



## ECOLOGY

# Quantifying longline bycatch mortality for pelagic sharks in western Pacific shark sanctuaries

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Marine protected areas are increasingly touted for their role in conserving large marine predators such as sharks, but their efficacy is debated. Seventeen “shark sanctuaries” have been established globally, but longline fishing continues within many such jurisdictions, leading to unknown levels of bycatch mortality levels. Using public data from Global Fishing Watch and Regional Fisheries Management Organizations, we quantified longline fishing within eight shark sanctuaries and estimated pelagic shark catch and mortality for seven pelagic shark species. Sanctuary mortality ranged from 600 individuals (Samoa) to 36,256 individuals (Federated States of Micronesia), equivalent to ~5% of hypothesized sustainable levels for blue sharks to ~40% for silky sharks, with high mortality levels in the Federated States of Micronesia, Palau, and the Marshall Islands. Unsustainable mortality rates were exceeded for silky sharks in two sanctuaries, highlighting a need for additional stock assessments and implementation of bycatch reduction measures. Big data integration workflows represent a transformative tool in fisheries management, particularly for data-poor species.

## INTRODUCTION

In the face of a looming biodiversity crisis, the global conservation community has increasingly turned toward spatial protection to conserve ocean ecosystems (1, 2), with particular emphasis being placed on the establishment of large-scale marine protected areas (LMPAs) (3). LMPAs, which are often implemented around remote island nations or areas containing high biodiversity and/or critical habitat for threatened, mobile marine species (4), seek to enhance ecological processes, connect oceanic habitats, and promote sustainable fisheries (5). One of the greatest expectations of LMPAs is the potential to conserve highly migratory species such as sharks (4), which can have home ranges up to 50,000 km<sup>2</sup> or more (6). This expectation has led to the recent establishment of 17 global shark sanctuaries, nations that have issued bans on the commercial targeting and retention of sharks within their entire exclusive economic zones (EEZs).

Sharks were historically abundant throughout remote oceanic regions, islands, and archipelagos (7), but today, many shark populations are in decline, largely due to overfishing. More than 30% of shark species are threatened with extinction (8, 9). Spatial protective measures to encompass shark core habitats are thus a potentially important management tool to reverse their declines and protect remaining areas of high biodiversity (10). Shark sanctuaries are a unique form of LMPA that provide regulations specifically for the protection of sharks but do not necessarily restrict the targeting of other species (such as establishment of full no-take zones). Throughout these nations, all commercial shark fishing is prohibited, and trade in shark parts is made illegal (11). As we are just beginning to understand how much space is needed to effectively protect populations of large sharks (12, 13), the true conservation benefits of these spatial management tools remain poorly understood or otherwise contested (14–17).

One of the most common criticisms of shark sanctuaries and the legislation that establishes them is a relative lack of bycatch mitigation measures (e.g., gear restrictions) in most of these jurisdictions (11). While targeted shark fishing is prohibited in shark sanctuaries, tuna and billfish pelagic longline fisheries operate in many of these locations. Although precise quantification remains challenging because of data limitations, shark bycatch in these regional fisheries is substantial (18, 19), with sharks potentially representing up to 10% or more of the total individual catch of longline fisheries operating in the Western Central Pacific Ocean (WCPO) (20). Even with sanctuary regulations prohibiting the retention of sharks captured as bycatch, a substantial portion of longline-captured sharks are killed incidentally during bycatch interactions, either dying while on the line [capture mortality (CM)] (21) or after live release [postrelease mortality (PRM)] (22). The risk of mortality from these interactions varies substantially among shark species, where some species, such as the blue shark (*Prionace glauca*), are seemingly more robust to capture (CM rates ranging from ~6 to 15% and PRM rates ranging from ~17 to 38%) (22–24) than others, including most notably hammerhead species (*Sphyrna* sp.; CM rates ranging from ~56 to 100% and PRM rate of ~87.5%) (22, 23, 25). Furthermore, a large portion of these unintended catches are either unreported (26, 27) or reported in a format where they are of little use for fisheries analyses (e.g., catch not identified to the species level) (28).

