mako, the only appropriate comparative data were from the north-west Atlantic Ocean (Campana et al., 2016) and for silky shark, additional studies included data from Hawaii and American Samoa (Hutchinson, Bigelow & Carvalho, 2019), Palau (Musyl & Gilman, 2018), and Costa Rica and Ecuador (Schaefer et al., 2019).

2.4 | Estimates of mortality and influences on PRS

Estimation of the mortality rate (i.e. 1 − S (survival rate)) at 60 days and the effect of potential predictor variables were calculated with semi-parametric Cox proportional hazards models (Cox, 1972). Variables considered in the models were: species, FL, condition (injured or not), tagging region, tag site (tagged in the water or on deck) and trailing branchline ratio (the ratio between the amount of trailing branchline left on the released shark and its FL). Two variables, sex and hook type, were not considered as the recorded sex was often missing or could not be verified, and hook type showed no contrast, with most sharks being caught on circle hooks. The proportional hazards assumption was tested by examining Schoenfeld residuals and log–log-survival plots (Grambsch &

TABLE 1 Details of tagging studies that were used in the combined analyses

Year	Species	Region	Sample size	Tag type	Max deploy duration	Hook type	Tagging location	Reference
2017–2018	Mako	New Zealand, Fiji, New Caledonia	57	sPAT	60 days	Circle (mainly)	Mostly in water	This study
2011–2013	Mako	North-west Atlantic	27	MK-10 PAT	12 months	Circle (mainly)	50% in water[a]	Campana et al. (2016)
2018–2019	Silky	Fiji, Marshall Islands	53	sPAT	60 days	Circle (mainly)	Mostly in water	This study
2016–2018	Silky	American Samoa	29	sPAT	30 days	Circle	Mostly in water	Hutchinson, Bigelow & Carvalho (2019)
2016–2017	Silky	Ecuador, Costa Rica	38	Mini PAT	180 days	Circle (mainly)	All on deck	Schaefer et al. (2019)
2016	Silky	Palau	35	sPAT	30 days	Circle	All on deck	Musyl & Gilman (2018)

[a]location unknown ($n = 4$).

Therneau, 1994). Initial results showed that condition and trailing branchline ratio were time-dependent (i.e. the proportional hazards assumption was violated, Figure S2) so an additional analysis was completed where these variables were refitted with a time-transforming function (Figure S3). The least informative variables were removed by stepwise backward selection using the Akaike information criterion (AIC). Predictors selected from the best fitting hazards model were then used to calculate predicted survivorship for both species, and at FL, condition (uninjured or injured) and trailing branchline ratio. Each predictor was assessed independently, with the remaining predictors held at their medians. Median FLs were taken from Pacific Community (SPC) observer data holdings (120 and 103 cm for mako and silky shark, respectively). Median trailing branchline ratios were taken from the analysed tag dataset (0.57 and 3.96 for mako and silky shark, respectively). Predicted survivorship and Cox models were fitted with the *survival* and *flexsurv* packages in R (Therneau, 2015; Jackson, 2016; R Core Team, 2020).

2.5 | Fishery interaction survival estimates

Tagged sharks were found to be broadly representative of observed species-specific captures for both condition at release and the proportion of individuals cut free across all fleets operating in the Convention Area (SPC, 2017). Overall survival rates were estimated for the three stages of a pelagic longline fishery interaction – haulback (period of time during which gear is hauled from the water back to the fishing vessel), handling (removal of the shark from gear) and release (the shark is returned to the sea). To obtain these estimates, PRS rates under selected predictors were applied to estimates of the percentage of sharks released alive and not dying as represented from SPC observer data:

$$Fish_{Int} = Catch \times PRS$$

where *Catch* is the proportion of catch released alive (from SPC observer data); *PRS* is the PRS rate at 60 days for uninjured sharks; and $Fish_{Int}$ is the proportion of catch surviving a fishery interaction (haulback, handling and release). This definition of 'fishery interactions' includes sharks that are caught and remain on the gear until they are cut free or released either alongside or onboard the fishing vessel. As such, hooked sharks that bite through the branchline during the soak or haulback, i.e. bite-offs, were not considered when calculating fishery interaction survival rates.

3 | RESULTS

3.1 | Tagged sharks

A total of 117 sharks were tagged (mako = 60 and silky shark = 57). Mako were tagged in New Zealand (58%, $n = 35$), Fiji (25%, $n = 15$) and New Caledonia (17%, $n = 10$). Silky sharks were tagged in Fiji (75%, $n = 43$) and RMI (25%, $n = 14$; Figure 1a; Supporting Information). Of the tagged mako, 32 were female (86–350 cm FL, mean ± SD: 139.4 ± 49.7 cm FL), seven were male (117–250 cm FL, 173.1 ± 43.9 cm FL) and were 21 unsexed (110–250 cm FL, 172.8 ± 41.8 cm FL). For tagged silky sharks, 30 were female (90–250 cm FL, 140.0 ± 38.0 cm FL), 14 were male (105–200 cm FL, 127.7 ± 26.7 cm FL) and 13 were unsexed (94–160 cm FL, 121.3 ± 20.0 cm FL). The lengths of many sharks were estimated because they were tagged in the water, so these distributions are approximate (Figure 2). Based on reported length at maturity (Francis & Duffy, 2005; Joung et al., 2008), most tagged individuals of both species would have been immature.

