

Quantitative estimates of post-release survival rates of sharks captured in Pacific tuna longline fisheries reveal handling and discard practices that improve survivorship

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Contents

Abstract.....	iv
Key words:.....	iv
List of Acronyms.....	v
Introduction.....	1
Methods.....	3
Fishing and Tagging.....	3
Survival Analysis.....	6
Covariates.....	6
Proportional hazard model.....	6
Survival Curves.....	8
Survival Rate Projections to the Observer Data Set.....	9
Focus on Oceanic Whitetip Mortality Mitigation.....	10
Individual Post-interaction Survival.....	10
Hindcast Survival of Observed Interactions.....	11
Results.....	11
Fishery Characteristics, Observer Data Collections, and Tagging.....	11
Survival Analysis.....	14
Proportional hazard model fit.....	14
Survival Curves.....	14
Expected Survival Projections.....	15
ESA Listed Oceanic Whitetip Shark Mortality Mitigation.....	16
Individual Post-interaction Survival.....	16
Hindcast Survival of All Observed Interactions.....	16
Discussion.....	17
Species specific survival rates.....	18
Silky shark.....	18
Blue shark.....	19
Bigeye thresher shark.....	20
Shortfin mako shark.....	21
Oceanic whitetip shark.....	22
Fishery and handling method effects on survival.....	22
Delayed Mortality.....	25
Conclusions, Recommendations, and Next Steps.....	28

Acknowledgements	29
References	30
Tables and Figures	35
Appendix	47
Supplementary Material.....	55

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Abstract

Shark catch rates are higher in pelagic longline fisheries than in any other fishery, and sharks are typically discarded (bycatch) at sea. The post-release fate of discarded sharks is largely unobserved and could pose a significant source of unquantified mortality that may change stock assessment outcomes and prevent sound conservation and management advice. This study assessed post-release mortality rates of blue (*Prionace glauca*), bigeye thresher (*Alopias superciliosus*), oceanic whitetip (*Carcharhinus longimanus*), silky (*C. falciformis*) and shortfin mako (*Isurus oxyrinchus*) sharks discarded in the Hawaii deep-set and American Samoa longline fisheries targeting tuna in the central Pacific Ocean. The impacts on survival rates were examined considering species, fishery, fishing gear configuration, handling method, animal condition at capture and at release, and the amount of trailing fishing gear remaining on discarded sharks. Bayesian survival analysis showed that the condition at release (good vs. injured), branchline leader material, and the amount of trailing fishing gear left on the animals were among the factors that had the largest effect on post-release fate—animals captured on monofilament branchline leaders and released in good condition without trailing fishing gear had the highest rates of survival. This study shows that fisher behavior can have a significant impact on pelagic shark post-release mortality. Ensuring that sharks are handled carefully and released with minimal amounts of trailing fishing gear may reduce fishing mortality on shark populations.

Key words:

Bycatch, mortality, shortfin mako, bigeye thresher, silky, blue, oceanic whitetip, best handling practice

List of Acronyms

ASLL – American Samoa
ASOP – American Samoa Observer Program
BSH – Blue shark
BTH – Bigeye thresher shark
CITES – Convention on International Trade in Endangered Species
CMM – Conservation and management measures
CPUE – Catch per unit effort
FAL – Silky shark
HIDS – Hawaii deep-set fishery
HISS – Hawaii shallow-set fishery
MSA – Magnuson-Stevens Fishery Conservation and Management Act
NMFS – National Marine Fisheries Service
OCS – Oceanic whitetip shark
PAT – Pop-off archival tag
PIROP – Pacific Islands Region Observer Program
RFMO – Regional Fisheries Management Organization
SMA – Shortfin mako shark
SPAT – Survivorship pop-off archival tag
WCPFC – Western and Central Pacific Fisheries Commission
WCPO – Western Central Pacific Ocean
WPFMC – Western Pacific Fisheries Management Council

Introduction

It is estimated that two-thirds of global elasmobranch species are threatened with extinction, with overfishing identified as a major contributor (Worm et al. 2013). Shark catch rates are higher in pelagic longline fisheries than in any other fishery, and sharks are typically unwanted and discarded at sea (Oliver et al. 2015). Identifying strategies that reduce commercial fishing impacts on discarded (bycatch) shark populations is a critical fisheries science and conservation need. Our research focuses on identifying best practices to reduce mortality using data collected from the Hawaii deep-set (HIDS) and American Samoa (ASLL) longline fisheries that target bigeye tuna (*Thunnus obesus*) and albacore (*Thunnus alalunga*), respectively. Both the HIDS and ASLL fisheries interact with several shark species, most of which are of low commercial value and are discarded at sea. In these fisheries, the highest shark catch rates consist of the following (in descending order): blue sharks (*Prionace glauca*), thresher (*Alopias spp.*), mako (*Isurus spp.*), oceanic whitetip (*Carcharhinus longimanus*), and silky sharks (*C. falciformis*) (Walsh et al. 2009). A study of catch per unit effort (CPUE) trends in the Hawaii based longline fishery found significant declines in the relative abundance of oceanic whitetips and silky sharks since 1995 (Walsh and Clarke 2011, Brodziak and Walsh 2013). In the Pacific Ocean, stock assessments have been formally conducted for the western and central Pacific Ocean populations of oceanic whitetip and silky sharks, the North Pacific population of blue shark and shortfin mako sharks, and a sustainability risk assessment for the bigeye thresher (*A. superciliosus*). All of these assessments have called for research on post-release survival rates to improve mortality estimates.

Based on concerns about population declines from overfishing, several regional fisheries management organizations (RFMOs) have responded with a series of conservation and management measures (CMMs) for sharks. Within the Western and Central Pacific Fisheries Commission (WCPFC) convention area, measures have been adopted to enhance bycatch mitigation including Safe Release Guidelines to maximize the survival of sharks that are caught and are not to be retained (CMM 2019-04). Additionally, CMM 2019-04 requires all vessels flying the flags of cooperating members and non-members to the WCPFC ‘to release any oceanic whitetip shark or silky shark that is caught as soon as possible after the shark is brought alongside the vessel, and to do so in a manner that results in as little harm to the shark as

possible', following any applicable safe release guidelines for these species. Additional international protections for oceanic whitetip, silky and the thresher shark species complex include listing in Appendix II of the Convention on International Trade in Endangered Species (CITES) which provides the legal framework to regulate trade and or introduction from the sea. In the United States, the oceanic whitetip shark was listed as threatened globally under the Endangered Species Act in 2018, requiring the US National Marine Fisheries Service (NMFS) to elucidate the steps necessary to restore the species to ecological health.

Measures banning retention are a step in the right direction but may not have the intended consequence of reducing mortality (Tolotti et al. 2015). According to a general consensus among shark and fishery scientists, three main factors have the largest impact on shark bycatch mortality rates in longline fisheries: 1) the underlying physiological sensitivity to stress, where impacts are species specific; 2) the amount of time an animal spends on the fishing line; and 3) the handling methods used to release/remove sharks from fishing gear. Many studies have identified which species are most sensitive to capture stress through physiological investigations and by quantifying at-vessel mortality rates (e.g., Beerkircher et al. 2002; Marshall et al. 2012). Yet the physiological and/or physical damage resulting from an interaction with fishing gear or handling procedures used to release sharks often results in undocumented and or delayed mortality (Campana et al. 2009). Effective fisheries management requires knowledge of the direct effects of fishing mortality on species that are retained and discarded. There is an urgent need to estimate levels of delayed mortality, account for these levels in stock assessments, and adopt measures to mitigate sources of mortality, such as identifying best handling and release practices (Gilman et al. 2013).

In the last few years, several studies have begun to focus on elucidating post-release mortality rates through satellite linked electronic tag technologies to ascertain total fishing mortality rates for shark bycatch species. Total mortality is the combination of mortality that is observed at the vessel and the more cryptic mortality that may occur post-release for species that are discarded at sea (Musyl and Gilman 2018; Campana et al. 2016). Until very recently the magnitude of post-release fishing mortality in shark bycatch species has been largely unknown where post-release mortalities of blue sharks released "alive" from longline fishing gear were found to range from 17% to 19% (Campana et al. 2016; Musyl and Gilman 2018). Similar studies have been conducted for mako and silky sharks around the Pacific Ocean (Francis et al.

2019; Musyl and Gilman 2018; Schaeffer et al. 2019, Schaefer et al. 2021) in various longline fisheries with results that show survival rates differ across fishing fleets, target species, fishing gear configurations and handling methods. Highlighting the need for post-release survival studies across ocean basins and fisheries.

In this study, post-release survival rates are quantified through the use of pop-off archival tags (PATs) for five of the WCPFC “key species” and the Western Central Pacific Fisheries Management Council’s (WPFMC) pelagic management unit shark species. These include blue (BSH), bigeye thresher (BTH), oceanic whitetip (OCS), shortfin mako (SMA) and silky (FAL) sharks that are incidentally captured in the HIDS and ASLL tuna target longline fisheries. We also investigate the effects that standard handling and discard practices may have on post-release fate with the goal of identifying best handling practices for fishers to improve survivorship of discarded species. We also expand survival estimates from tagged sharks across all observed shark interactions using data collected by fishery observers to generate a suite of survival rates across different scenarios that encompass catch condition, release method and the effect of gear configuration for integration into stock assessments.

Methods

Fishing and Tagging

Pacific Islands Regional Observer Program (PIROP) and American Samoa Observer Program (ASOP) fisheries observers were trained to collect additional details on shark condition, fisher handling and release methods, and in tagging during commercial longline fishing trips on Hawaii deep-set (HIDS, bigeye tuna target) and American Samoa (ASLL, albacore target) permitted vessels. Shark condition and handling data were collected during Hawaii shallow-set (HISS, swordfish target) permitted trips, to a lesser extent, and no sharks were tagged during these trips. Gear configurations (e.g., hook sizes, hooks set, branchline lengths and materials) and fishing method details (e.g., set and haul timing) vary across these fishing sectors and these details are also collected by both observer programs. All trips departed from the ports of San Diego, California; Honolulu, Hawaii; and Pago Pago, American Samoa.

Data collected by fisheries observers during shark interactions were used to assess factors that influence post-release survival rates of sharks discarded in HIDS and ASLL longline fisheries and to identify the handling and release methods that enhance survivorship. While there is a spectrum of vitality for sharks at haul back of the gear, PIROP and ASOP observers are only required to record whether an animal is alive or dead at haul back and a release disposition of alive, dead, or kept. Additional condition indices were created for observers that participated in this study to more accurately reflect how capture condition may impact post-release fate. Handling and injury codes were also developed and tested to ascertain how sharks were removed from the fishing gear and to provide details on any injuries that the animal may have incurred during the process. This was an iterative process. The data codes were created with definitions, and observers were deployed with video cameras to assess whether or not they interpreted the definitions accurately. This process began during the summer of 2015, and final definitions (Table 1) were adopted and implemented in December 2016 prior to the onset of tagging activities.

To quantify post-release survival rates of blue (BSH), bigeye thresher (BTH), oceanic whitetip (OCS), shortfin mako (SMA) and silky (FAL) sharks captured in the HIDS and ASLL, PIROP and ASOP observers were trained to tag sharks captured and released during normal fishing operations. Tags were placed on sharks over the rail of the vessel while the shark was still in the water, using extendable tagging poles. Vessel crew then removed the shark from the fishing gear via whichever release methods they typically employed. Observers recorded additional metrics about the tagging event (date, time, latitude and longitude, and sea surface temperature), the captured shark (species, condition at capture and release, sex, and approximate length) and the handling methods employed to release the sharks (composition and quantity of trailing gear attached to the shark at release, any damage to the shark from gear removal, if and how the shark was landed, and time out of the water). Observers also recorded video of the tagging events using a GoPro mounted to a head strap worn while tagging for scientific review and validation of data recorded for each shark interaction by project staff. The videos were also used to determine whether or not the tagging event (tag placement location, number of attempts to tag, and total time to tag and release) may have had an impact on survival.

This study used two different satellite linked pop-off archival tags (PAT), survivorship PATs (SPAT) and miniPATs (Wildlife Computers, Inc., Redmond, WA). The first model of the

SPAT was programmed for 30-day deployment periods while later models (from 2017 onwards) were programmed to 60 days. SPATs archived and then transmitted binned light, temperature, and depth data to the tag manufacturer. The tag manufacturer analyzed these data to interpret whether the animal died (“Sinker”—tag sank to a depth beyond 1400 m or it sank and sat at a constant depth (shallower than 1400 m for > 3 days); the animal survived (“Completed Deployment”—tag remained on the animal to the end of the programmed deployment period of 30 or 60 days); or if the tag came off prematurely due to an attachment failure (“Floater”—tag floated to the water’s surface after detaching from shark). The fate of the tag (“Sinker,” “Completed Deployment,” or “Floater”), the daily minimum and maximum depth and temperature, and the tag’s release (“pop-off”) location were then communicated from the manufacturer to us, as the tag owner.

The project was expanded to assess the long-term effects of trailing gear on survivorship after the initial phases of data collection revealed that most sharks were released by cutting the branchline with varying amounts of trailing gear attached to the animal (Table 2). Long-term survivorship was assessed with miniPAT tags placed on blue sharks incidentally captured in the HIDS fishery (n=25) and oceanic whitetip sharks captured in both the HIDS (n=6) and the ASLL fisheries (n=8). Of the 25 long-term miniPATs placed on BSH, 13 tags were deployed on trips where the vessel was using branchlines with monofilament leaders, while the remaining BSH (n=12) were tagged and released with trailing gear composed of branchlines with wire leaders. All 6 of the long-term miniPATs placed on OCS in the HIDS were on trips where the vessel was using branchlines with wire leaders, whereas all 8 miniPATs placed on OCS in the ASLL fishery were on trips with branchlines completely composed of monofilament. The long-term miniPATs used in this study archived light, temperature, and depth time series data, with sampling intervals of 10 minutes and deployment periods programmed for 180 days (n=2) or 360 days (n=37). Only sharks that were alive and in good condition (AG) at haul back were tagged with miniPATs and were released by cutting the line. Fishery participation in this study was voluntary. Observers were only asked to tag a small number of sharks (2–3) per trip to ensure that vessels did not bear a large burden for participating in the project and to avoid observer or trip-specific data biases. This research was conducted in accordance with the institutional animal care and use guidelines at the University of Hawaii.

Survival Analysis

Covariates

Factors associated with the fishery interaction were used to generate covariates for the survival analysis. A dummy variable (0, 1) was included for whether the fishery interaction occurred in the HIDS or ASLL fishery and for each tagged shark's post-release fate of dead or alive. The approximate length of the individual and the amount of trailing gear in meters were included as continuous variables and the mean per species was assumed when data were missing. Covariates were also included in the analysis for the shark condition at capture and release and the handling and discard practices. The data recorded by the scientific reviewer superseded that recorded by the fishery observer when discrepancies occurred, and if the reviewer was unable to ascertain a particular condition from the video or notes, the data recorded by the observer was used in the analyses. Additional covariates were used for the type of branchline leader material (wire or monofilament) and for the location the animal was hooked in the body. Hooking location only applied to BTH, which are often hooked in the tail or in the mouth because of their feeding strategies.