Big-data approaches are now revealing insights into fishing vessel activities happening at the global scale (29, 30). Vessel positioning data broadcast from onboard Automatic Identification System (AIS) equipment have been leveraged for identifying areas where highly migratory sharks overlap with elevated levels of fishing effort (31–33). These approaches have also detected cases where fishing activities occurred inside marine protected areas (34, 35). Remotely sensed fisheries monitoring thus represents an alternative source of data to traditional fisheries management methods such as the historical reliance on data reporting, which can be characterized by taxonomic uncertainty, a lack of geolocation data, and a general underreporting of catch (27, 36–38). Given the challenges in

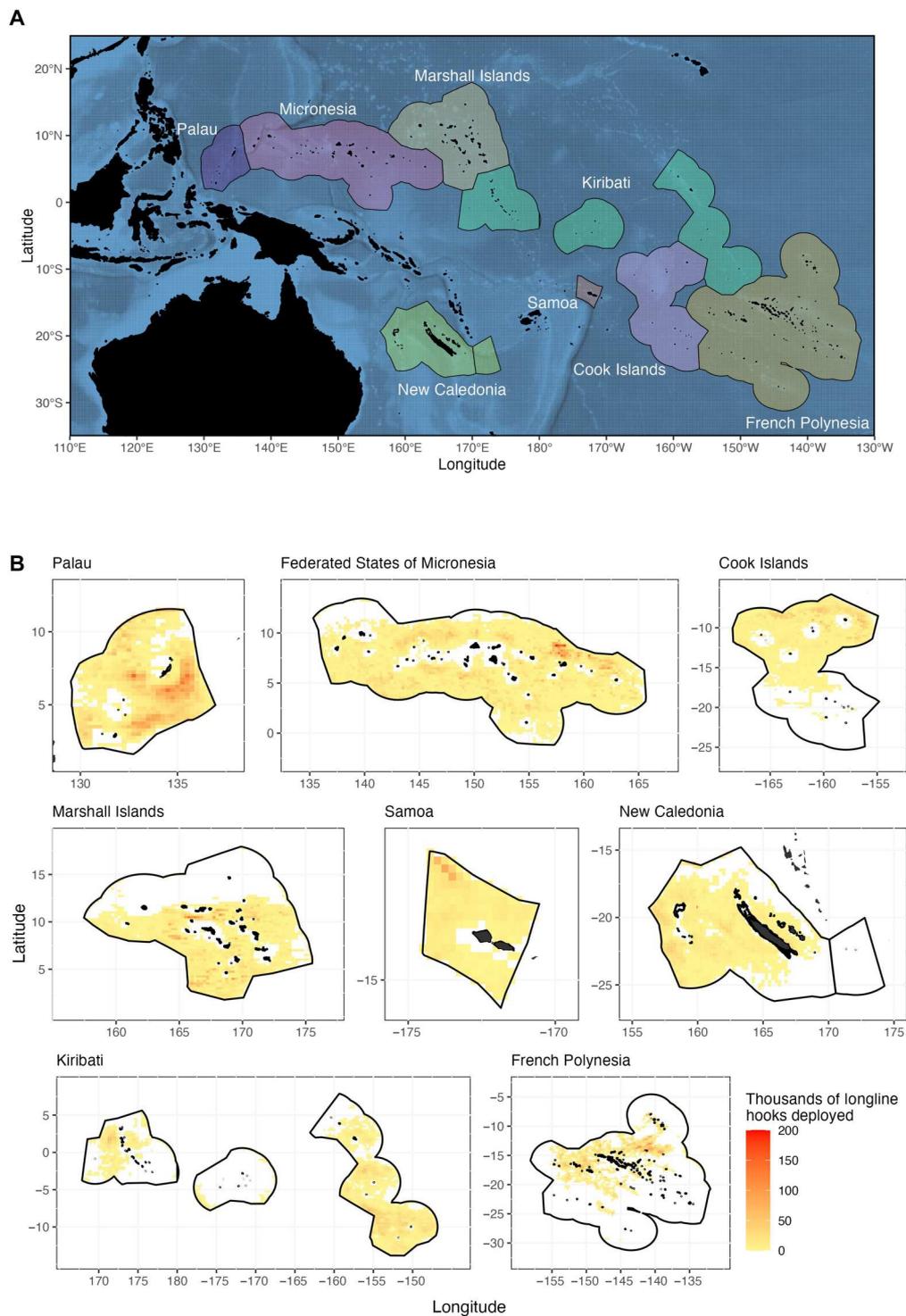
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quantifying shark bycatch in the face of these limitations, we took a big data approach to quantifying longline fishing effort, in terms of the number of hooks deployed, and the resulting pelagic shark bycatch mortality in WCPO shark sanctuaries [Cook Islands, the Federated States of Micronesia (FSM), French Polynesia, Kiribati,