3.2 | Movement

Based on straight-line trajectories from deployment to pop-up locations, mako generally showed pronounced latitudinal movement patterns between temperate and tropical waters (Figure 1b). While New Zealand-tagged mako moved mostly northwards and remained within the New Zealand Exclusive Economic Zone; several individuals travelled further (two to Norfolk Island and one to the outer islands of Fiji). Fiji-tagged mako showed southerly movements directed towards New Zealand. Mako tagged in New Caledonia showed a predominantly southward movement pattern, with one individual reaching the coast of Tasmania, Australia and one reaching the north-west coast of the North Island, New Zealand. From the Marshall Islands, silky sharks tagged in July all headed eastward (as far as Palmyra Atoll) whereas those tagged in November showed little to no directed movements away from the RMI (Figure 1c). Fiji-tagged silky sharks seemed to remain in the area with no directed movements away from the archipelago and their activity patterns were random.

Minimum and maximum daily depth and temperature values were available for all sharks throughout their deployments (except for tags in which the depth sensor failed, $n = 5$). Mako experienced a broad range of temperatures across their expansive latitudinal and depth range (temperature: 3.4–25.7°C, mean ± SD: 13.5 ± 3.1°C; depth: 0–1,407 m). The depth and temperature profiles for silky sharks were different between Fiji (temperature: 4.7–30.3°C, 22.6 ± 3.6°C; depth: 0–928 m) and the Marshall Islands (temperature: 6.8–30.3°C, 21.0 ± 5.3°C; depth: 0–621 m). The deepest dive recorded by a mako was 1,407 m (water temperature 3.4°C). This shark made repeated dives to depths of more than 1,000 m on multiple days, alternating with shallower dives at 200–400 m depth. Five mako were recorded to dive below 1,000 m, with three of the sharks repeating the behaviour on multiple days. The deepest dive recorded by a silky shark was 928 m (water temperature 4.7°C) and five silky sharks were recorded below 600 m.

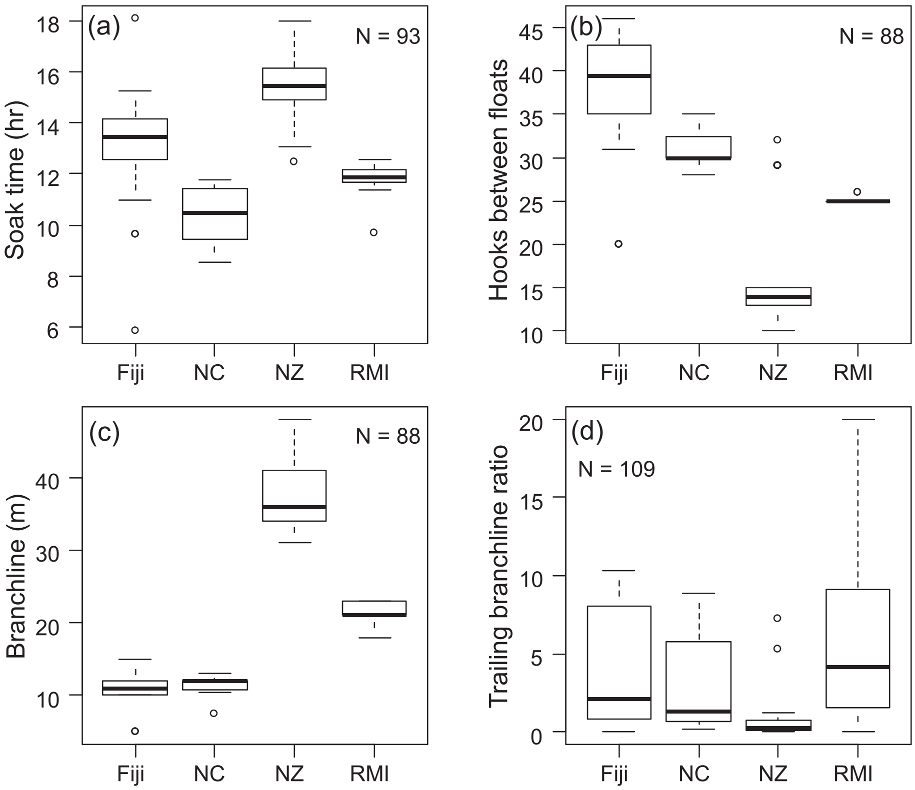

FIGURE 2 Distributions of pelagic longline operating parameters by fleet derived from Western and Central Pacific Fisheries Commission (WCPFC) data from which sharks were tagged: (a) soak time; (b) hooks between floats; (c) branchline length; and (d) trailing branchline ratio (ratio of trailing branchline left on shark to fork length). N, number of tagged sharks; NC, New Caledonia; NZ, New Zealand; RMI, Marshall Islands. The central black bar is the median, the box spans the first to third quartiles and the whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box. Circles represent outliers.