Proportional hazard model

A proportional hazard model was implemented in a Bayesian framework in order to explicitly model the baseline hazard, h_0 , and not rely on a pseudo-likelihood as in the frequentist framework. We assumed that the survival function was equal to the probability of the survival time, T , being greater than a given time, t (Equation 1):

$$P(T > t) = S(t) = e^{-H(t)} \quad \text{Equation 1}$$

where $S(t)$ is the survival function and $H(t)$ is the cumulative hazard (Equation 2) equal to integrating the hazard rate, $h(t)$, from time zero to time t .

$$H(t) = \int_0^t du h(u) \quad \text{Equation 2}$$

$$h(t; X_p) = h_0(t)e^{X_p^T \beta} \quad \text{Equation 3}$$

where $h_0(t)$ is assumed to be equivalent to the baseline hazard, h_0 , X_p is a vector of hazard covariates describing the individual's fishery interaction and β is a vector of hazard covariate

effects. Equation 3 can be reparameterized to follow a more traditional linear model formulation (Equation 4):

$$h(t; X_p) = e^{X_p' \beta + \gamma} \quad \text{Equation 4}$$

where e^γ is equivalent to the baseline hazard. The baseline hazard (i.e. the comparison to which all hazard covariate effects, β , are compared) was assumed to vary by shark species and tag deployment period. The survival time, T , can be explicitly written as being distributed following an exponential model with rate, $h(t)$, conditioned on the observed survival (right-censorship in survival analysis parlance), z , where $z = 1$ if the individual survived (Table 4) (Equation 5):

$$T \sim \begin{cases} z = 0 & \text{Exp}(e^{X_p' \beta + \gamma}) \\ z = 1 & \text{Exp}(1 - e^{X_p' \beta + \gamma}) \end{cases} \quad \text{Equation 5}$$

Covariate effects, β , were assumed to have normal priors with mean zero and a standard deviation of 2. The baseline hazard rate was assumed to have a normal prior with a standard deviation of 2 and varying means equal to $-\log(\mu)$, where μ equals the mean survival time by species and tag deployment period. All priors were specified using weakly informative priors, such that minor structural information is provided and the inference is weakly regularized (Gelman et al. 2017). The Bayesian hierarchical proportional hazard model was implemented in *rstan* (STAN Development Team 2020) using 5,000 iterations for burn-in (discarded), and 2,500 iterations from 4 chains using the No U-Turn variant of the Hamiltonian sampling algorithm with default parameters. Convergence was assessed visually and using the Gelman-Rubin convergence statistic, \hat{R} (less than 1.1 when chains converged) (Gelman et al. 2013).

We also completed a posterior predictive check by estimating predicted survival times of the dead (uncensored) individuals, \hat{T} , and comparing these predicted survival times to observed survival times (Rubin 1984). As the uncensored survival times are bounded by tag deployment period (30, 60, 180 or 360 days in this study), we utilized an exponential draw with an upper bound limit for these individuals (Equations 6–8) and an unbounded draw for censored individuals (Equation 5):

$$p = 1 - e^{-(X_p' \beta + \gamma)\omega} \quad \text{Equation 6}$$

$$u \sim \text{Uniform}(0, p) \quad \text{Equation 7}$$

$$\hat{T} = -\frac{\log \log (1-u)}{e^{(x_p^\beta + \gamma)}} \quad \text{Equation 8}$$

where p is equal to cumulative distribution function of the exponential distribution evaluated at the upper bound, ω , and u is a draw from a uniform distribution between 0 and p . Two versions of the model goodness of fit, R^2 , was assessed using Equations 9–11.

$$R^2 = 1 - \frac{SS_{pred}}{SS_{tot}} \quad \text{Equation 9}$$

$$SS_{pred} = \sum_i (T - \tilde{T})^2 \quad \text{Equation 10}$$

$$\text{Equation 11}$$

where SS_{pred} is the predicted sum of squares, SS_{tot} is the total sum of squares, \tilde{T} is the median predicted survival time, and \underline{T} is the mean of the observed survival times, T . The first version of the model goodness of fit, R_0^2 only used \tilde{T} values for uncensored individuals. The second version used all the \tilde{T} values but assumed that the model adequately predicted the individual to survive past the tag deployment period if $\tilde{T} > T$. To do such, \tilde{T} values satisfying the condition $\tilde{T} > T$ were set equal to T . The significance of each fishery interaction covariate was assessed by taking the average of posterior parameter samples less than zero (Equation 12) and evaluating if this value was less than $\frac{\alpha}{2}$ or greater than $1 - \frac{\alpha}{2}$, where $\alpha = 0.1$.

$$p(\beta) = \frac{\sum(\beta < 0)}{n} \quad \text{Equation 12}$$

where n is the number of posterior samples.

Survival Curves

Survival curves were estimated from the posterior samples of the hazard model effects over a sequence of potential survival times from 1 day to the maximum observed survival time (360 days) with a daily step. For each survival curve, the median and the 90% credible interval were calculated from the posterior samples. Species-specific survival curves were estimated at the mean conditions across all tagged individuals by species and by fishery (only relevant for OCS) and the mean baseline hazard rate for the species (e.g., the mean of h_0 varying by tag deployment period). Survival curves were also estimated to explore the marginal effects of specific conditions and, for these estimates, all other effects were multiplied by the proportion of conditions observed in the tagged individuals. A comparison was made of the survival curves

between each of the following: 1) caught conditions (Alive, Alive Good, Alive Lethargic, and Alive Injured); 2) between hooking location (BTH only) and between using wire leader or mono leaders, 3) between each of the handling methods involving direct contact with the shark or the hook in its mouth (Gear Removed, Jaw Damaged, Dehooking, and Part Removal), and 4) between each of the handling methods involving only the line attached to the shark (Line Cut, Drag Line, and Escaped. See Table 1 for descriptions). For the tail hooking comparison, the mean interaction conditions across BTH were used rather than the mean across all species. Lastly, the effect of increasing length of trailing gear was explored by determining the 25th percentiles of the observed length of trailing gear and estimating survival curves for each length. These comparisons were also summarized by extracting the survival rate at the unique programmed tag deployment periods.

Survival Rate Projections to the Observer Data Set

Using the hazard model's parameter estimates, we projected the expected survival of BSH, OCS, SMA, FAL, and BTH in the HIDS and ASLL fisheries across the observer data set. We used the PIROP and ASOP data sets for the HIDS and the ASLL fisheries collated between January 3, 2005 and December 4, 2019. For all of the observed fishing sets, a shark's individual length was assigned from the approximate length (estimated) and the total length (measured) values recorded by the observers. A small subset of the total observed longline sets recorded the same covariates used in the hazard model and were used directly in the projection estimation. Only the handling codes used in the hazard model were used in the projection estimation. For the rest of the observed fishing sets without the survival covariates or missing part of the necessary covariate set, the mean condition(s) for each species by each caught condition was used. Survival estimates were projected to 1, 30, 60, 180, and 360 days post-release. The proportion of individuals that were caught and assessed as dead at the vessel was tallied by species, and results were reported both with and without these dead individuals. The mean intercept by species was used in lieu of using the tag-specific intercepts. In addition, for the HIDS fishery a wire leader effect was included.

Focus on Oceanic Whitetip Mortality Mitigation

OCS are federally listed as threatened under the US ESA, and as such, steps are required by action agencies to reduce mortality for this species in the fisheries they manage. This analysis details the expected survival of OCS following interactions with the HIDS fishery based on the survival of tagged animals and tabulated to reflect management options that include changes to gear configurations. One option under consideration by the fishing industry is converting from wire leader materials (currently in use) to monofilament leader materials, as well as reducing the trailing gear left on each animal. In this analysis we explored how potential changes in gear and handling may impact mortality rates through two examinations: 1) the change in the individual post-release survival under a range of interaction conditions, and 2) the proportion of historic OCS interactions with the HIDS fishery observed by the PIROP that would have survived given a set of interaction conditions.

Individual Post-interaction Survival

The individual post-interaction survival analysis was conducted using a Bayesian hazard model. Other than the branchline leader material and trailing gear effects in the model, all other interaction conditions were held at the mean across tagged sharks. All species were included in this analysis with species-specific effects included in the baseline hazard rate, the expected survival at the baseline, and for each tag deployment duration. The species-specific survival was estimated, as the average over the tag deployment duration. For OCS, three effects for each tag deployment duration were included in the whole model. The baseline for OCS for each particular tag deployment duration was capture in the HIDS on monofilament leaders. While this leader material was not in regular use in the HIDS during the study period, a subset of BSH were tagged in this fishery on a vessel using monofilament leaders, thus using this as a baseline allowed the model to achieve some separation between the fishery and leader material effects. All other effects in the model: caught condition (Alive, Good, Injured, Lethargic), handling condition (Line Cut, Gear Removed, Drag Line, Jaw Damaged, Escaped, Dehooking, Part Removed), hooked condition (tail hooked, leader material), amount of trailing gear left on the animal, fishery (HIDS or ASLL), and the individual animal's length were informed by all species due to the data constraints.

Hindcast Survival of Observed Interactions

Two sets of prospective hindcast configurations were considered for observed OCS interactions in the HIDS fishery. The interaction conditions examined in this hindcast were 1) using monofilament branchline leader material instead of a wire leader, and 2) the effects of the remaining trailing gear of either the observed trailing gear length or no trailing gear remaining on the animal at release. For this analysis, the observed interaction conditions were used unless the specific condition was missing, in these cases, the mean condition across all species was used. The observed conditions were missing 62% of the shark length data 99% of the trailing gear data from all shark interactions recorded in the observer data set. The proportion of observed oceanic whitetip shark interactions that would have survived post-interaction given the prospective interactions were tabulated.

Results

Fishery Characteristics, Observer Data Collections, and Tagging

Observers collected shark condition and handling data on 19,572 elasmobranchs incidentally captured during 128 fishing trips on 76 different vessels that occurred between January 2016 and June 2019. During 84 of these trips (ASLL, $n = 14$; HIDS, $n = 70$), 224 sharks were tagged by observers and fishers. Tagging was not conducted on Hawaii shallow-set (HISS) trips targeting swordfish. The handling and damage data recorded by trained observers indicated that most of the five species of sharks considered in this study (BSH, BTH, FAL, OCS, SMA $n = 16,527$ animals) were released by cutting the line (LC = 81.1%). Followed by gear removal with jaw damage (JD = 11.5%), gear removal with no damage to the shark (GR = 3%), gear removal with removal of part of the shark (e.g., lobe of tail on tail-hooked BTH, PR = 0.3%). A small proportion of these sharks escaped the gear on their own (ES = 3%). Other handling methods that were observed included the use of a dehooker (DH = <1%) and a drag line (DL = < 1%). While 1.2 % of sharks were released using some other (OT) method.

The longline gear configurations differ across fishing sectors (Table 3). In the ASLL fishery, branchlines are composed of all monofilament from the clip to the hook. Circle hook

sizes are also a bit smaller than those used in the HIDS and HISS fisheries. The HIDS has a seabird bycatch mitigation measure requiring a weight of at least 45 g be within 1.0 m of the hook. Many fishers choose to use wire leaders between the hook and the weight to increase crew safety and reduce the risk of weights flying back at the vessel if the leader breaks while under tension. The HISS sector does not have a line-weighting requirement but there is a requirement to set at night to reduce seabird interactions. Many vessels still use weights but the leader and branchlines are composed of all monofilament. The length and composition of the trailing gear recorded by observers varied by fishery (Figure 1A) and by species (Figure 1B, Table 2). The HIDS fishery left the greatest amount of trailing gear on sharks, where sharks were released with an average of 8.75 m of trailing gear (Figure 1B). This typically includes a stainless-steel circle hook, 0.5 m of braided stainless steel wire leader, a 45-g weighted swivel, and monofilament branchline ranging in length from 0 to 30.0 m. Whereas sharks released by cutting the line in the ASLL had an average of 2.98 m of trailing gear which is composed of a stainless-steel circle hook to an all monofilament line ranging in length from 0 to 10.0 m. In the HISS fishery sharks were released with an average of 7.74 m of trailing gear, composed of an 18/0 stainless steel circle hook, with a range of 1–18.0 m of all monofilament line and weighted swivels (Figure 1A). Some species were released with more trailing gear than others (Figure 1B, Table 2). This was primarily due to how quickly the fishers were able to ascertain that the catch was a shark and not a target species. The behavior of some species often predicts where the line will be cut; for example, blue sharks tend to surface far away from the vessel and are easy to identify so the line was often cut farther away from the vessel than for some other species. Observers were also asked to record hooking location for thresher sharks. Thresher sharks use their elongated tail to stun prey and are often hooked in the tail. When a thresher shark is tail hooked, it is brought to the vessel backwards and more often (67%) than not (33%), the tip of the tail is removed so that the fishers can get their hooks back (Part Removal; Supplementary Material Table S1).

A total of 224 sharks captured incidentally in the ASLL and HIDS were tagged by fisheries observers (Table 4). ASLL observers tagged a total of 57 sharks: 30 FAL and 19 OCS with SPATs and 8 OCS with miniPATs programmed for a 360-day deployment period. In the HIDS fishery, observers tagged a total of 167 sharks: 44 BSH, 43 BTH, 29 OCS, and 20 SMA with SPATs and 25 BSH with miniPATs (two programmed for 180-day and 23 with 360-day

deployment periods); and 6 OCS with miniPATs programmed for 360-day deployment periods. Six sharks tagged with SPATs were removed from the survival analyses because the effect of the tagging event on post-release fate could not be ruled out after video review (Table 4; Removed). In addition, several tags failed to report any data (Table 4; Non-reporters, n=14) and were also discarded from further analysis.

BSH had the lowest post-release survival rates (62%) of the 5 species tagged in this study. BSH tags also revealed delayed mortalities recorded out to 307 days post-release. Several of the BSH tags were ingested post-release (n = 6, on days 6, 9, 26, 30, 148 and 307 post-release). The ingestions were also considered mortalities and contributed to the overall mortality estimate. Of the BSH mortalities that were not ingestions, 53% occurred within 1 day of release and 76.5% were within 13 days of release. OCS was the only other species tagged with long-term tags programmed out to 360 days yet most (90%) of the mortalities occurred within 4 days of release. Only one delayed mortality occurred for OCS at 22 days post-release. Interestingly, none of the OCS tags were ingested. One of the OCS tagged with a miniPAT was recaptured by a Tongan longline vessel 197 days after tagging. This animal was recorded as dead at capture by the longliner and the tag was recovered and returned to us. BTH were only tagged with SPATs programmed for 30- and 60-day deployment periods and had the second lowest post-release survival rate of 82%. All of the BTH mortalities occurred between 0 to 3 days post-release with the exception of one tag that was ingested on day 24. FAL were only tagged with 30 day SPATs and had the highest post-release survival rate out to this period of 97%. The only mortality for this species occurred within 6 days post-release. SMA were tagged with SPATs programmed for both 30- and 60-day deployment periods revealing a relatively high post-release survival rate (94%). This species had the lowest sample size in this study because tagging of SMA commenced only recently and tagging is ongoing. To date, only 1 mortality occurred immediately after release as the animal had swallowed the hook and was injured. Tag deployment and release (pop-off) locations are illustrated in Figures 2A (HIDS) and 2B (ASLL).