Marshall Islands, New Caledonia, Palau, and Samoa; Fig. 1]. We chose to focus on WCPO shark sanctuaries as Caribbean shark sanctuaries are difficult to monitor via AIS because of low rates of equipment use and receiver coverage, and longline fishing is banned in the lone Indian Ocean sanctuary of the Maldives. We created a



**Fig. 1. WCPO shark sanctuaries.** (A) Map of WCPO shark sanctuaries. (B) Estimated longline hook deployments in 2019 in WCPO shark sanctuaries projected at 0.25° by 0.25° resolution.

data integration workflow (see Fig. 2) using AIS data from Global Fishing Watch (GFW; Fig. 2A) and publicly available data from Regional Fisheries Management Organizations (RFMOs; Fig. 2B) to (i) produce robust estimates of longline fishing effort (in terms of the number of hooks deployed; Fig. 2C) for eight shark sanctuaries in the WCPO; (ii) develop standardized catch rates [catch per unit effort (CPUE)] for three species, three genera, and one group of large pelagic sharks in the region (Fig. 2D); and (iii) estimate in-sanctuary shark bycatch (Fig. 2E) and, in turn, associated mortality (Fig. 2F) using CM and PRM rates gleaned from the literature (table S2).

## RESULTS

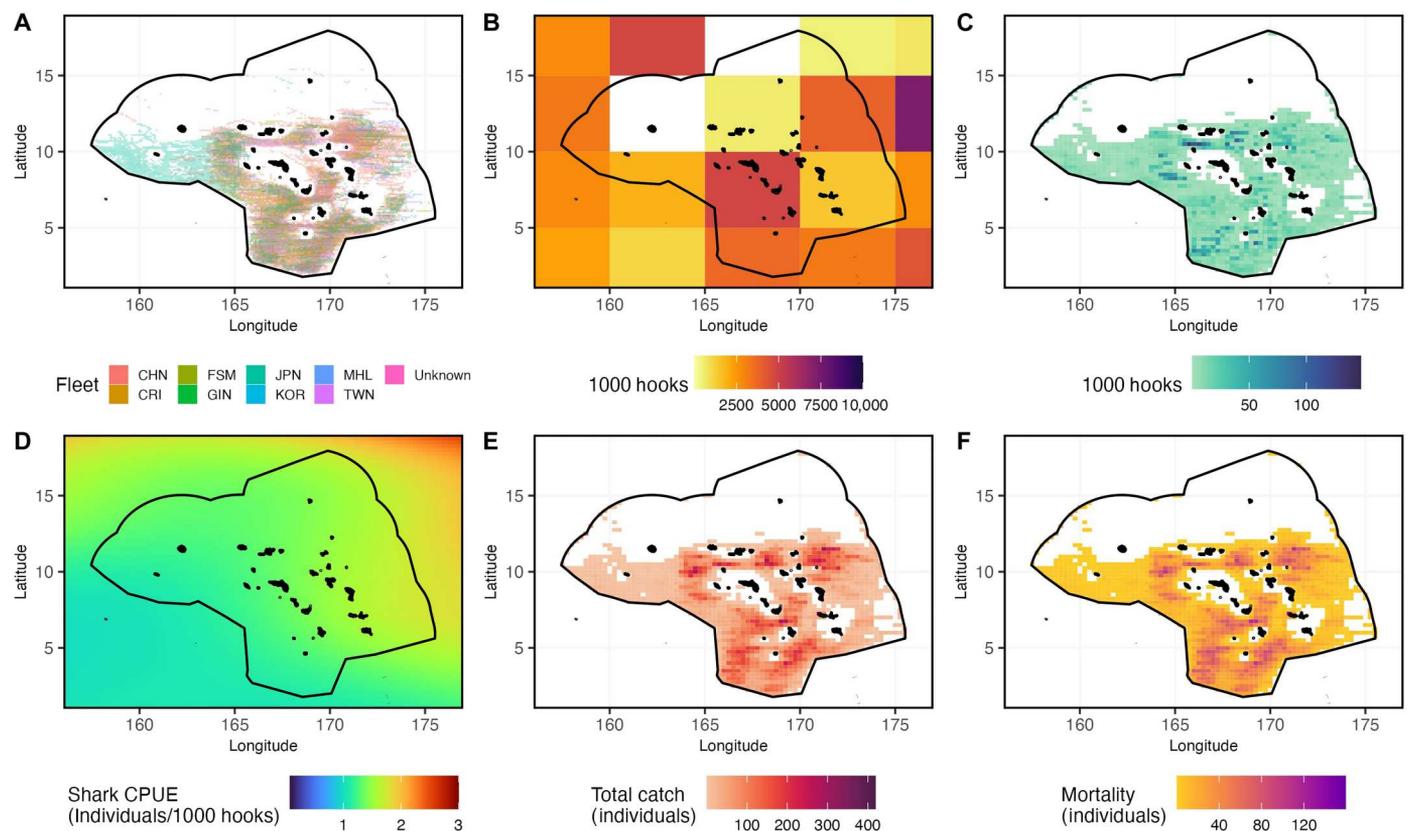
### Longline fishing effort

Our global dataset of apparent fishing effort from vessels deploying drifting longlines in 2019 represented approximately 7.4 million fishing hours from 56 national fleets (39), of which about 536,000 hours (7.2%) corresponded to fishing in WCPO shark sanctuaries (table S1). After modeling the relationship between hours and hooks using a generalized additive mixed model (GAMM), we estimated this level of fishing effort to result in approximately 228 million longline hooks deployed across the eight sanctuaries, with the most hooks deployed in the FSM (74 million hooks; table S1) and the Marshall Islands (49 million). The fewest hooks were deployed in Samoa (3.6 million) and New Caledonia (8.0 million).