3.3 | Pelagic longline gear operating parameters

High-level comparisons of gear configurations by national fishery (flag-level) demonstrated some variability (Figure 2). Soak times (length of time the longlines remained in the water) were highest for New Zealand-flagged vessels (12.5–18.0 hours, median ± SD: 15.5 ± 1.3 hours) and lowest for New Caledonia-flagged vessels (8.5–11.8 hours, 10.5 ± 1.2 hours). The mean number of hooks between floats (hbf) was highest for Fiji-flagged vessels (20.0–46.0 hbf, 39.5 ± 7.7 hbf) and lowest for New Zealand-flagged vessels (10.0–32.0 hbf, 14.0 ± 6.8 hbf). Branchline lengths were longest for New Zealand-flagged vessels (31.0–48.0 m, 36.0 ± 4.4 m) and shortest for Fiji-flagged vessels (5.0–15.0 m, 11.0 ± 2.8 m) and the trailing branchline ratio was highest for RMI-flagged vessels (0.0–20.0 m/FL, 4.1 ± 5.9 m/FL) and lowest for New Zealand-flagged vessels (0.0–7.2 m/FL, 0.3 ± 1.5 m/FL).

3.4 | Tag deployment and mortality

Most tagged sharks of both species were uninjured upon release (89%) and most sharks (88%, median number of days at liberty: mako AU = 51, mako AI = 60, silky AU = 38, silky AI = 56) survived until tag loss (i.e. released pre-programmed pop-up date) or the programmed pop-up date. Data suitable for assessing PRS were received from 110 sharks (94% of tags, mako = 57 and silky = 53). The remaining seven tags either did not transmit via satellite or did not transmit sufficient data for proper interpretation of fate. Data on depth and temperature were successfully transmitted for 108 sharks, and sufficient depth and/or temperature data were obtained from 104 sharks (89%). Only 47% of the tags on mako and 36% of tags on silky sharks reached their pre-programmed deployment term of 60 days (Figure 3). Eight sharks died post-release (mako = 3 and silky = 5), with most mortalities occurring in the first 15 days.

Data transmitted from four tags attached to mako and one attached to a silky shark were consistent with ingestion by endothermic predators, as evidenced by an abrupt increase in the temperature and a decrease in light intensity (Supporting Information). Tag ingestions occurred throughout the deployment period. Ingested tags were eventually regurgitated, after which they floated to the surface and transmitted data via the Argos constellation of polar orbiting satellites. The fate of the sharks with tags that were later ingested cannot be confidently determined from the transmitted data as several scenarios for tag ingestion were hypothesized: (i) the tag detached and was later consumed by a predator and the tagged shark survived; (ii) the predator bit off the tag while it was still attached to the tagged shark but the shark survived; or (iii) the predator attacked the tagged shark and consumed the tag, and the tagged shark died. It is also not known if these tagged sharks were more susceptible to predation, which may have been influenced by the fishing and/or tagging event. Without determining the true fate of these sharks, a conservative approach was taken and all ingested tags were treated as mortalities. Therefore, the total numbers of mortalities (including ingested tags) were seven mako and six silky sharks.

3.5 | Kaplan–Meier survivorship model

Analysis of K-M survival curves indicated no significant differences between mako and silky shark survival rates from tagged WCPFC sharks. There were no immediate steep declines in survival, with 94.7% of released mako (CI: 89.1–100%) and 94.3% of released silky sharks (CI: 88.3–100%) surviving beyond 1 day (Figure 4a). Both species exhibited similar overall rates of mortality shown by considerable overlap in the 95% CIs of the K-M survival curves across the 60 day period, but silky shark exhibited acute mortality outcomes within 10 days of release (92.3% survival, CI: 85.3–99.9%). At 30 days, survival was estimated at 90.2% for mako (CI: 82.3–98.9%) and 92.3% for silky shark (CI: 85.3–99.9%). By 50 days, the proportion of sharks surviving was nearly equivalent in the two species, at 84.8% for mako (CI: 74.7–96.1%) and 85.0% for silky shark (CI: 74.1–97.6%). These estimates remained virtually unchanged after 60 days (mako: 84.7% (CI: 74.7–96.1%) and silky: 85.0% (CI: 74.1–96.1%).