Survival Analysis

Proportional hazard model fit

The proportional hazard model converged with all chains visually mixing (Figure S1) and the Gelman-Rubin statistic was less than 1.1 for all parameters. The posterior predictive check indicated that the model predicted higher survival times than observed for individuals dying within a few days of the fishing interaction and lower than observed for individuals surviving longer than 50 days (Figure 3). For a few BSH individuals in the former group, \tilde{T} was between 84 and 122 days and far higher than the observed T . The model goodness of fit for the uncensored individuals, R_0^2 , was 0.23, while the model goodness of fit overall was 0.86. The latter resulted from 96% of the censored individuals having the condition $\tilde{T} > T$.

The median log-transformed baseline hazard rates, γ , varied from -7.1 to -2.0, resulting in baseline survival times of 10 days to 1,318 days (Figure 4A). In general, 30-day tags had lower γ values than the 60-day tags (resulting in higher hazard rates in 60-day tags) but higher γ values than 180- or 360-day tags. Among the 5 species, BSH had the highest hazard rate (0.076), followed by OCS (0.033), BTH (0.020), SMA (0.017), and FAL (0.012). The fishery interaction covariates, β , had wide credible intervals generally and only the individual's length and tail hooking (BTH only) were significantly different from zero (Figure 4B). The covariates with median hazard ratios that increased the hazard were the Injured caught condition, Jaw Damaged handling condition, Part Removal handling condition, trailing gear length, tail hooking, wire leader material, and ASLL fishery interaction. All other covariates reduced the hazard (Figure 4C).

Survival Curves

Between the species caught in the HIDS fishery, BSH had the lowest survival rate, followed by BTH, OCS, and SMA at their mean interaction conditions (Figure 5A). For the species caught in the ASLL fishery, OCS had a lower survival rate than FAL at their mean interaction conditions (Figure 5A). The only species tagged in both fisheries, OCS, had lower survival in the ASLL fishery than the HIDS fishery (Figure 5A); this result is not unexpected given the positive effect size (hazard ratio > 1) of the ASLL fishery (Figure 4B). Between caught conditions, sharks caught in Good condition had the highest survival rates, followed by the Alive

condition, Lethargic, and then the Injured condition (Figure 5B). Using wire leader material lowered the survival rate (Figure 5C), as well as, tail hooking (BTH; Figure 5C) lowered the species-specific survival rate relative to mean conditions (Figure 5A). For handling methods involving direct contact with the shark or the hook, damaging the jaw (Jaw Damaged) had the lowest survival rate, then removing parts (Part Removal), then removing the gear (Gear Removed), then dehooking (Figure 5D). Between handling methods involving the line, sharks escaping the gear (Escaped) had the highest survival rate, followed by cutting the line (Line Cut), and then dragging behind the boat (Drag Line) (Figure 5E). Although the median survival rates for Line Cut and Drag Line are similar, the 90% credible interval of the Drag Line condition encompasses far lower survival rates than those within the 90% credible interval for the Line Cut. Increasing the amount of gear on the shark negatively affected the survival rate with the best survival occurring with no gear or only up to a meter of gear left on the shark at release (Figure 5F). These results are also summarized at 1, 30, 60, 180, and 360 days post-interaction in the Appendix, for all species (Table A1) and for each individual species; BSH (Table A2), BTH (Table A3), SMA (Table A4), FAL (Table A5) and OCS (Table A6).

Expected Survival Projections

Of the 5 shark species considered here, BSH were most frequently caught, followed by BTH, SMA, FAL, and OCS in the observed sets of the HIDS and the ASLL fisheries between January 3, 2005 and December 4, 2019 (Table 5). It should be noted that both fisheries have, on average, approximately 20% observer coverage, and thus, the shark interactions used in this analysis do not account for the total fishery interactions. Between 2017 and 2019, observer coverage on ASLL trips ranged from 15.7% to 20% and was consistently around 20.4% in HIDS over the same period. The majority of individuals were alive when captured in both fisheries, and close to 20% across species were assigned a Dead caught condition in the HIDS with the exception of BSH where at vessel mortality is much lower. It is noteworthy that the proportion of sharks that were caught Dead in the ASLL fishery was much higher for SMA (44.4%), FAL (35.8%) and OCS (35.8%) (Table 5). Of the 5 species, BSH had the lowest proportion of dead animals at capture in both fisheries (Table 5). The observer data set was missing data for several of the influential survival covariates; only one third of all shark interactions contained animal length data, about 1% had data on trailing gear lengths, and between 2% to 5% had fisher

handling methods with the vast majority recorded as No Damage (the default designation for the observer program outside of this study focusing on shark interactions) (Table 6).

Projections of expected survival to the observed data set revealed BTH to have the lowest initial survival for sharks that were assigned as 1 of the 3 Alive caught conditions (Table 7). Not surprisingly, this species also had the lowest estimated survival 360 days later followed by OCS caught in the American Samoa fishery. SMA, had the highest survival across all projected time points. When including the sharks that also were assigned a Dead caught condition, FAL had the lowest initial survival but BTH had the lowest long-term survival (Table 7). The most numerous species caught, BSH, had extremely high initial survival for those caught alive and only a 5% reduction in the median when factoring in those that were dead at capture (Table 7).

ESA Listed Oceanic Whitetip Shark Mortality Mitigation

Individual Post-interaction Survival

Two prospective gear configurations considered for individual OCS interactions with the HIDS fishery were 1) wire or monofilament leaders on branchlines, and 2) different trailing gear lengths (0, 1.8, 3, 5.15, 10, 14 m) for sharks at release. The latter represents the 20th percentiles of trailing gear lengths observed remaining on sharks at release during tag deployments on OCS in this study. These two prospective post-interaction conditions were crossed so that trailing gear at various lengths with wire or monofilament leaders was evaluated (Table 8). The model revealed that over a 360-day time duration, switching from wire leader material to monofilament has a small improvement in survival rates while trailing gear length has a much larger impact on survivorship.

Hindcast Survival of All Observed Interactions

A total of 4,322 OCS interactions with the HIDS fishery were observed by the PIROP between 2005 and 2019 (3,392 alive and 930 dead at haul back). In this comparison of leader material and trailing gear effects on survival for OCS that were alive at the vessel and for all sharks captured (Alive and Dead) the tabulations also show that leader material has a small effect on survival where sharks captured and released with monofilament gear have a higher survival

rate over time (Table 9). The effect of trailing gear on survival is greater than leader material, where OCS survival rates are higher when it is minimized for both leader materials.

Discussion

Longline fisheries have the largest impact on pelagic shark populations due to the scale and magnitude of global fishing effort, such that finding strategies that can increase post-release survival is paramount. This study used satellite linked PATs to generate quantitative estimates of post-release survival rates for 5 of the most frequently captured and discarded shark species, BSH, BTH, OCS, SMA and FAL sharks, in 2 tuna target longline fisheries in the Pacific Ocean. By working directly with observer programs and fishers to record detailed information about each interaction, our modeling approach was able to estimate realistic, scenario-based survival rates to predict post-release survivorship for inclusion in stock assessments and population projections. This study also elucidates the handling and discard methods that improve survival probabilities post release.

For fisheries where no-retention measures have been implemented to reduce mortality, it is important that post-release fate is well understood to assess the efficacy of the measures. In the WCPFC, no-retention measures have been adopted for both OCS and FAL. In the eastern half of the Pacific Ocean the Inter-American Tropical Tuna Commission has also adopted a no retention resolution for OCS [C-11-10] and has enacted longline fishing restrictions for FAL in nursery areas and established FAL catch limits for some fleets [Resolution C-19-05]. In the Atlantic Ocean the International Convention for the Conservation of Atlantic Tuna adopted no-retention measures for; BTH [BYC-09-07], FAL [BYC-11-8], OCS [BYC-10-07] and SMA [BYC-19-06 (with caveats)]. In the Indian Ocean, the Indian Ocean Tuna Commission enacted no retention measures for *Alopias spp.* [Resolution 12/09] and for OCS [Resolution 13/06]. All of the measures outlined above call for fishers to release sharks in manner that minimizes harm but do not outline exactly how to minimize harm during the fishing interaction. The data generated in this study will help RFMOs address issues surrounding conservation and management measures by providing quantitative estimates of post-release survival for 5 of their key shark bycatch species, as well as data derived recommendations for improving handling and discard practices and details on the effects of leader material on survival.

Species specific survival rates

Some species are physiologically more sensitive to capture related stress, and at-vessel mortality rates tend to reflect which species are more resilient than others (e.g., Marshall et al 2012; Mandelman and Skomal 2009). In this study we assessed survival in pelagic species that occupy a range of ecological niches, vertical depth distributions, aerobic capacities and span the spectrum of differential sensitivities for highly mobile obligate ram ventilators. Here at-vessel mortality ranged from 4% in BSH to 29.2% for FAL when data from both fisheries was combined. FAL, BTH, OCS and SMA all had very similar at-vessel mortality rates of 20.6%–23.2% in the HIDS fishery but these rates increased dramatically in the ASLL.

Silky shark

Silky sharks had the highest at-vessel mortality rate (29.2%) and also the highest post-release survival rate (97%) compared to all other species examined in this study. FAL were only tagged in the ASLL fishery and only if they were in good condition at the vessel. In addition, these sharks were consistently released with short lengths of trailing gear. Capture condition has been shown to be the most influential factor on post-release survival probabilities in this and in other studies (e.g., Musyl and Gilman, 2018, Hutchinson et al. 2015, Francis et al. 2019). Thus, the post-release survival rates generated in our study are likely an optimistic estimate and should be taken in consideration with similar studies that have been conducted on this species. Other studies on post-release fate of FAL also found high post-release survivorship for sharks captured in longline fisheries. In the equatorial western Pacific Ocean, FAL had 91% post-release survival out to 60 days if uninjured, this estimate dropped to 44% if injured (Francis et al. 2019). In a Palauan fishery post-release survival rates were 80% for sharks tagged in all conditions with all mortalities occurring within 1 day of release (Musyl and Gilman 2018). On the eastern side of the Pacific Ocean in Central America and Mexico, FAL tagged in panga style longline fisheries using long-term tags also had high post-release survival rates of 94% to 20 days and 91% to 132 days, respectively (Schaeffer et al. 2019; Schaeffer et al. 2021). They also found that injured individuals were likely to die within 1 to 3 days of release and the delayed mortalities that did occur in some individuals after 133 and 168 days were not attributed to the fishing interaction (Schaeffer et al. 2019; Schaeffer et al. 2021).

Blue shark

BSHs represent the highest proportion of total shark bycatch in longline fisheries worldwide. In 2019, the Hawaii longline fleets caught 114,317 BSH, with only 2 sharks retained and the rest of these individuals discarded at sea (PIFSC 2020). Observer data shows that this species has the lowest at-vessel mortality rate of all the shark species assessed in this study (4.9%) where most sharks are released alive. Other studies have shown that hook type, leader material and shark size are important predictors of at-vessel condition for BSH across longline fisheries. At-vessel mortality rates of BSH across these studies are as follows: 11.9% for Canadian Northwest Atlantic Ocean (AO) swordfish (Campana et al. 2009); 13.3% for Portuguese AO swordfish (Coelho et al. 2012); 31% for US Southwest AO swordfish and tuna (Diaz and Serafy 2005); and 31% for AO swordfish and tuna (Afonso et al. 2012). The fishery characteristics likely not only affect at-vessel condition for BSH but also their post-release survival rates. Our tagging data revealed that this species is highly susceptible to mortality post-release and had the lowest post-release survival rate (62%) of the 5 species tagged. Projections of survival rates, out to 360 days under the average interaction conditions, using the observed data set estimated only 18% of sharks survive (see Appendix for species-specific scenario based survival rates). These estimates are alarming and may have broad impacts for population projections and should be integrated into future stock assessments. Other studies that have investigated PRS rates of blue sharks found relatively high post-release survival rates after longline fishery interactions; 83% to 30 days (Musyl and Gilman 2018). In a swordfish target longline fishery in the Northwest Atlantic BSH survival was dependent on at-vessel conditions where all healthy individuals survived, while only 77% survived if injured (Campana et al. 2009, 2016). In both of these studies a proportion of animals were brought on board for tagging and trailing gear was removed. Trailing gear at a shark's release appears to be one of those important interaction conditions that has a large impact on survival for this and other species. In our study BSH were released with a wide range of trailing gear and sharks released with more gear had lower post-release survival. Our study also highlights the susceptibility of BSH to predation with the highest proportion of tags that were ingested (9.7%) by other animals. Of the mortalities that were not due to ingestions, most (53%) occurred within one day of release and 76.5% were within 13 days of release. It is possible that differences in mortality rates across studies are due to fishery characteristics, handling (no trailing gear in the other studies), and the temporal period

of monitoring fate where the 30-day tags capture most mortality events but miss delayed events that could be due trailing gear.

Bigeye thresher shark

This study has demonstrated relatively high post-release survival rates (82%) for BTH captured in the HIDS fishery. Yet, this species is still susceptible to overexploitation because it is one of the least productive of all epipelagic shark species (e.g., ICCAT 2012; Fu et al. 2016) and it is one of the most frequently captured shark bycatch species in longline fisheries targeting tuna and swordfish worldwide (e.g., Walsh et al. 2009; Coelho et al. 2012; Afonso et al. 2012; Fu et al. 2016). In the US Pacific longline fisheries, BTH represent the second most frequently captured shark species behind BSH (Walsh et al. 2009). In 2019, 8,748 BTH were caught in the HIDS with only 58 sharks retained and the rest discarded (PIFSC 2020). The at-vessel mortality rate (21.5%) in the PIROP data set was much lower than those reported rates in other fisheries: US longline fisheries targeting swordfish and tuna in the Western AO, 53.7% (Beerkircher et al. 2004); in the Gulf of Mexico, 55.1% (Gallagher et al. 2014); and in the Portuguese longline fisheries, 50.6% (Coelho et al. 2012). Most of the data from the AO fisheries include periods before J-style hooks were phased out and may account for some of the differences in at-vessel mortality rates with the PIROP data. Further regulatory changes in the Pacific Islands region, including finning prohibitions and fishery closures, have also been shown to reduce BTH mortality (Walsh et al. 2009). In this study, BTH post-release survival rates of tagged animals was 82% where hooking location (mouth vs. tail) and discard methods were very influential on post-release survival. Tail-hooked BTH are in poorer shape at the vessel than if they are mouth-hooked. Additionally tail-hooked animals are often subject to the “Part Removal” handling method where fishers cut the tip of the tail off to retain their hooks (see Supplementary Materials Table S1 for details on handling methods by species and impacts to release condition). These effects were shown to significantly increase the risk of mortality for BTH in this study. Only a few other studies have published BTH post-release survival data after fisheries interactions. Musyl et al. (2011) tagged 8 sharks during scientific longline surveys in the central Pacific Ocean with only 3 tags reporting data with no mortalities. A post-release survival study is currently underway in the Indian Ocean and preliminary data suggests that survival rates are 41% (IOTC 2020). Other tagging experiments for this species reported post release survival rates of

86%–93% after capture in experimental deep-set buoy gear and linked buoy gear targeting swordfish in Southern California (Aalbers et al. 2021; Sepulveda et al. 2019).

A risk assessment of the Pacific population estimated that fishing mortality for this species may far exceed population growth rates when the precautionary approach (no post-release survival) is taken (Fu et al. 2016). Improved estimates of post-release survival and strategies to further improve survivorship such as improved handling will greatly enhance assessments, population projections and the resultant advice that can be confidently conveyed to fishery managers.