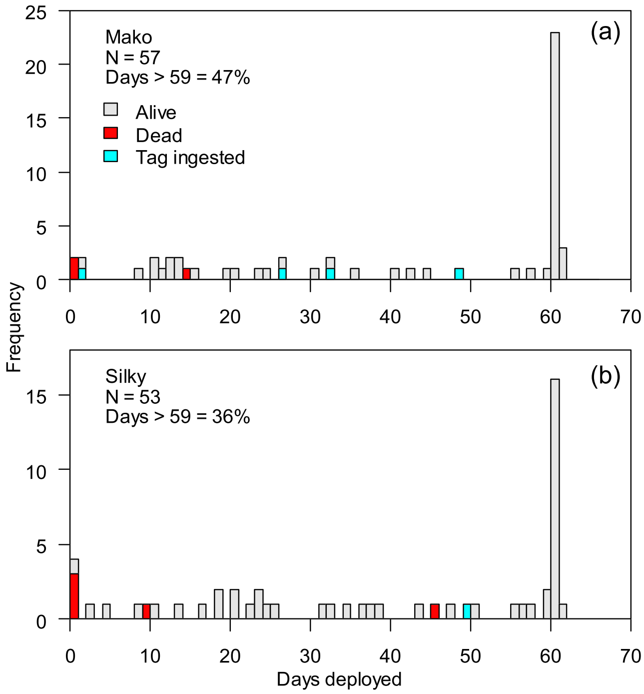

FIGURE 3 Distributions of tag deployment durations for (a) mako and (b) silky sharks, classified by whether the sharks were alive or dead at the time of tag release, or the tag was ingested by a warm-blooded predator.

Given a lack of difference in species-specific survival rates in this study, five Pacific datasets (four silky and one mako) were combined and compared with survival rates for mako in the north-west Atlantic (Campana et al., 2016). The K-M survival curve from the Campana et al. (2016) study steeply declined during the initial period but over time began to approximate the slope of the survival curve from this study (Figure 4b). Overall, PRS of mako after 60 days was lower in the north-west Atlantic (68.7%, CI: 52.8–89.4%) compared to the 60 day survival estimate for mako in this study.

3.6 | Influences on PRS

An initial Cox hazard model fitted to the WCPFC tag data sequentially excluded all variables in the model, leaving FL as the only retained variable. However, because of missing variable values, only 59 of the tagged sharks across both species could be used in the model. Consequently, variables with many missing values (soak time, branchline length, hbf) were dropped to increase sample size and to avoid overfitting the model given the small number of mortalities (Musyl & Gilman, 2019). The resulting model (selected variables: species, FL and trailing branchline ratio) had a larger sample size ($n = 96$; AIC = 101.97). In order to test the species interactions,

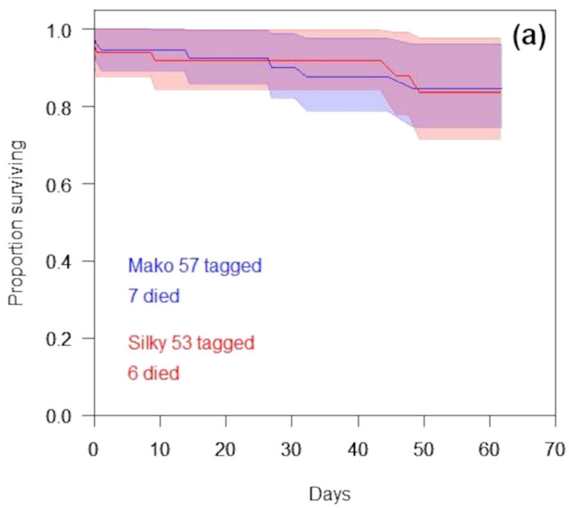

FIGURE 4 (a) Kaplan–Meier survivorship curves for Western and Central Pacific Fisheries Commission (WCPFC) mako (blue) and silky (red) sharks, with 95% confidence limits. The number of deaths for each species included ingested tags; (b) Kaplan–Meier survivorship curves compared for north-west Atlantic mako (green) and five Pacific datasets (four silky and one mako; blue), with 95% confidence limits.

separate models were run (species*FL interaction and species* trailing branchline ratio interaction). Interaction terms did not improve the model fit (species*FL interaction AIC = 102.88; species*trailing branchline ratio AIC = 103.93). Thus, the best fitting model based on the AIC included the predictors: species, FL and trailing branchline ratio.

Combining the WCPFC silky and mako shark data with the supplementary Pacific silky shark datasets further increased the available sample size (n = 209), and the best fitting model (the 'combined dataset' model) included the predictors: condition and trailing branchline ratio. There was no evidence of variation in survival rates between the tagging region, and so the 'combined dataset' model was used to estimate PRS rates, and fishery interaction survival rates.