Shortfin mako shark

High post-release survival rates and low at-vessel mortality rates were observed for SMA in the HIDS; caution, however, is still warranted for SMA populations as they are currently overfished in the AO and the third most frequently encountered shark bycatch species in the US Pacific longline fisheries. This species is generally discarded in the HIDS, but is sometimes retained as it is considered a marketable consumer product. In 2019, total discards in the US Pacific longline fisheries was 4,522 animals with ~ 11% retained (PIFSC 2020). At-vessel mortality rates (22.7%) for this species in the PIROP data set were low compared to other studies in longline fisheries: 100% in the IO (Coelho et al. 2011); 26% (Campana et al. 2016), 35.6% (Coelho et al. 2012), and 75% (Afonso et al. 2012) in the AO; and 35.0% (Beerkircher et al. 2004) and 29.3% (Gallagher et al. 2014) in the US longline fisheries targeting swordfish and tuna in the Western AO and Gulf of Mexico. Post-release survival rates for SMA that were discarded were estimated to be relatively high (94%) in this study with only 1 mortality observed out of 18 tags that reported. Other studies with much larger sample sizes also found high post-release survivorship for SMA captured in longline fisheries: in the equatorial western Pacific Ocean, 88.4% in uninjured SMA out to 60 days, this estimate dropped to 36.8% if the SMA were injured (Francis et al. 2019). A study on SMA post-release survival in the AO also noted that condition was a factor where 70% of healthy SMA survived while 67% of injured SMA survived (Campana et al. 2016). The disparity in post-release survival estimates from this study in comparison to others with larger sample sizes warrants further investigation.

Oceanic whitetip shark

The WCPFC oceanic whitetip shark population is overfished and experiencing overfishing (Tremblay-Boyer et al. 2019). It is also now an ESA listed species and the United States NMFS is mandated to determine strategies to rebuild the population. Because the largest threat to this species is overfishing, reducing mortality in US fisheries and in foreign fleets that impact the same populations is imperative. In the 2019 stock assessment, several scenarios included survivorship estimates (Hutchinson and Bigelow 2019; Francis et al. 2019) for the first time. The combination of no retention measures and a proportion of discards surviving resulted in the most optimistic outcomes in the assessment with slight increases in spawning biomass (Tremblay-Boyer et al. 2019). Post-release survival rates from OCS tagged in both HIDS and ASLL was 85%. We know of no other studies with published post-release survival in commercial longline fishery data for comparison. This was the only species tagged in both fishing sectors and our analysis showed that fishery was indeed an important factor in which survival was higher in HIDS compared to ASLL. The projections of survival data across the observed data set may have been impacted by at-vessel mortality rates that were higher in ASLL (32.7%) than in HIDS (21.5%) for this species. The combined at-vessel mortality for both fisheries (21.9%) for the PIROP data set was lower than in other studies: 27.5% (Beerkircher et al. 2002), 34.2% (Coelho et al. 2012), 40% (Gilman et al. 2016), 33–62.5% (Nunes et al. 2019).

Fishery and handling method effects on survival

Survival estimates for shark bycatch may not only be species specific but also fishery specific, due to operational and gear configuration characteristics, but also on how fishers release animals from the gear. In this study, we found that most fishers cut the branchline while the shark was still in the water leaving different quantities and compositions of trailing gear attached to discarded animals. Other methods that were used less often included the following; bringing sharks onboard, or pulling them out of the water to get their hooks back, or using a drag line to drag the sharks behind the vessel until the hook pulled from the shark. Other handling methods observed that resulted in damage to the animal were gear removal with “Jaw Damage,” or “Part Removal.” Jaw damage occurred when fishers cut through the jaw’s cartilage to remove a hook. In these cases not only is there physical damage to the animal but it may often require additional

handling time or time out of water that would also impact their vitality post-release. Part removal in sharks almost exclusively applied to the removal of tail-hooked thresher sharks from the gear. Part removal and damaged jaws during discarding had a default release condition of Injured. Tail hooking, jaw damage, part removal, and injured condition were all significant variables that contributed to mortality.

Our analyses showed that leaving sharks in the water and removing as much trailing gear as possible by either using a dehooker or cutting the line had the best survival outcomes. A similar study on SMA and FAL also found that survival rates were higher when trailing gear was minimized particularly in relation to the size of the animal (Francis et al. 2019). This same study also concluded that even though there were no data showing that hauling sharks on deck contributed to mortality, it did show that injured sharks are less likely to survive and the probability of injury is higher when sharks are hauled onboard. In the Atlantic Ocean swordfish longline fisheries, a study that investigated post-release mortality of SMA, BSH, and porbeagle sharks did not investigate handling effects but brought sharks onboard the vessel for tagging and removal of fishing gear (Campana et al. 2016). They found the effect of the boarding to be negligible but also demonstrated much lower post-release survival rates in sharks that were released in good condition than the present study and the study published by Francis et al. (2019).

Because most sharks are released by cutting the line (~84%), fishers have the opportunity to make small changes in their operating procedure with significant impacts on bycatch survival. If they take time to remove as much trailing gear as possible, ideally leaving less than 1 m, survivorship can be improved by as much as 40% over 360 days. Notably, different species are released with different lengths of trailing gear. Some differences in trailing gear length are likely due to differences in fishery operations between the ASLL and HIDS fisheries with the ASLL fishers using shorter branchlines and smaller vessels allowing fishers to bring animals closer to the vessel to cut the line. Yet, across species we found that both BSH and BTH are typically released with longer lengths of trailing gear than both OCS and FAL amongst the different fisheries. This may be symptomatic of how the different species behave on the line. For example, BSH surface early and can be seen farther away from the vessel, thus the fisher can cut the line as soon as they see that it is a shark. Threshers often fight very hard against the gear and either come flying out of the water when mouth hooked or take deep dives when tail hooked; therefore,

these sharks can be identified quickly and their lines can then be cut when the animal is farther away from the vessel. Conversely, both FAL and OCS do not surface until they are closer to the boat. These species are also harder for some fishers to identify to species from further away, so they are brought closer to the vessel where the crew can cut more line off.

Leaving large quantities of trailing gear is not only energetically costly for the animal, but may also introduce infection, present an entanglement hazard and increase susceptibility to predation. Mortalities that would be due to the energetic drain of trailing gear would probably occur outside the 30–60 day window of the deployment period of the survivorship tags that were used for most of the sharks in this study. We found that delayed mortality (beyond 30 days) and ingestion rates were high in the small number of blue sharks that were tagged with miniPATs programmed for 360-day deployment periods and released with long lengths of trailing gear. OCS that were tagged with long-term tags and released with trailing gear did not show any delayed mortalities and none of the tagged OCS were ingested by other animals. This detail may have broad implications for the determinations of post-release mortality rates derived from survivorship tags since most survival studies use tags with 30–60 day deployment periods (this study; Musyl and Gilman 2018; Francis et al. 2019). It is nearly impossible to point directly to trailing gear as a cause of mortality however. Yet this study and the Francis et al. (2019) study both show that longer lengths of trailing gear have a negative impact on survivorship over time. Interestingly, mortality rates for oceanic whitetip sharks, the only species tagged in both fisheries were higher in the ASLL sector than in the HIDS sector, even though average trailing gear lengths were shorter in the ASLL fishery. At-vessel or haul-back mortality rates were also higher in ASLL than in HIDS. One potential variable that was not assessed independently because it is crossed with fishery, is the effects of temperature on survival rates. Temperature is known to have a profound effect on the physiology, metabolism, stress, fitness, performance, and survival of animals (Hochachka and Somero 2002; Angilletta 2009). Warmer seawater temperatures encountered in the ASLL fishery may exacerbate the stress response in sharks captured in fishing gear.

Some studies have shown that metabolic and respiratory acidosis are temperature-dependent reactions and may be the actual cause of mortality on longlines where obligate ram ventilation sharks are able to swim and respire while fighting on the line. Warmer temperatures for poikilothermic species that are physiologically less effective at clearing lactic acid buildup

from anaerobic exertion could induce lethal physiological disruptions in their acid base status. A study from the same region on juvenile silky sharks captured in purse seine nets showed that lactic acid concentrations in the blood was correlated to at-vessel condition and post-release mortality rates (Hutchinson et al. 2015). This same study concluded that these sharks died due to metabolic acidosis, where respiratory acidosis had less of an effect, which is counterintuitive for species that had been restrained in a net. This suggests that silky sharks and perhaps species that occupy similar niches such as OCS are less resilient to capture stress in warmer waters. A comparison of at-vessel mortality rates of 5 sharks species; BSH, SMA, FAL, BTH and smooth hammerhead sharks (*Sphyrna zygaena*) captured on longlines targeting swordfish in the Indian Ocean (IO) and the Atlantic Ocean (AO) found much higher at-vessel mortality rates across all 5 species in the IO where water temperatures are consistently warmer than the AO (Coelho et al. 2011).

Delayed Mortality

Detecting the difference between fishery-induced (both acute and tertiary) mortality and mortality as a result of tagging or even natural mortality over time is the subject of intense speculation. Most studies investigating post-release mortality rates somewhat arbitrarily assign a cut-off period for mortality that can be directly attributed to the acute effects of the fishery interaction. Most of the mortalities in this study occurred within a few days of the fishing interaction across species: OCS (0–4 days), FAL (7 days), BTH (0–3 days), SMA (0.5 days). BSH however, demonstrated a high rate of delayed mortalities out to 307 days post-release. Other post-release survival tagging studies on pelagic sharks captured in longline fisheries also show that most mortalities occur within 1–3 days of the interaction. Campana et al. (2009) showed that 95% of mortalities in the AO swordfish fishery occurred within 11 days of the fishing interaction for BSH. They used tags that recorded time-series depth data and a period of recovery behavior was noted out to 11 days where the animal either resumed normal vertical movements or died (Campana et al. 2009). While most mortalities for SMA occurred within 2 days of release in this same fishery (Campana et al. 2016). Most SMA mortalities also occurred within 2 days of the fishing interaction in the South Pacific study as well (Francis et al. 2019). Consensus on an appropriate duration for which to assign a mortality to a fishing event across studies seem to converge at a point of around 15 days where a 30-day tag deployment period

may be sufficient to capture approximately 90% of post-release mortality events related to the fishing interaction (Reviewed in Musyl and Gilman 2019).

Physiological damage from embedded hooks, trailing gear and from tag attachment has been documented in several shark species. Ingested hooks have shown evidence of induced disease, including coelomic carcinoma, hepatitis, necrotizing peritonitis, pericarditis and gastric perforation that contributed to low body weight in recaptured BSH (Borucinska et al. 2001, 2002, and 2003). Retained fishing hooks were also noted in 6 of 211 BSH captured by recreational fishers in New York over the 1-year period (Borucinska et al. 2003). Sharks are negatively buoyant so most mortalities of pelagic sharks result in the animal sinking out of the water column. In one report, however, a longfin mako washed ashore with an embedded hook surrounded by a pericardial mass and systemic diseased tissue (Adams et al. 2015). This report provided evidence of direct mortality as a result of systemic lesions from retained fishing gear. Retention of hooks and trailing gear from fishery interactions has also been photo documented in some shark species. A photo identification program in Tahiti observed that galvanized hooks rusted away after 2.5 years while stainless steel hooks persisted for at least 7.6 years in tiger sharks (Begue et al. 2020), suggesting that trailing gear may have long-term impacts on discarded sharks. Tagging might also be a source of infection or physical deformation. Some fin mount tags have been shown to cause permanent damage to dorsal fins but did not appear to impact vitality in white sharks (Jewell et al. 2011). It is difficult to verify whether or not the delayed BSH mortalities we saw in this study were a direct result of the initial fishing interaction, particularly since chondrichthyan fishes are well known for their capacity to heal from traumatic wounds (e.g., mating scars; Chin et al. 2015). Additional work to assess delayed mortality rates due to fishing interaction and potentially the trailing gear needs to be conducted.

Another scenario that may also comprise a significant portion of undetected mortality is recapture. In this study, a tagged OCS was recaptured by a Tongan longliner, and the tag was returned to us by the fishing company. Although the animal was dead at the vessel, the tag data showed that it was a “floater.” Without contact by the fishing company about the recapture, it would have been difficult to distinguish a recapture that goes unreported from other “floater” tags using the transmitted data alone. In survival analyses, a tag that was considered a “floater”

would be treated as a censored event, where the animal was alive at the time that it left the study prematurely.

Furthermore, the tag fates of the early SPATs communicated by the tag manufacturer is a simplistic interpretation of the tag data and may not always represent the myriad of potential fates for tagged animals. For example, several of the tags deployed in this study were ingested by thermo-regulating predators and subsequently regurgitated. The tag fate was determined to be a “floater” by the manufacturer (tag was shed as a result of attachment failure), but careful analysis of the tag report showed temperatures did not change with depth and or no changes in light levels. Ingested tags may be easier to detect when they are ingested by thermo-regulating species, but this may not be the case when tags are ingested by poikilotherms. There is also the potential for tags to be bitten off the animal, which would not always result in mortality for the tagged animal. In this study and in the Francis et al. study (2019), ingestions of tags were shown to occur throughout the deployment periods. Attributing the impact of the fishery interaction to susceptibility to predation is another tenuous venture and what we are seeing in these ingestions may actually be insight into food web dynamics at the top of the food chain.

Focus on Mortality Mitigation for ESA Listed OCS

The western and central Pacific Ocean (WCPO) OCS stock was determined to be overfished and experiencing overfishing as of the latest assessment in 2019 (Tremblay-Boyer et al. 2019). On May 4, 2020, the WPFMC was notified by NMFS of the overfished and overfishing status based on best scientific information available and of its obligations to take action within 1 year of that notice, pursuant to the Magnuson-Stevens Fishery Conservation and Management Act (MSA). To satisfy requirements under MSA Section 304(i) data regarding actions that will lead to ending overfishing and rebuild the WCPO OCS stock are necessary for both managers and stakeholders. One option that has been proposed by the fishing industry is to move away from using wire leaders in the HIDS fishery. We explored the OCS post-release survival data generated in this study to assess how changes to leader material in the HIDS may affect post-release survival rates. Our tabulations showed that the change from wire to monofilament leader materials do have a small (~2%–4%) increase in post-release survival rates over time in all of the scenarios considered in this study. A more significant improvement in post-release survival rates occur when sharks are captured in the HIDS over the ASLL (potential

temperature effects on shark survival between these fisheries is discussed above) and when trailing gear is removed (~28%).

The potential to reduce shark bycatch rates and mortality by using monofilament leaders vs. wire leaders has been investigated in other regions with a positive effect (e.g., Ward et al. 2008; Coelho et al. 2013). At-vessel mortality of BSH captured in a longline swordfish fishery showed that mortality rates were higher on lines composed of wire leaders as opposed to monofilament leaders (Coelho et al. 2013). In an AO fishery where the difference in mortality rates between monofilament and wire leaders was assessed they noted that this improvement was only present when J-style hooks were used compared to the circle hooks that are mandated in the HIDS and ASLL fisheries (Afonso et al. 2012). Further, when “bite-offs” (i.e., sharks bite through the monofilament leaders) were counted, the difference in shark catch rates between monofilament and wire leaders was non-existent (Afonso et al. 2012). As the United States moves forward in devising OCS mortality mitigation strategies, switching from wire leaders to monofilament leader material will allow some sharks to cut themselves free of the fishing gear, which may have a larger positive, albeit unmeasurable impact on improving survival of OCS bycatch. This analysis highlights the importance of reducing trailing gear, regardless of material, to improve the post-release survival rates of discarded sharks in addition to changes in leader materials.

Conclusions, Recommendations, and Next Steps

In this study, we show post-release survival rates are high to 30 days for BSH, BTH, FAL, SMA, and OCS if they are in good condition at release, the line is cut to release them from the gear and if trailing gear is minimized. We found that the amount of trailing gear left on an animal has a negative effect on post-release survival potential for multiple species and is correlated with high delayed mortality rates of BSH (beyond 30 days). Because most sharks are released by cutting the line, making recommendations to remove as much trailing gear as possible will enhance post-release survival rates. In the WCPFC, no-retention measures for silky and oceanic whitetip sharks may have the intended effect of reducing mortality if the measure included handling guidance and requirements to reduce the amount of trailing gear left on animals to less than 1 m.

Improved data collection for sharks will also improve estimation of post-release survival rates. Here we find that species, size, capture and release conditions, handling and release method, trailing gear, and hooking location all influence the post-release fate of discarded sharks, but only a small proportion of shark catch records contain these data. Roughly a third of all shark catch records have length estimates, while trailing gear was recorded for ~1% of sharks and handling information was available for ~3% of sharks. These details would facilitate good estimates of post-release fate and fill data gaps that have previously been unavailable for stock assessments. As the United States continues to work towards shark bycatch mortality reduction it is important that the number of ‘bite-offs’ are also recorded by observers so that fishery impacts can still be estimated (Afonso et al. 2012). Emerging technologies such as eDNA may also be effective in identifying ‘bite-offs’ to species (Kraft et al. 2020) and should be explored further.

Further investigation of post-release survival rates is required to refine the estimates garnered in this study. The survival rate credible intervals were quite large for several of the species across scenarios. Future FAL tagging effort should also include sharks in compromised conditions and in the HIDS fishery to get a more encompassing understanding of the impacts of US longline fishing on Pacific populations. Additional tagging is also necessary for SMA as tag numbers were relatively low for this species. Because delayed mortality rates for BSH were so high, it is also recommended that more long-term tags be used in future studies.

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Tables and Figures

Table 1. Condition and handling metrics. Condition, handling and damage codes, definitions and criteria for shark bycatch species captured during trips with observers participating in this post-release survivorship study.

Condition at Capture and at Release		
Condition	Definition and Criteria	Code
Alive, in Good Condition	Animal appears lively and healthy with no obvious signs of injury or lethargy (animal should appear active). This condition code is used when ALL of the following criteria are observed and met: 1) no bleeding, 2) shark is actively swimming, 3) not upside down and/or sinking, 4) no external injury, 5) not hooked in the esophagus, stomach or the gills.	AG
Alive	Animal was observed to exhibit signs of life, but its level of activity or injury could not be established or the criteria for the AG or AI codes are not met. This code is the default for any live animals that could not be further categorized for any reason including the animal was too far away to discern whether or not the AG or AI criteria were met.	A
Alive but Injured	Animal was alive but there was clear evidence of serious injury. The serious injury category is met when ONE OR MORE of the following injury criteria exists: 1) the hook has been swallowed (e.g., the bend of the hook is not in the tissue surrounding the jaw but has been ingested posterior to the esophageal sphincter or deeper), 2) bleeding is seen from the vent and/or gills, 3) stomach is everted (please specify in comments), or 4) other damage (e.g., depredation, entangled in gear) occurred prior to or as a result of hook/gear removal. This code should also be used if the animal is boarded through the use of a gaff or grappling hook. Gaffed animals should have a brief comment on where the gaff was embedded e.g., head, gills, back, pectoral fin, etc.	AI
Alive but Lethargic*	Animal is alive but does not meet criteria for AG or AI. Appears extremely lethargic at the vessel and makes little to no effort to swim or fight against the gear.	AL*
Kept	Animal retained by the vessel	K
Dead	Animal showed no signs of life.	D
Handling and Damage		
Line Cut	Shark/ray is released by the crew cutting any portion of the branchline. In the measurements column please specify the	LC

	quantity of gear still attached to the animal.	
Gear Removed	The fishermen attempt or successfully remove the fishing gear from the animal. Some fishermen may bring the shark to the fish door of the vessel and lift and drop it so that the hook tears out or lift the shark and cut the hook out or bring them onto the deck near the cutout or a combination of these. To remove the gear, fishermen may also cut the lip to remove the hook. If they must cut into the jaw or pieces of the jaw come off as a result of the handling please use JW code to record the jaw was damaged (JW) during the interaction. Furthermore, if there was more damage to the shark during the interaction (e.g., they gaffed the animal to bring it on board) please mark the comments box and describe the handling and damage to live animals. When gaffs are used, please note the location where the gaff was embedded (e.g., body, gills, eye, mouth, etc.).	GR
Escaped	Shark/ray freed itself (e.g., throws the hook, breaks the line, or becomes disentangled in the gear).	ES
Jaw Damaged	Anytime a shark/ray's jaw is cut or damaged to remove the gear. This would include sharks/rays whose jaws are removed in part or wholly or if the shark's jaw is cut to remove a hook.	JW
Part Removal	If any part of a shark/ray is cut or removed to retrieve the gear. This would include partial or complete removal of any portion of a fin, tail, spine, or other body part. Tail-hooked thresher sharks that get their tails (any portion of it) cut off, and stingrays that get their "stingers" cut off are common examples covered by this code. This code would not refer to any situation covered by the JW code. If a shark/ray disposition is undetermined, the default Release code for this handling method is AI.	PR
Dehooker	This code is only used when a dehooking device successfully removes the gear from a shark/ray without the use of any other handling methods.	DH
Drag Line Employed	If the shark/ray is connected to a long line at the stern of the vessel and dragged until the line breaks, the hook becomes dislodged or the shark comes off the line. Please record in the comments sections if there are portions of jaw still attached to the hook when it is retrieved or the animal is dragged for a long time period, record the time.	DL
Other	This code is only used when the handling technique you wish to describe is not covered by any other code, and must be accompanied by comments describing the situation (e.g., a bang stick, firearms, and spine).	OT
Disposition Not Observed	Use this code when you did not see the dispatch and or handling methods used to remove the shark from the gear	DN

*This code was not available to observers, but could be assigned by the reviewer after examining the observer notes or video and deemed the animal to be lethargic.

Table 2. Trailing gear lengths. The average length and range (m) of trailing branchline remaining on sharks after release from longline gear as recorded by observers participating in this study by species and fishery.

Species	ASLL	HIDS	HISS
BTH	2.35 (1–8)	7.39 (1–25)	6
BSH	3.27 (0–9)	8.93 (1–30)	7.77 (1–18)
FAL	1.73 (0–8)	6.07 (2–15)	2.33 (2–3)
OCS	1.86 (0–3)	5.44 (1–12)	3 (2–3)
SMA	2	6.07 (2–15)	8.55 (2–18)

Table 3. Fishery characteristics. Gear configurations by fishery for American Samoa tuna (ASLL), Hawaii deep-set for tuna (HIDS) and Hawaii shallow-set for swordfish (HISS) longline fisheries. The mean and range (in parentheses) are reported for number of hooks per float, number of hooks set and branchline length.

<i>Gear</i>	Fishery		
	<i>ASLL</i>	<i>HIDS</i>	<i>HISS</i>
Circle hook sizes	13/0, 14/0	14/0, 15/0, 16/0	18/0
Hooks per float (N)	29 (28–35)	25 (21–38)	5–6
Hooks set (N)	2,827 (1,684–3,457)	2,777 (1,252–4,349)	974 (472–1,313)
Branchline composition	All monofilament	Stainless steel braided wire leader (0.5 m–1.0 m), 45-g weighted swivel, monofilament to clip.	All monofilament (some vessels use weighted swivels several meters above hook).
Branchline length (meters)	11.0 m (11.0 m–13.0 m)	12.5 m (10.0 m–17.0 m)	10.9 m (7.0 m–13.0 m)

Table 4. Tag deployment details. The total number of tags deployed by species, along with the number of mortalities, number and proportion of sharks surviving during tag deployment, number of tags that did not report data (Non-reporters) and the number of tags that were removed from the analyses due to possible effects on survival from tagging.

Species	Died	Survived	Proportion surviving (%)	Non-reporters	Removed	Total tags deployed
BSH	23	38	62	7	1	69
OCS	8	47	85	4	3	62
BTH	7	33	82	1	2	43
FAL	1	29	97	0	0	30
SMA	1	17	94	2	0	20

Table 5. Observed shark capture conditions. Number of sharks by species caught alive or dead by either the HIDS or ASLL fisheries between January 3, 2005, and December 4, 2019, along with percentage of the total numbers caught that were dead when brought to the vessel (capture condition).

Species	Alive			Dead			%Dead		
	ASLL	HIDS	Combined	ASLL	HIDS	Combined	ASLL	HIDS	Combined
BTH	403	21,378	21,781	114	5,861	5,975	22.1	21.5	21.5
SMA	508	11,754	12,262	406	3,058	3,464	44.4	20.6	22
FAL	2,485	3,278	5,763	1,387	988	2,375	35.8	23.2	29.2
OCS	912	3,392	4,304	443	930	1,373	32.7	21.5	24.2
BSH	7,833	250,500	258,333	477	10,302	10,779	5.7	4	4

Table 6. Observed data coverage for survival metrics. Percentage (%) of individual shark interactions from the PIROP and ASOP data sets where the survival covariates (Length, Trailing gear, and Handling method) were recorded. For the handling conditions, the percentage was calculated based on having any of the handling conditions used in the survival analysis (from Table 1).

Species	Length (%)	Trailing gear (%)	Handling method (%)
BTH	35.27	1.01	2.56
SMA	32.36	0.92	2.08
FAL	28.56	1.17	4.95
OCS	37.81	0.95	3.18
BSH	41.61	1.3	2.82

Table 7. Survival projections. The proportion of sharks estimated to have survived the interaction to the time specified using the mean condition from the survival model and extrapolated across the observer data set between January 3, 2005, and December 4, 2019, is presented below by capture condition, species, and fishery. For the “Any” capture condition this includes sharks that were alive and sharks that were dead at the vessel.

Capture condition	Fishery	Species	1 day	30 days	60 days	180 days	360 days
Alive	HIDS	BTH	0.96 (0.81–0.99)	0.43 (0.09–0.81)	0.26 (0.02–0.67)	0.05 (0–0.38)	0.01 (0–0.21)
Alive	HIDS	SMA	1 (0.98–1)	0.89 (0.61–0.98)	0.8 (0.45–0.96)	0.57 (0.19–0.88)	0.41 (0.06–0.79)
Alive	HIDS	OCS	0.99 (0.94–1)	0.84 (0.34–0.98)	0.73 (0.18–0.97)	0.45 (0.02–0.91)	0.27 (0–0.83)
Alive	HIDS	BSH	0.99 (0.94–1)	0.77 (0.39–0.96)	0.63 (0.25–0.92)	0.37 (0.05–0.78)	0.22 (0.01–0.64)
Alive	ASLL	FAL	0.99 (0.89–1)	0.78 (0.2–0.98)	0.65 (0.08–0.96)	0.41 (0.02–0.89)	0.24 (0.01–0.8)
Alive	ASLL	OCS	0.99 (0.88–1)	0.72 (0.18–0.97)	0.57 (0.06–0.94)	0.31 (0.01–0.83)	0.15 (0–0.71)
Any	HIDS	BTH	0.75 (0.64–0.78)	0.34 (0.07–0.63)	0.2 (0.01–0.53)	0.04 (0–0.3)	0 (0–0.16)
Any	HIDS	SMA	0.78 (0.76–0.78)	0.69 (0.48–0.76)	0.62 (0.35–0.75)	0.45 (0.14–0.69)	0.32 (0.04–0.62)
Any	HIDS	OCS	0.8 (0.76–0.81)	0.68 (0.27–0.8)	0.59 (0.15–0.78)	0.36 (0.02–0.73)	0.22 (0–0.67)
Any	HIDS	BSH	0.94 (0.9–0.95)	0.73 (0.37–0.91)	0.6 (0.23–0.87)	0.35 (0.05–0.75)	0.21 (0.01–0.61)
Any	ASLL	FAL	0.64 (0.57–0.64)	0.5 (0.13–0.63)	0.42 (0.0–0.62)	0.26 (0.01–0.57)	0.15 (0–0.52)
Any	ASLL	OCS	0.66 (0.59–0.67)	0.49 (0.12–0.65)	0.38 (0.04–0.63)	0.21 (0.01–0.56)	0.1 (0–0.48)

Table 8. OCS survival projections by gear types in HIDS. Individual survival of oceanic whitetip sharks at five time points (in days (d)) after interaction with the HIDS fishery on two types of branchline leader material and with various lengths of trailing gear remaining on the animal after release from the fishing gear. The median shark survival is given with the 90% credible interval provided in the parentheses.