3.7 | Estimates of PRS

Predicted survivorship at 60 days for the WCPFC tagged sharks was considerably higher for uninjured sharks (mako: 88.4%, CI: 74.0–95.2%; silky shark: 90.5%, CI: 82.5–94.9%) than for injured sharks (mako: 36.8%, CI: 6.3–69.1%; silky shark: 44.3%, CI: 14.3–71.5%) when FL and trailing branchline ratios were fixed at their median values (Figure 5a,b). For both species, survivorship was greater in

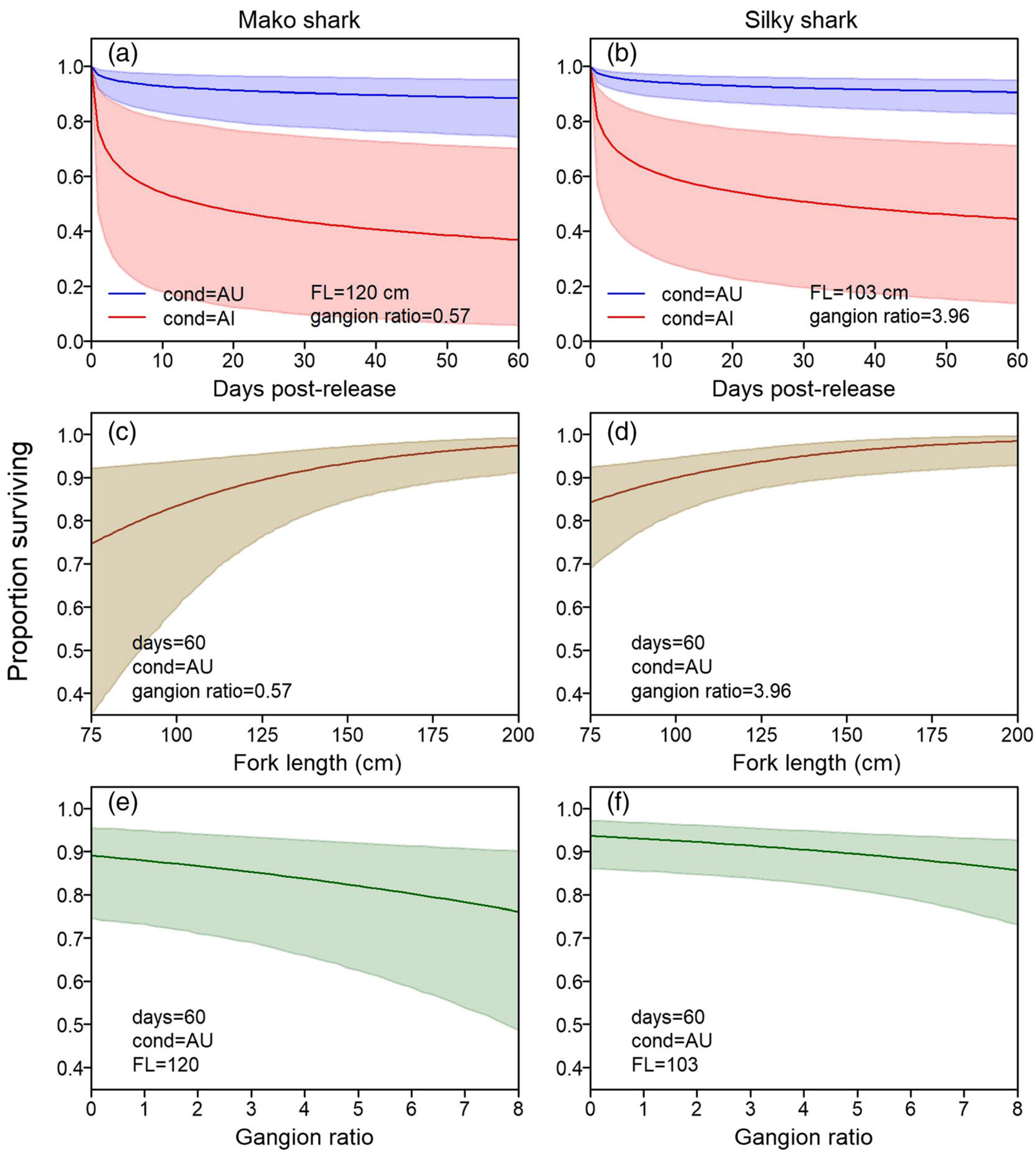

FIGURE 5 Predicted survivorship (with 95% confidence limits) for the parameters from the 'combined dataset' (i.e. the five Pacific datasets, Table 1) model for mako (a, c, e) and silky sharks (b, d, f). (a, b) Effect of number of days post-release on survivorship of uninjured (AU) and injured (AI) sharks, with fork length (FL, in cm) and branchline ratio fixed at their median values; (c,d) effect of fork length on survivorship at 60 days of uninjured sharks, with branchline ratio fixed at its median value; (e,f) effect of branchline ratio on survivorship at 60 days of uninjured sharks, with fork length fixed at its median value.

large (>150 cm FL) uninjured sharks (mako at 150 cm FL: 93.4%, CI: 84.6–97.2%; silky shark at 150 cm FL: 96.1%, CI: 90.2–98.5%; Figure 5c,d). Survivorship was also greater when the trailing branchline ratio was shorter (Figure 5e,f) and the effect of the trailing branchline ratio on survival was more pronounced for mako. A trailing branchline ratio of 1 produced a predicted survivorship of 87.9% for uninjured mako (CI: 73.3–94.9%) and 93.0% for uninjured silky shark (CI: 85.3–96.7%). Predicted survivorship was reduced to 76.1% (CI: 48.3–90.2%) and 85.7% (CI: 73.4–92.6%) for uninjured mako and silky sharks, respectively, when the trailing branchline ratio was increased 8-fold (see Supporting Information for all outcomes).

With the time-transforming function, condition was found to have a large effect on initial shark survival, but this reduced to near zero with time (Supporting Information). Inversely, branchline ratio had little effect on survival initially, but its effect increased with time. Inclusion of the time-transforming function had little effect on predicted survivorship outcomes with the exception of 'alive and injured' sharks where the initial mortality estimate was steeper and gradually increased over time. This is biologically impossible, i.e. morbid sharks cannot improve their condition over time, and this effect is probably influenced by the small number of mortalities observed in this study.

3.8 | Fishery interaction survival estimates

Overall PRS estimates for all sharks captured and released from WCPFC pelagic longline fisheries in the SPC observer data records during the study period were obtained by applying the PRS rates from this study to the percentage of sharks released alive and not dying in the observer database. Based on available SPC data holdings, a total of 3,581 and 2,409 mako and silky shark captures were recorded by observers, respectively, across all WCPFC longline fleets during the tagging period. Of these, 55.0% of mako and 66.0% of silky shark were released alive as recorded on observer reports. The remainder of catches were discarded in a dead or dying condition, or retained in the case of mako. Condition was found to be an important predictor for silky shark PRS for the combined five Pacific datasets so a condition class weighted average was calculated using the proportion of WCPFC silky sharks in each condition class (i.e., 75.7% were alive and uninjured and 24.3% alive and injured according to SPC observer data) and condition-specific PRS for uninjured silky shark (79.3% at 60 days; Supporting Information). The proportion of sharks estimated to survive all three stages of a fishery interaction at 60 days were 48.6% and 52.3% for mako and silky shark, respectively.

4 | DISCUSSION

Post-release survival rates after 60 days were estimated at 88.4% and 90.5% for uninjured mako and silky shark, respectively, after capture and release in pelagic longline fleets operating in the WCPFC Convention Area. PRS estimates between species were similar and explained by two factors: (i) the size of the shark (i.e. larger sharks had higher survival rates); and (ii) the trailing branchline ratio after release (i.e. minimal gear left on the shark increased survival rates). PRS rates for silky sharks (90.5%) here were very similar to those reported from Hawaii and American Samoa, Palau, and Costa Rica and Ecuador (Musyl & Gilman, 2018; Hutchinson, Bigelow & Carvalho, 2019; Schaefer et al., 2019; Hutchinson et al., 2021; Schaefer et al., 2021). For mako, the PRS rate (88.4%) was higher here than those reported for ongoing work across the International Commission for the Conservation of Atlantic Tunas (ICCAT)-managed region in the Atlantic (77.2%) (Miller et al., 2019), and in the north-west Atlantic, where PRS was about 70% and has shown little change over a 17-year period (2001–2018) (Campana et al., 2016; Bowlby et al., 2020). While the PRS estimates in this study suggest that capture and release of healthy sharks in the WCPFC Convention Area may not result in elevated post-release mortalities, these estimates are likely to be conservative given low (<5%) observer coverage across the WCPO (WCPFC, 2018).

4.1 | Mortality

Most shark mortalities (7/8) occurred within 2 weeks from release, indicating that the 30-day deployment period was sufficient to account for immediate PRS rates associated with fishing interactions. Five of these sharks (mako = 2 and silky shark = 3) died within the first 2 days post-release. These results correspond with other PRS studies on pelagic sharks where most mortalities were reported to occur within 3 days of a longline fishing interaction (Campana et al., 2016; Musyl & Gilman, 2018). One mako and one silky shark died within 2 weeks (14 and 11 days, respectively). One additional delayed (>30 days) mortality of a silky shark occurred at 46 days. Delayed mortalities have often been reported up to 50 days post-release, and as long as 307 days post-release (Hutchinson et al., 2015; Musyl & Gilman, 2019). Delayed fishing-associated mortalities are difficult to quantify but have been shown to be associated with physiological and physical damage from fishing gear or handling techniques and reduced activity levels upon release, leading to increased susceptibility to predation or disease, or cessation of feeding (Campana et al., 2016). It is possible that additional delayed mortalities occurred beyond the 60-day reporting period (Campana, Joyce & Manning, 2009; Hutchinson et al., 2015). Longer tagging periods would be informative with regard to background mortality and are thus preferred, but longer deployments also represent higher costs and higher probability of tag failure (Hays et al., 2007; Musyl et al., 2011).