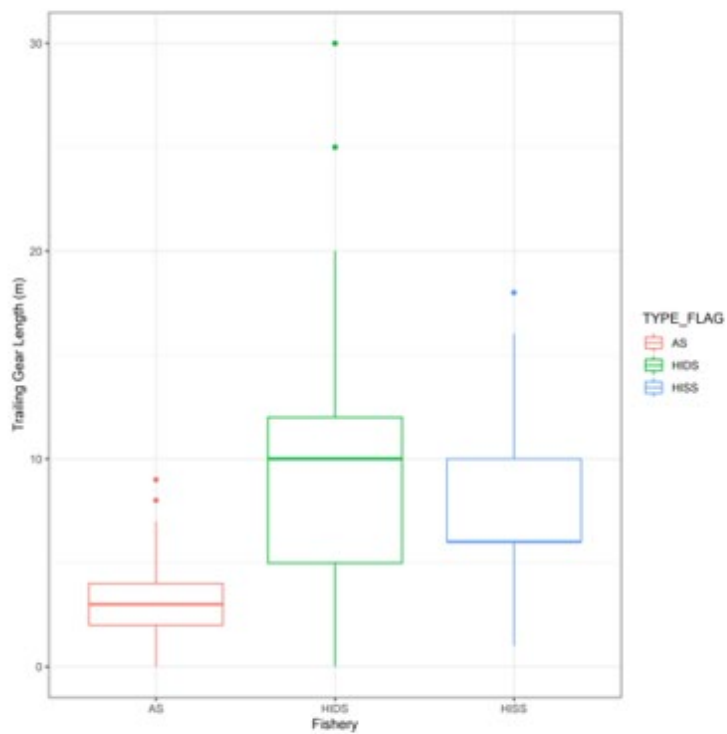
Leader material	Trailing gear (m)	1 day	30 days	60 days	180 days	360 days
Wire	0	1 (1–1)	0.98 (0.95–0.99)	0.96 (0.9–0.99)	0.89 (0.72–0.96)	0.79 (0.52–0.93)
Wire	1.8	1 (1–1)	0.98 (0.94–0.99)	0.95 (0.89–0.99)	0.87 (0.7–0.96)	0.76 (0.49–0.92)
Wire	3	1 (1–1)	0.97 (0.94–0.99)	0.95 (0.88–0.98)	0.86 (0.69–0.95)	0.74 (0.47–0.91)
Wire	5.15	1 (1–1)	0.97 (0.93–0.99)	0.94 (0.87–0.98)	0.84 (0.65–0.94)	0.7 (0.42–0.89)
Wire	10	1 (1–1)	0.96 (0.9–0.99)	0.92 (0.81–0.97)	0.78 (0.52–0.92)	0.6 (0.27–0.85)
Wire	14	1 (0.99–1)	0.94 (0.84–0.98)	0.89 (0.71–0.97)	0.71 (0.36–0.91)	0.51 (0.13–0.82)
Mono	0	1 (1–1)	0.98 (0.94–0.99)	0.97 (0.89–0.99)	0.9 (0.7–0.97)	0.81 (0.48–0.95)
Mono	1.8	1 (1–1)	0.98 (0.94–0.99)	0.96 (0.88–0.99)	0.89 (0.67–0.97)	0.79 (0.45–0.94)
Mono	3	1 (1–1)	0.98 (0.93–0.99)	0.96 (0.87–0.99)	0.88 (0.65–0.96)	0.77 (0.42–0.93)
Mono	5.15	1 (1–1)	0.97 (0.92–0.99)	0.95 (0.84–0.99)	0.86 (0.6–0.96)	0.74 (0.36–0.92)
Mono	10	1 (1–1)	0.96 (0.88–0.99)	0.93 (0.77–0.98)	0.8 (0.45–0.95)	0.64 (0.2–0.9)
Mono	14	1 (0.99–1)	0.95 (0.81–0.99)	0.91 (0.66–0.98)	0.74 (0.29–0.94)	0.56 (0.082–0.88)

Table 9: OCS total survival by gear type in HIDS The estimated proportion of oceanic whitetip sharks observed to be caught alive or caught at all (Any scenario) that were estimated to survive capture in the HIDS. For the “Any” scenario, the “Alive” scenario results are modified to account for sharks that were assigned as Dead at haul back by an observer. The prospective leader (Leader) material was either wire or mono and the trailing gear length (Trailing gear) was either the observed trailing gear length in the PIROP data set (or the mean for OCS when missing) or specified as zero.

Capture condition	Leader	Trailing gear	1 day	30 days	60 days	180 days	360 days
Alive	Wire	PIROP	0.99 (0.95–1)	0.85 (0.36–0.98)	0.74 (0.19–0.97)	0.46 (0.02–0.91)	0.28 (0–0.83)
Alive	Mono	PIROP	1 (0.95–1)	0.87 (0.38–0.99)	0.76 (0.21–0.97)	0.5 (0.03–0.92)	0.32 (0–0.85)
Alive	Wire	0	1 (0.97–1)	0.9 (0.46–0.99)	0.81 (0.28–0.98)	0.57 (0.06–0.94)	0.38 (0.01–0.88)
Alive	Mono	0	1 (0.97–1)	0.91 (0.48–0.99)	0.83 (0.3–0.98)	0.6 (0.07–0.95)	0.41 (0.01–0.89)
Any	Wire	PIROP	0.8 (0.77–0.81)	0.69 (0.29–0.8)	0.6 (0.16–0.78)	0.37 (0.02–0.74)	0.23 (0–0.67)
Any	Mono	PIROP	0.81 (0.77–0.81)	0.7 (0.31–0.8)	0.62 (0.17–0.79)	0.4 (0.02–0.75)	0.26 (0–0.69)
Any	Wire	0	0.81 (0.78–0.81)	0.72 (0.37–0.8)	0.65 (0.22–0.79)	0.46 (0.05–0.76)	0.31 (0.01–0.71)
Any	Mono	0	0.81 (0.78–0.81)	0.73 (0.39–0.8)	0.67 (0.24–0.79)	0.49 (0.06–0.76)	0.33 (0.01–0.72)

isher

A.



B.

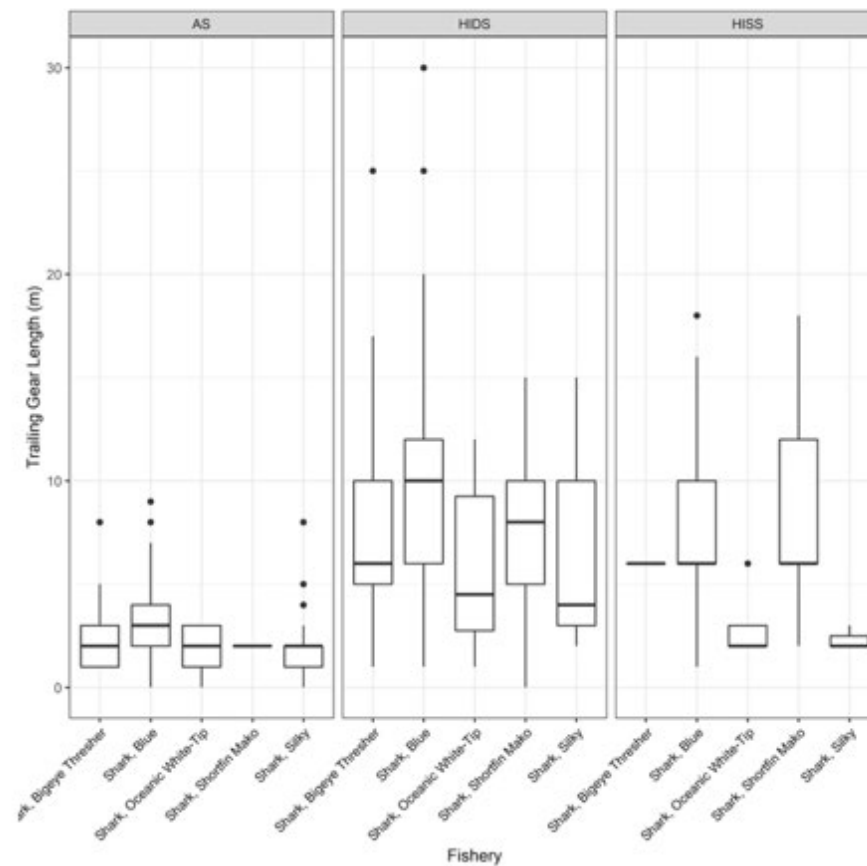
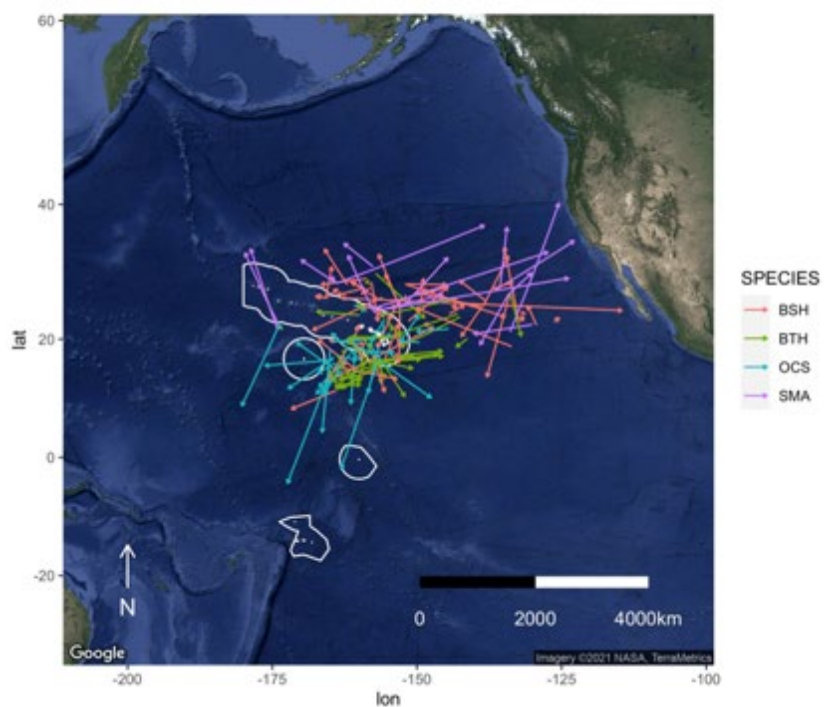


Figure 1. Trailing gear. Length (m) of trailing gear remaining on sharks captured and released (A) by longline fishery (all shark species combined) and by species and longline fishery (B).

A.



B.

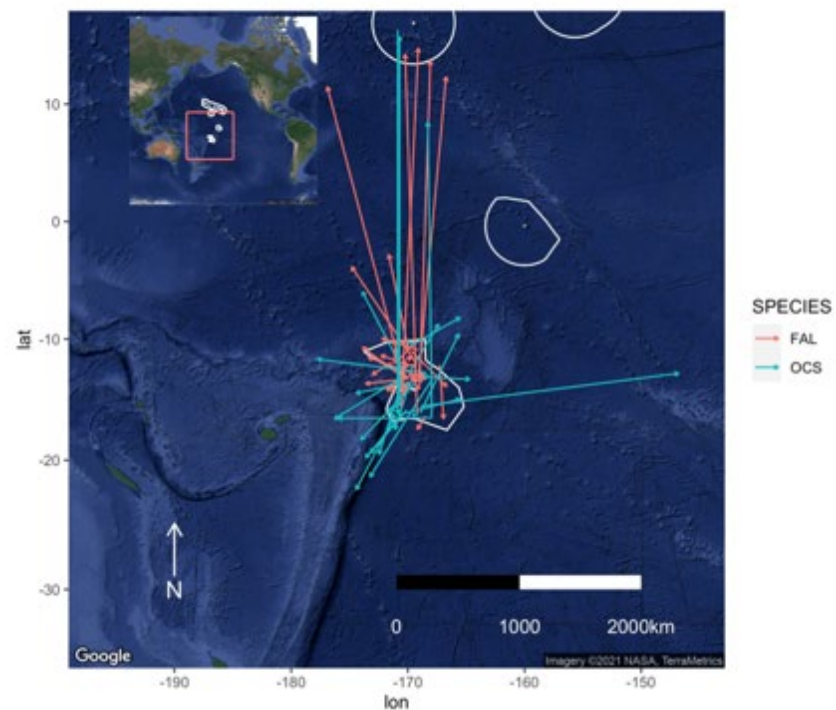


Figure 2. Tagging and tag release (“pop-off”) locations (arrow tip) for (A) blue (BSH), bigeye thresher (BTH), oceanic whitetip (OCS) and shortfin mako sharks (SMA) in the HIDS fishery and (B) for silky (FAL) and OCS sharks in the ASLL fishery.

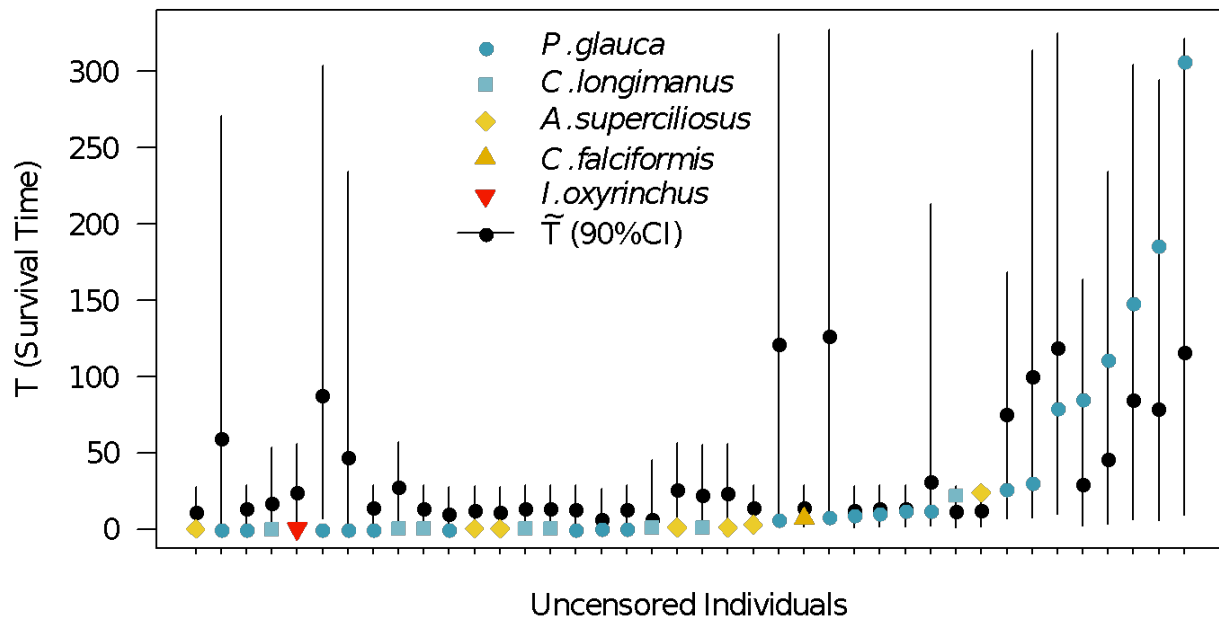


Figure 3. Survival times predictive check. Posterior predictive check of the uncensored survival times for each individual (post release mortalities from tagging data), colored by species, using the median predicted survival time (\tilde{T}) and the 90% credible interval (line).

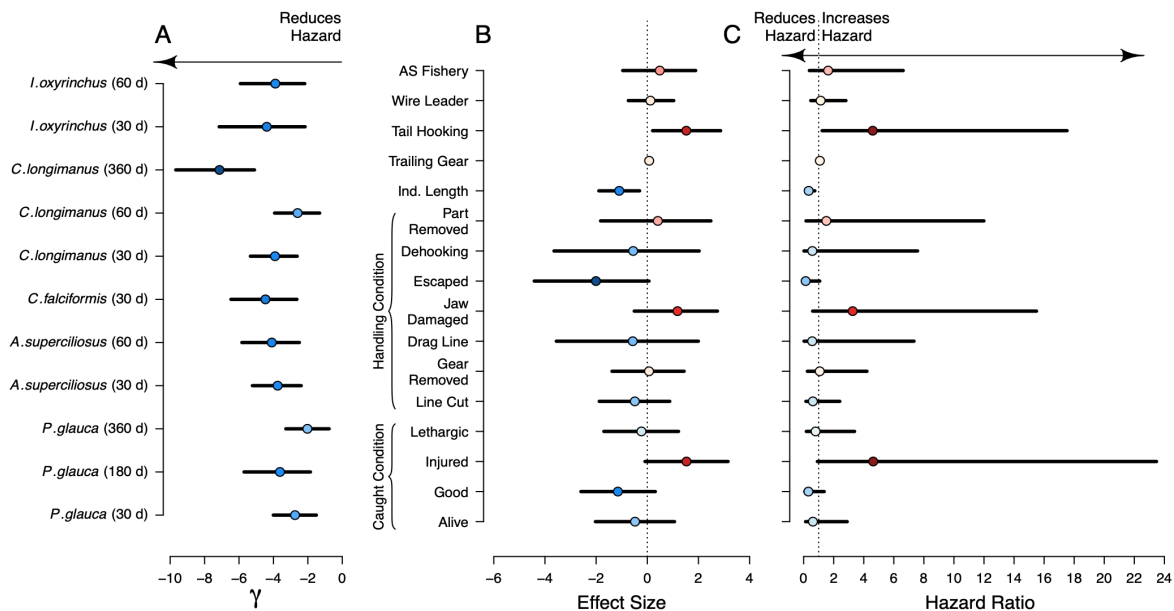


Figure 4. Hazard ratio and effect sizes. The negative log-transformed baseline hazard ratio, γ from the tagging data (A), the effect size of the fishery interaction covariates (B), and the hazard ratio (C). For each, the 90% credible interval (line) and the median (point) are shown; for the latter, warmer colors indicate values increasing the hazard and cooler colors indicate values reducing the hazard.