Five tags, and possibly five sharks (mako = 4, silky shark = 1), were presumed ingested by endothermic predators over the duration of this study as indicated by the light and temperature data. Increased activity and accumulated stress during a tagging event may make tagged sharks more likely to attract predators, and smaller and/or injured sharks may be more impaired by tagging (e.g. reduced swimming performance, hindered defensive abilities) than larger or uninjured sharks making them more susceptible to predation (Raby et al., 2014). Marine mammals and lamnid sharks (e.g. mako, porbeagle and great white sharks) could all have been responsible for the ingestions as these species maintain their visceral temperatures above ambient (Carey et al., 1971). However, the presence of lengthy dives (to >1,000 m for long periods of time) probably rules out marine mammals, which surface regularly to breathe and maintain body temperatures generally exceeding 36°C whereas temperature data did not exceed 29°C (Reisinger et al., 2015).

4.2 | Factors affecting survival

Shark size and shark condition were important factors in determining PRS. Most sharks tagged in this study were estimated to be juveniles and subadults and seven of the eight sharks that died (88%) were relatively small in size (estimated length of <150 cm FL). Larger mako were more likely to survive capture encounters, which may be related to a lower likelihood of being hauled on deck (Francis & Finucci, 2019; Miller et al., 2019). In the north-east Atlantic, the PRS rate for large mako (>180 cm FL) was 84.5%, while PRS for small individuals (<180 cm FL) was estimated at 76.2% (Miller et al., 2019). The tagging location of sharks was not reported, although previous work in the region reported unusually high mortality rates associated with small (110 cm FL) sharks tagged onboard (Campana et al., 2016). No such effect was expected in the current study because, with the exception of one shark hauled on deck, all sharks assessed as mortalities were tagged alongside the fishing vessel.

Increased survival is correlated with shark condition at haulback and release, and the probability of injury is higher when sharks are hauled onboard (Poisson et al., 2014; Musyl & Gilman, 2018). Survival, particularly for injured sharks, may be increased if sharks are tagged in the water (Poisson et al., 2014). Most sharks in this study were tagged in the water, so comparison of survival rates with sharks tagged onboard vessels was not possible. In the case of mako, some tagged individuals were hauled on deck but this was not found to be a significant factor in their PRS, which may be due to low statistical power. Campana et al. (2016) compared the effects of tagging mako, porbeagle (*Lamna nasus*) and blue shark (*Prionace glauca*) onboard versus in the water and also noted no significant statistical difference in survival outcomes by tagging location. Controlling for tagging effects, however, is difficult. Processes that increase physical and physiological trauma to released sharks, such as handling and time spent out of water incurred during fishing events, are associated with longer recovery times, which may affect survival (Ellis, McCully & Poisson, 2017). In the north-west Atlantic median recovery times were found to be 1 and 1.5 days longer for shortfin mako and porbeagle, respectively, when sharks were hauled onboard for tagging (Bowlby et al., 2020). Bowlby et al. (2020) also noted changes in diving behaviour for sharks with delayed mortality, with individuals generally staying at a constant, relatively shallow depth (instead of commonly observed oscillatory dive patterns). Changes in diving behaviour can reflect lower activity levels associated with recovery from physiological and metabolic stress upon capture (Whitney et al., 2016). Evidence from behavioural classification models and free-tagged striped marlin (*Kajikia audax*) suggested tagged animals may resume normal behavioural patterns after approximately 2 weeks at liberty (Sippel et al., 2011). Of the mortalities in this study, 50% ($n = 4$) of the sharks were reported to have swam away quickly, three swam away slowly and the behaviour of one shark was not recorded.

The length of trailing gear left on the shark, as a function of body length, was found to be a significant factor in determining PRS for both mako and silky shark. The effect trailing gear has on mortality and survival rates is not well understood. The increasing effect over time of branchline ratio on survival observed here may suggest trailing gear becomes more problematic for sharks the longer it is attached to the shark (e.g. increases risk of entanglement, Wegner & Cartamil, 2012). Longer trailing line may eventually entangle the shark, restricting its ability to capture prey or evade predators or incur higher energy expenditure (Hutchinson et al., 2021). Long trailing branchlines were found to increase delayed mortalities in blue sharks captured on Hawai'in longline vessels (Hutchinson, Bigelow & Carvalho, 2019), and by limiting as much trailing gear as possible (i.e. leaving <1 m), survivorship for pelagic sharks was increased by up to 40% over the course of one year (Hutchinson et al., 2021). Other studies, however, have noted that trailing gear had little effect on the mortality rates of pelagic sharks, including silky and blue sharks (Musyl & Gilman, 2018). Nonetheless, it is well recommended in the literature to reduce the amount of fishing gear left on a shark before release (Musyl & Gilman, 2018; Hutchinson et al., 2021; Schaefer et al., 2021).

4.3 | Management

This study shows that despite relatively high PRS rates for mako and silky shark in the Pacific, these estimates are markedly reduced by nearly 40% (mako = 39.8%, silky = 38.2%) when the proportion of overall catch surviving a fishery interaction (haulback, handling and release) is taken into consideration. Thus, while no-retention policies offer sharks an increased chance of survival, continued efforts should be made to avoid catching sharks altogether to minimize fishing impacts on shark populations. Many shark populations have undergone declines in the western Pacific Ocean (Clarke et al., 2012). Currently, there are no-retention measures implemented in the WCPFC Convention Area for silky, oceanic whitetip (*Carcharhinus longimanus*) and whale (*Rhincodon typus*) sharks, and manta and mobulid rays (family Mobulidae), and the release condition (dead or alive) of silky and oceanic whitetip sharks must be recorded. Additional management measures are in place to reduce shark bycatch (e.g. discouraging use of wire traces as branch lines or leaders, or shark lines) and it is encouraged that any bycaught shark be released alive using techniques that result in minimal harm (WCPFC, 2019).

Results herein provide guidelines to encourage best practice for safe release, which should include reducing any gear left on released sharks. Uninjured sharks are more likely to survive than injured sharks, so efforts should be made to minimize the number of sharks brought on board to limit possible injuries often obtained during haulback (Poisson et al., 2014). To minimize the length of trailing gear left on the shark, sharks should be brought close to the vessel while remaining in the water, and the line should be cut as close to the hook as possible. This recommendation may differ from current fishing practices, where sharks that surface early (and are thus spotted further away from the vessel) may be cut from the line as soon as it is identified (Hutchinson, Bigelow & Carvalho, 2019). Hauling the shark close to the vessel before release would not only facilitate the removal of trailing gear from the shark but also aid species identification by either an observer or an electronic monitoring system.

PRS estimates should be incorporated into future stock assessments and projections. However, there is a paucity of data on species-specific PRS rates in the WCPO region. Several shark species have been identified as future priority species to examine, including oceanic whitetip shark (high conservation interest) and bigeye thresher shark (*Alopias superciliosus*, to resolve mortality rates by hooking location) (Brouwer & Griggs, 2009; ABNJ, 2019). In the absence of species-specific PRS estimates, at-vessel condition could be useful for other pelagic sharks as an indicator of post-release fate. At-vessel mortality rates may be an indicator of species-specific sensitivities to fishing related stressors and therefore PRS (Braccini, Van Rijn & Frick, 2012). Assessment of at-vessel mortality is more cost-effective than tagging studies and has the potential to include considerably larger sample sizes, although factors that may affect condition (e.g. internal injuries, time spent hooked) must also be accounted for (Butcher et al., 2015). Additionally, information on discarding is also required. Discard data (e.g. species, sex, size) has become limited, particularly for no-retention species such as silky shark. Reporting species-specific discarding is highly encouraged.

Mako and silky shark are now assessed as globally Endangered and Vulnerable, respectively, under the IUCN Red List of Threatened Species, highlighting the need to continue research on mitigating fishing mortality (IUCN, 2022). Additional mako PRS studies should be considered and conducted on other fleets where appropriate to augment results for input into regional assessments, with the north-west Pacific stock assessment scheduled for 2024 (Brouwer & Hamer, 2020). A useful framework for understanding the various components of shark mortality was developed by Harley et al. (2015). It is recommended that the model be further developed and the input parameters (e.g. probability of mortality at time of retrieval and upon release, and probability of release in water) updated to the extent possible in a follow-on study. Such a study would be useful in providing specific advice to managers considering the effectiveness of WCPFC shark mitigation measures in general, and specifically, no-retention measures. Several meta-analyses synthesizing PRS in pelagic fishes and sharks have been published or are underway around the world (Ellis, McCully & Poisson, 2017; Musyl & Gilman, 2019). These reviews have indicated PRS results from different studies and fisheries should be subject to further joint analyses in order to better understand PRS in various regions and to work towards harmonizing best practices for safe release. One forum where such efforts could be carried out is the Joint Tuna Regional Fishery Management Organization (Kobe) Bycatch Working Group (Anon, 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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