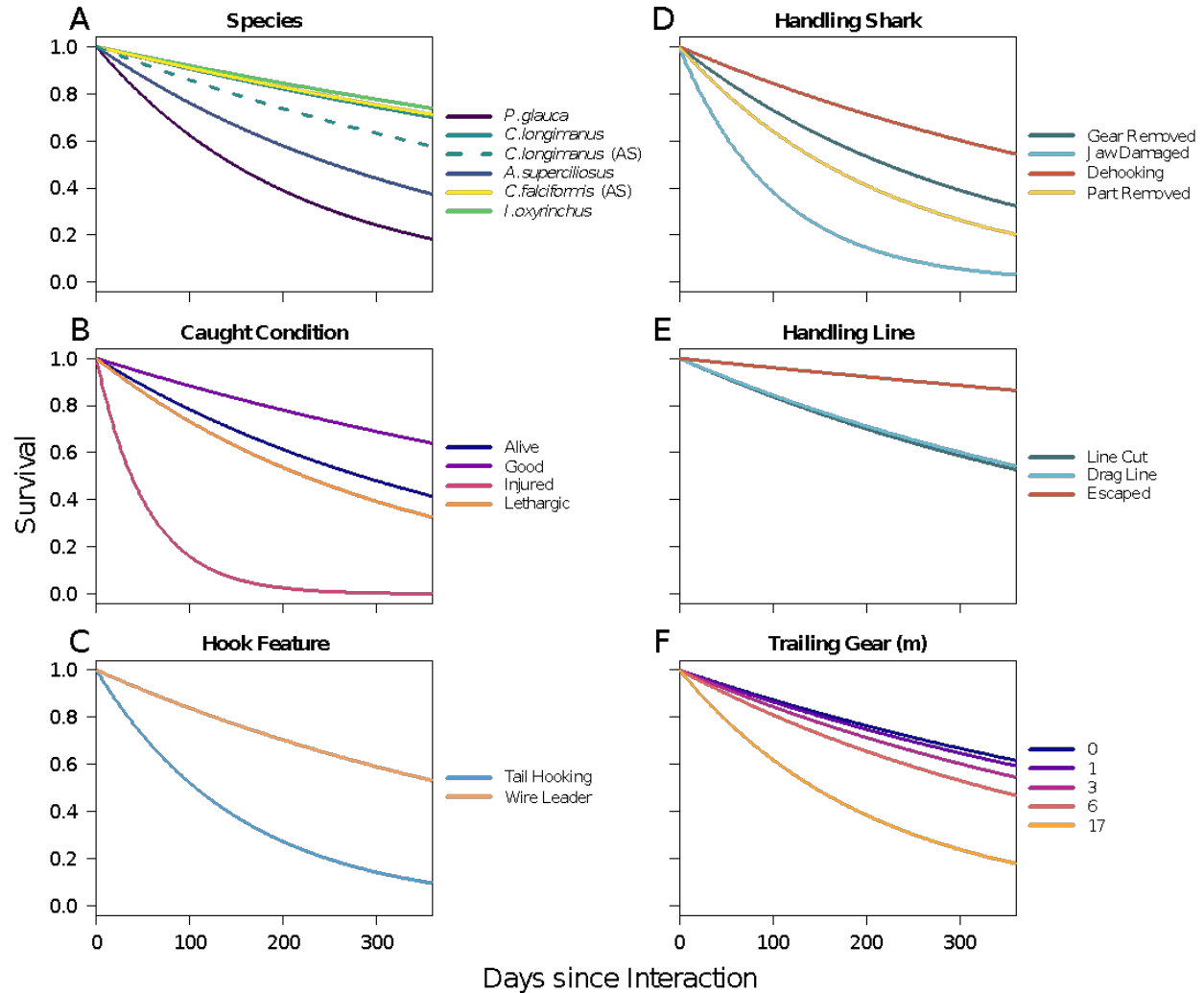


Figure 5. Bayesian survival curves. Bayesian survival curves of the mean interaction conditions for 1 to 360 days since the interaction occurred: for each species (A), by caught condition (B), by hook feature (C), by handling condition involving the shark (D), handling condition involving the line (E), and by length of trailing gear (F) from 1 to 360 days since interaction. For B and D–F, the baseline hazard rate, h_0 , was the mean across species and tag deployment periods while all other conditions were assumed to be at their respective mean. In (C), the baseline hazard rate was the mean across all species tagged for the wire leader. For tail hooking the baseline hazard is the mean across *A. superciliosus* (BTH) only.

Appendix

Table A 1. Scenario-based survival projections. The estimated proportion of sharks surviving to the specified time period after a fishery interaction with analyses grouped by the following scenarios: 1) by species and by fishery; 2) all species combined by capture condition; 3) by hook feature with all species combined for wire leader or only bigeye thresher shark (BTH) for tail-hooked; 4) all species combined by fisher handling method involving direct contact with the shark or the hook (see Table 1 for definitions); 5) all species combined by fisher handling method involving contact with only the branchline line (see Table 1 for definitions); 6) all species combined by the amount of trailing gear remaining on the shark at release. The median proportion of sharks surviving is reported with the 90% credible interval in parentheses. More details on analyses can be found in the Methods under the “Survival Curves” section of the “Survival Analysis.”

Scenario	1 days	30 days	60 days	180 days	360 days
Mean for species					
BTH	1 (0.99–1)	0.92 (0.84–0.97)	0.85 (0.71–0.93)	0.61 (0.36–0.81)	0.37 (0.13–0.66)
SMA	1 (1–1)	0.97 (0.91–1)	0.95 (0.82–0.99)	0.86 (0.56–0.97)	0.74 (0.31–0.95)
FAL (AS)	1 (1–1)	0.97 (0.91–0.99)	0.94 (0.82–0.99)	0.84 (0.55–0.97)	0.71 (0.31–0.94)
OCS	1 (1–1)	0.97 (0.93–0.99)	0.94 (0.87–0.98)	0.84 (0.65–0.94)	0.7 (0.42–0.89)
OCS (AS)	1 (1–1)	0.95 (0.88–0.99)	0.91 (0.78–0.97)	0.76 (0.47–0.93)	0.58 (0.22–0.86)
BSH	0.99 (0.99–1)	0.87 (0.77–0.94)	0.75 (0.6–0.88)	0.43 (0.21–0.67)	0.18 (0.046–0.45)
Caught Condition					
Alive	1 (0.99–1)	0.93 (0.85–0.97)	0.86 (0.73–0.94)	0.64 (0.38–0.83)	0.41 (0.15–0.7)
Good	1 (1–1)	0.96 (0.94–0.98)	0.93 (0.88–0.96)	0.8 (0.68–0.89)	0.64 (0.46–0.79)
Injured	0.98 (0.95–0.99)	0.58 (0.24–0.82)	0.33 (0.06–0.67)	0.037 (0–0.31)	0.001 (0–0.094)
Lethargic	1 (0.99–1)	0.91 (0.83–0.96)	0.83 (0.69–0.92)	0.57 (0.33–0.77)	0.33 (0.11–0.59)
Hook Feature					
Tail Hook (BTH only)	0.99 (0.98–1)	0.82 (0.52–0.95)	0.68 (0.28–0.9)	0.31 (0.021–0.73)	0.096 (0–0.54)
Wire Leader	1 (1–1)	0.95 (0.91–0.97)	0.9 (0.82–0.95)	0.73 (0.56–0.85)	0.53 (0.31–0.73)
Handling Shark					
Gear Removed	1 (0.99–1)	0.91 (0.77–0.97)	0.83 (0.59–0.94)	0.57 (0.2–0.84)	0.32 (0.041–0.71)
Jaw Damaged	0.99 (0.96–1)	0.75 (0.31–0.95)	0.56 (0.095–0.9)	0.18 (0.001–0.74)	0.032 (0–0.54)
Dehooking	1 (0.98–1)	0.95 (0.49–1)	0.9 (0.24–1)	0.74 (0.015–0.99)	0.54 (0–0.98)
Part Removed	1 (0.97–1)	0.88 (0.43–0.98)	0.77 (0.19–0.97)	0.45 (0.007–0.91)	0.2 (0–0.83)
Handling Line					

Scenario	1 days	30 days	60 days	180 days	360 days
Line Cut	1 (1-1)	0.95 (0.92-0.97)	0.9 (0.84-0.94)	0.73 (0.59-0.83)	0.53 (0.35-0.7)
Drag Line	1 (0.98-1)	0.95 (0.5-1)	0.9 (0.25-1)	0.74 (0.016-0.99)	0.54 (0-0.98)
Escaped	1 (1-1)	0.99 (0.92-1)	0.98 (0.84-1)	0.93 (0.6-0.99)	0.86 (0.35-0.99)
Trailing Gear					
0 m	1 (1-1)	0.96 (0.93-0.98)	0.92 (0.86-0.96)	0.79 (0.63-0.89)	0.62 (0.4-0.79)
1 m	1 (1-1)	0.96 (0.93-0.98)	0.92 (0.86-0.96)	0.77 (0.63-0.87)	0.59 (0.39-0.76)
3 m	1 (1-1)	0.95 (0.92-0.97)	0.9 (0.85-0.94)	0.74 (0.61-0.84)	0.55 (0.37-0.71)
6 m	1 (1-1)	0.94 (0.9-0.96)	0.88 (0.82-0.93)	0.68 (0.54-0.8)	0.47 (0.3-0.65)
17 m	0.99 (0.99-1)	0.87 (0.66-0.95)	0.75 (0.44-0.91)	0.42 (0.084-0.76)	0.18 (0.007-0.58)

Table A 2. Blue shark survival scenario projections. Proportion of blue (*Prionace glauca*: BSH) sharks surviving fishery interactions at different days since interaction for different scenarios (see Materials and Methods –Survival Curves). The median is reported with the 90% credible interval in the parentheses.

Scenario	1 day	30 days	60 days	180 days	360 days
Caught Conditions					
Alive	1 (0.99–1)	0.91 (0.67–0.98)	0.83 (0.45–0.96)	0.57 (0.091–0.88)	0.33 (0.008–0.78)
Good	1 (0.99–1)	0.92 (0.82–0.97)	0.84 (0.67–0.93)	0.59 (0.3–0.82)	0.34 (0.088–0.67)
Injured	0.98 (0.91–1)	0.55 (0.05–0.9)	0.31 (0.002–0.8)	0.029 (0–0.52)	0.001 (0–0.27)
Lethargic	1 (0.98–1)	0.89 (0.64–0.97)	0.8 (0.41–0.95)	0.5 (0.07–0.85)	0.25 (0.005–0.72)
Handling Conditions					
Line Cut	1 (0.99–1)	0.88 (0.79–0.94)	0.77 (0.62–0.89)	0.46 (0.23–0.7)	0.21 (0.055–0.5)
Gear Removed	0.99 (0.98–1)	0.86 (0.57–0.97)	0.74 (0.32–0.93)	0.41 (0.034–0.81)	0.17 (0.001–0.66)
Drag Line	1 (0.96–1)	0.93 (0.33–1)	0.85 (0.11–0.99)	0.62 (0.001–0.98)	0.39 (0–0.96)
Jaw Damaged	0.99 (0.94–1)	0.66 (0.14–0.93)	0.43 (0.019–0.86)	0.082 (0–0.64)	0.007 (0–0.41)
Hook Feature					
Wire Leader	0.99 (0.99–1)	0.86 (0.77–0.94)	0.75 (0.59–0.88)	0.42 (0.2–0.67)	0.18 (0.041–0.45)
Trailing Gear					
0 m	1 (0.99–1)	0.92 (0.82–0.97)	0.84 (0.67–0.94)	0.59 (0.29–0.82)	0.35 (0.087–0.67)
1 m	1 (0.99–1)	0.91 (0.81–0.96)	0.83 (0.66–0.93)	0.57 (0.29–0.8)	0.33 (0.083–0.64)
3 m	1 (0.99–1)	0.9 (0.8–0.95)	0.8 (0.65–0.91)	0.52 (0.27–0.75)	0.27 (0.072–0.57)
6 m	0.99 (0.99–1)	0.87 (0.78–0.94)	0.76 (0.61–0.88)	0.44 (0.22–0.68)	0.19 (0.05–0.46)
17 m	0.99 (0.97–1)	0.73 (0.44–0.9)	0.54 (0.2–0.81)	0.15 (0.007–0.54)	0.024 (0–0.29)

Table A 3. Bigeye thresher shark survival scenario projections Proportion of bigeye threshers (*Alopias superciliosus*: BTH) sharks surviving fishery interactions at different days since interaction for different scenarios (see Materials and Methods – Survival Curves). The median is reported with the 90% credible interval in the parentheses.

Scenario	1 day	30 days	60 days	180 days	360 days
Caught Conditions					
Alive	0.95 (0.79–0.99)	0.9 (0.62–0.98)	0.72 (0.24–0.93)	0.52 (0.057–0.87)	0.95 (0.79–0.99)
Good	0.96 (0.87–0.99)	0.92 (0.76–0.98)	0.78 (0.45–0.93)	0.61 (0.2–0.86)	0.96 (0.87–0.99)
Injured	0.71 (0.14–0.94)	0.5 (0.021–0.89)	0.12 (0–0.69)	0.016 (0–0.48)	0.71 (0.14–0.94)
Lethargic	0.93 (0.79–0.98)	0.87 (0.62–0.96)	0.66 (0.23–0.89)	0.43 (0.055–0.8)	0.93 (0.79–0.98)
Handling Conditions					
Line Cut	1 (0.99–1)	0.93 (0.85–0.97)	0.86 (0.72–0.94)	0.64 (0.38–0.83)	0.41 (0.14–0.69)
Gear Removed	1 (0.99–1)	0.92 (0.71–0.98)	0.84 (0.5–0.96)	0.6 (0.13–0.89)	0.36 (0.016–0.8)
Escaped	1 (1–1)	0.99 (0.9–1)	0.98 (0.81–1)	0.94 (0.53–0.99)	0.87 (0.28–0.99)
Part Removed	1 (0.97–1)	0.89 (0.37–0.99)	0.79 (0.14–0.98)	0.49 (0.002–0.93)	0.24 (0–0.87)
Hook Feature					
Tail Hooking	0.99 (0.98–1)	0.8 (0.59–0.92)	0.64 (0.35–0.85)	0.26 (0.045–0.62)	0.069 (0.002–0.38)
Wire Leader	1 (0.99–1)	0.92 (0.84–0.97)	0.85 (0.71–0.93)	0.61 (0.36–0.81)	0.37 (0.13–0.66)
Trailing Gear					
0 m	1 (0.99–1)	0.94 (0.87–0.98)	0.89 (0.76–0.96)	0.7 (0.44–0.87)	0.49 (0.2–0.76)
1 m	1 (0.99–1)	0.94 (0.87–0.97)	0.88 (0.75–0.95)	0.68 (0.43–0.86)	0.46 (0.18–0.74)
3 m	1 (0.99–1)	0.93 (0.85–0.97)	0.86 (0.73–0.94)	0.64 (0.39–0.83)	0.41 (0.15–0.69)
6 m	1 (0.99–1)	0.91 (0.82–0.96)	0.83 (0.68–0.93)	0.57 (0.31–0.79)	0.33 (0.097–0.63)
17 m	0.99 (0.98–1)	0.81 (0.49–0.95)	0.66 (0.24–0.9)	0.29 (0.014–0.72)	0.082 (0–0.51)

Table A 3. Shortfin mako survival scenario projections. Proportion of shortfin mako (*Isurus oxyrinchus*: SMA) sharks surviving fishery interactions at different days since interaction for different scenarios (see Materials and Methods –Survival Curves). The median is reported with the 90% credible interval in the parentheses.

Scenario	1 day	30 days	60 days	180 days	360 days
Caught Conditions					
Alive	1 (11)	0.98 (0.89–1)	0.97 (0.8–1)	0.91 (0.51–0.99)	0.83 (0.26–0.98)
Good	1 (1–1)	0.98 (0.92–1)	0.96 (0.85–0.99)	0.89 (0.62–0.98)	0.79 (0.39–0.96)
Injured	1 (0.97–1)	0.9 (0.43–0.99)	0.81 (0.18–0.98)	0.53 (0.006–0.94)	0.28 (0–0.88)
Lethargic	1 (1–1)	0.98 (0.88–1)	0.96 (0.77–0.99)	0.89 (0.45–0.99)	0.79 (0.2–0.97)
Handling Conditions					
Line Cut	1 (1–1)	0.97 (0.91–1)	0.95 (0.82–0.99)	0.86 (0.56–0.97)	0.74 (0.31–0.95)
Hook Feature					
Wire Leader	1 (1–1)	0.97 (0.9–1)	0.95 (0.82–0.99)	0.86 (0.55–0.97)	0.73 (0.3–0.95)
Trailing Gear					
0 m	1 (1–1)	0.98 (0.93–1)	0.97 (0.86–0.99)	0.9 (0.64–0.98)	0.81 (0.41–0.97)
1 m	1 (1–1)	0.98 (0.93–1)	0.96 (0.86–0.99)	0.9 (0.63–0.98)	0.8 (0.39–0.96)
3 m	1 (1–1)	0.98 (0.92–1)	0.96 (0.84–0.99)	0.88 (0.59–0.98)	0.77 (0.35–0.96)
6 m	1 (1–1)	0.97 (0.9–0.99)	0.95 (0.81–0.99)	0.85 (0.53–0.97)	0.72 (0.28–0.95)
17 m	1 (0.99–1)	0.94 (0.73–0.99)	0.88 (0.53–0.98)	0.69 (0.15–0.95)	0.48 (0.022–0.91)

Table A 4. Silky shark survival scenario projections. Proportion of silky (*Carcharhinus falciformis*: FAL) sharks surviving fishery interactions at different days since interaction for different scenarios (see Materials and Methods –Survival Curves). The median is reported with the 90% credible interval in the parentheses.

Scenario	1 day	30 days	60 days	180 days	360 days
Caught Conditions					
Good	1 (1–1)	0.97 (0.91–0.99)	0.95 (0.83–0.99)	0.85 (0.57–0.97)	0.72 (0.32–0.95)
Lethargic	1 (0.99–1)	0.98 (0.86–1)	0.96 (0.74–0.99)	0.88 (0.41–0.99)	0.77 (0.17–0.97)
Handling Conditions					
Line Cut	1 (1–1)	0.97 (0.91–1)	0.95 (0.83–0.99)	0.85 (0.57–0.97)	0.73 (0.33–0.95)
Gear Removed	1 (0.99–1)	0.97 (0.84–1)	0.94 (0.71–0.99)	0.84 (0.36–0.98)	0.7 (0.13–0.96)
Escaped	1 (1–1)	1 (0.95–1)	0.99 (0.91–1)	0.97 (0.75–1)	0.95 (0.57–1)
Trailing Gear					
0 m	1 (1–1)	0.97 (0.92–1)	0.95 (0.84–0.99)	0.86 (0.59–0.97)	0.74 (0.35–0.95)
1 m	1 (1–1)	0.97 (0.91–0.99)	0.95 (0.83–0.99)	0.85 (0.57–0.97)	0.72 (0.32–0.95)
3 m	1 (1–1)	0.97 (0.9–0.99)	0.94 (0.8–0.99)	0.83 (0.52–0.97)	0.69 (0.27–0.94)
6 m	1 (0.99–1)	0.96 (0.87–0.99)	0.93 (0.76–0.99)	0.79 (0.44–0.96)	0.62 (0.19–0.92)
17 m	1 (0.98–1)	0.92 (0.61–0.99)	0.84 (0.37–0.98)	0.6 (0.051–0.94)	0.36 (0.003–0.88)

Table A 5. Oceanic whitetip shark survival scenario projections. Proportion of oceanic whitetip (*Carcharhinus longimanus*: OCS) sharks surviving fishery interactions at different days since interaction for different scenarios (see Materials and Methods—Survival Curves). The median is reported with the 90% credible interval in the parentheses.

Scenario	Fishery	1 day	30 days	60 days	180 days	360 days
Caught Conditions						
Alive	HIDS	1 (1–1)	0.98 (0.91–1)	0.96 (0.83–0.99)	0.89 (0.56–0.98)	0.79 (0.32–0.96)
Good	HIDS	1 (1–1)	0.98 (0.94–0.99)	0.96 (0.89–0.99)	0.89 (0.71–0.97)	0.79 (0.51–0.94)
Injured	HIDS	1 (0.97–1)	0.88 (0.45–0.98)	0.78 (0.2–0.96)	0.47 (0.008–0.89)	0.22 (0–0.8)
Lethargic	HIDS	1 (1–1)	0.98 (0.89–0.99)	0.95 (0.79–0.99)	0.87 (0.5–0.97)	0.75 (0.25–0.95)
Handling Conditions						
Line Cut	HIDS	1 (1–1)	0.97 (0.93–0.99)	0.95 (0.87–0.98)	0.85 (0.66–0.95)	0.72 (0.44–0.9)
Gear Removed	HIDS	1 (0.99–1)	0.97 (0.87–0.99)	0.94 (0.75–0.99)	0.83 (0.42–0.97)	0.69 (0.18–0.93)
Jaw Damaged	HIDS	1 (0.98–1)	0.91 (0.6–0.99)	0.83 (0.36–0.97)	0.58 (0.046–0.93)	0.34 (0.002–0.86)
Hook Feature						
Wire Leader	HIDS	1 (1–1)	0.97 (0.93–0.99)	0.94 (0.87–0.98)	0.84 (0.65–0.94)	0.7 (0.42–0.89)
Trailing Gear						
0 m	HIDS	1 (1–1)	0.98 (0.95–0.99)	0.96 (0.9–0.99)	0.89 (0.72–0.96)	0.79 (0.52–0.93)
1 m	HIDS	1 (1–1)	0.98 (0.94–0.99)	0.96 (0.89–0.99)	0.88 (0.71–0.96)	0.77 (0.5–0.92)
3 m	HIDS	1 (1–1)	0.97 (0.94–0.99)	0.95 (0.88–0.98)	0.86 (0.69–0.95)	0.74 (0.47–0.91)
6 m	HIDS	1 (1–1)	0.97 (0.93–0.99)	0.94 (0.86–0.98)	0.83 (0.63–0.94)	0.68 (0.4–0.88)
17 m	HIDS	1 (0.99–1)	0.93 (0.78–0.98)	0.87 (0.6–0.97)	0.65 (0.22–0.9)	0.43 (0.049–0.81)
Caught Conditions						
Alive	ASLL	1 (0.99–1)	0.97 (0.83–1)	0.94 (0.7–0.99)	0.84 (0.34–0.98)	0.71 (0.12–0.95)
Good	ASLL	1 (1–1)	0.98 (0.91–1)	0.96 (0.84–0.99)	0.88 (0.58–0.97)	0.77 (0.34–0.95)
Injured	ASLL	0.99 (0.96–1)	0.83 (0.35–0.97)	0.69 (0.12–0.95)	0.33 (0.002–0.85)	0.11 (0–0.72)
Lethargic	ASLL	1 (0.99–1)	0.96 (0.87–0.99)	0.92 (0.75–0.98)	0.78 (0.42–0.95)	0.61 (0.18–0.9)
Handling Conditions						
Line Cut	ASLL	1 (1–1)	0.96 (0.89–0.99)	0.92 (0.79–0.98)	0.77 (0.49–0.93)	0.59 (0.24–0.87)

Scenario	Fishery	1 day	30 days	60 days	180 days	360 days
Escaped	ASLL	1 (1-1)	0.99 (0.94-1)	0.99 (0.88-1)	0.96 (0.68-1)	0.92 (0.46-0.99)
Dehooking	ASLL	1 (0.99-1)	0.97 (0.67-1)	0.95 (0.45-1)	0.86 (0.091-0.99)	0.73 (0.008-0.99)
Trailing Gear						
0 m	ASLL	1 (1-1)	0.96 (0.89-0.99)	0.92 (0.8-0.98)	0.78 (0.51-0.94)	0.61 (0.26-0.88)
1 m	ASLL	1 (1-1)	0.96 (0.89-0.99)	0.92 (0.79-0.98)	0.77 (0.48-0.93)	0.59 (0.24-0.86)
3 m	ASLL	1 (0.99-1)	0.95 (0.87-0.99)	0.9 (0.76-0.97)	0.74 (0.43-0.92)	0.55 (0.19-0.84)
6 m	ASLL	1 (0.99-1)	0.94 (0.83-0.98)	0.88 (0.69-0.97)	0.69 (0.33-0.9)	0.47 (0.11-0.81)
17 m	ASLL	0.99 (0.98-1)	0.87 (0.49-0.97)	0.76 (0.24-0.95)	0.43 (0.014-0.86)	0.19 (0-0.74)

Supplementary Material

Table S 1. Handling effects on release condition. Proportions of all sharks and by species, released with a particular handling or damage code (LC – Line Cut, GR – Gear Removed, DL – Drag Line, JW – Jaw Damaged, ES – Escaped, DH – Dehooking, PR – Part Removed) with given caught condition and release condition as recorded by the tagging observer as well as the total number (N). The proportion of sharks does not necessarily sum to one as more than one handling code can be assigned per individual.

Species	Caught Condition	Release Condition	LC	GR	DL	JW	ES	DH	PR	N
All species	Alive	Alive	0.95	0.05	0	0	0	0	0	19
All species	Good	Alive	1	0	0	0	0	0	0	4
All species	Good	Good	0.9	0.06	0.01	0	0.03	0.01	0	147
All species	Good	Injured	0.15	0.38	0	0.38	0	0	0.15	13
All species	Injured	Injured	0.83	0.13	0	0	0.04	0	0	23
BTH	Alive	Alive	1	0	0	0	0	0	0	5
SMA	Alive	Alive	1	0	0	0	0	0	0	1
OCS	Alive	Alive	0.88	0.12	0	0	0	0	0	8
BSH	Alive	Alive	1	0	0	0	0	0	0	5
BTH	Good	Alive	1	0	0	0	0	0	0	1
SMA	Good	Alive	1	0	0	0	0	0	0	1
FAL	Good	Alive	1	0	0	0	0	0	0	1
OCS	Good	Alive	1	0	0	0	0	0	0	1
BTH	Good	Good	0.88	0.08	0	0	0.04	0	0	26
SMA	Good	Good	1	0	0	0	0	0	0	15
FAL	Good	Good	0.86	0.07	0	0	0.07	0	0	29
OCS	Good	Good	0.93	0.02	0	0	0.02	0.02	0	41
BSH	Good	Good	0.86	0.11	0.03	0	0	0	0	36
BTH	Good	Injured	0.33	0	0	0	0	0	0.67	3
OCS	Good	Injured	0.33	0.33	0	0.33	0	0	0	3
BSH	Good	Injured	0	0.57	0	0.57	0	0	0	7
BTH	Injured	Injured	0.6	0.4	0	0	0	0	0	5
SMA	Injured	Injured	1	0	0	0	0	0	0	1
OCS	Injured	Injured	0.33	0.33	0	0	0.33	0	0	3
BSH	Injured	Injured	1	0	0	0	0	0	0	14

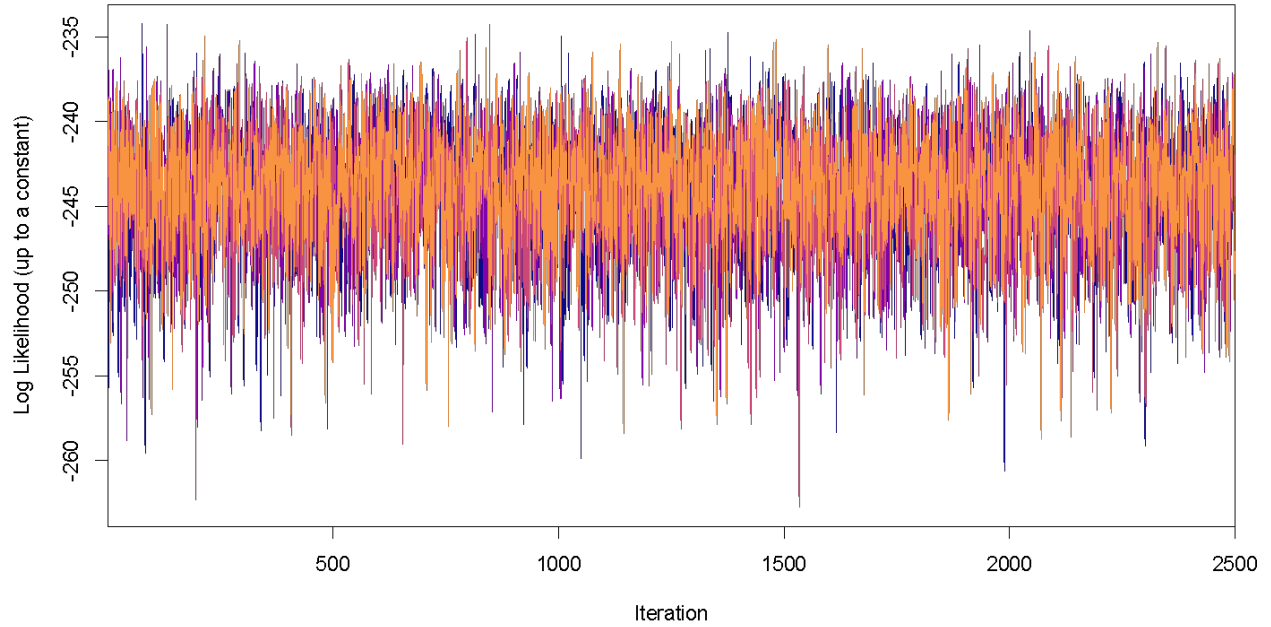


Figure S 1. Convergence. Trace of the log likelihood for each chain (different colors) of the No U-Turn variant of the Hamiltonian sampling algorithm for the proportional hazard model.