We also calculated in-sanctuary hook deployments for the years 2016–2018 to evaluate potential temporal trends for in-sanctuary longline fishing and, in turn, potential bycatch mortality. Overall, longline fishing effort in WCPO sanctuaries was higher in 2019 than either of the previous 2 years but consistent with the level of effort from 2016. Most sanctuaries were relatively consistent in total effort year over year, although Kiribati saw a decrease in fishing from 2016 to 2018, likely due to the establishment of the Phoenix Islands Protected Area, before a small increase in 2019. Conversely, the longline fishing effort in the FSM increased each year from 2016 to 2019. GFW data are increasingly improving, and these across-years patterns may not reflect actual changes in fishing effort.

### Catch per unit effort

We standardized CPUEs for seven species and/or genera (figs. S2 and S3) using observer data from the Western and Central Pacific Fisheries Commission (WCPFC) (40) by fitting a generalized additive model (GAM), then used a Monte Carlo approach combining our hook-deployment estimates, CPUEs, and published CM and PRM rates to predict pelagic shark catch and mortality for each of the seven groups. Blue, silky (*Carcharhinus falciformis*), and oceanic whitetip (*Carcharhinus longimanus*) sharks were modeled at the species level, while thresher (*Alopias* sp.), mako (*Isurus* sp.), and hammerhead sharks were modeled at the genus level due to taxonomic uncertainty within the WCPFC observer data. A final group,



**Fig. 2. Data integration workflow.** Visualized complete workflow for Marshall Islands. (A) AIS-detected longline fishing effort by fleet ( $0.1^\circ$  resolution; color codes are national fishing fleets). (B) RFMO-declared fishing effort ( $5^\circ$  resolution). (C) Model-estimated hook deployment ( $0.25^\circ$  resolution). (D) Standardized CPUEs, all species and genera combined ( $0.25^\circ$  resolution). (E) Total pelagic shark catch ( $0.25^\circ$  resolution). (F) Total pelagic shark mortality ( $0.25^\circ$  resolution).

“other sharks,” reflects a corresponding category within the WCPFC observer data that pools species not otherwise identified.

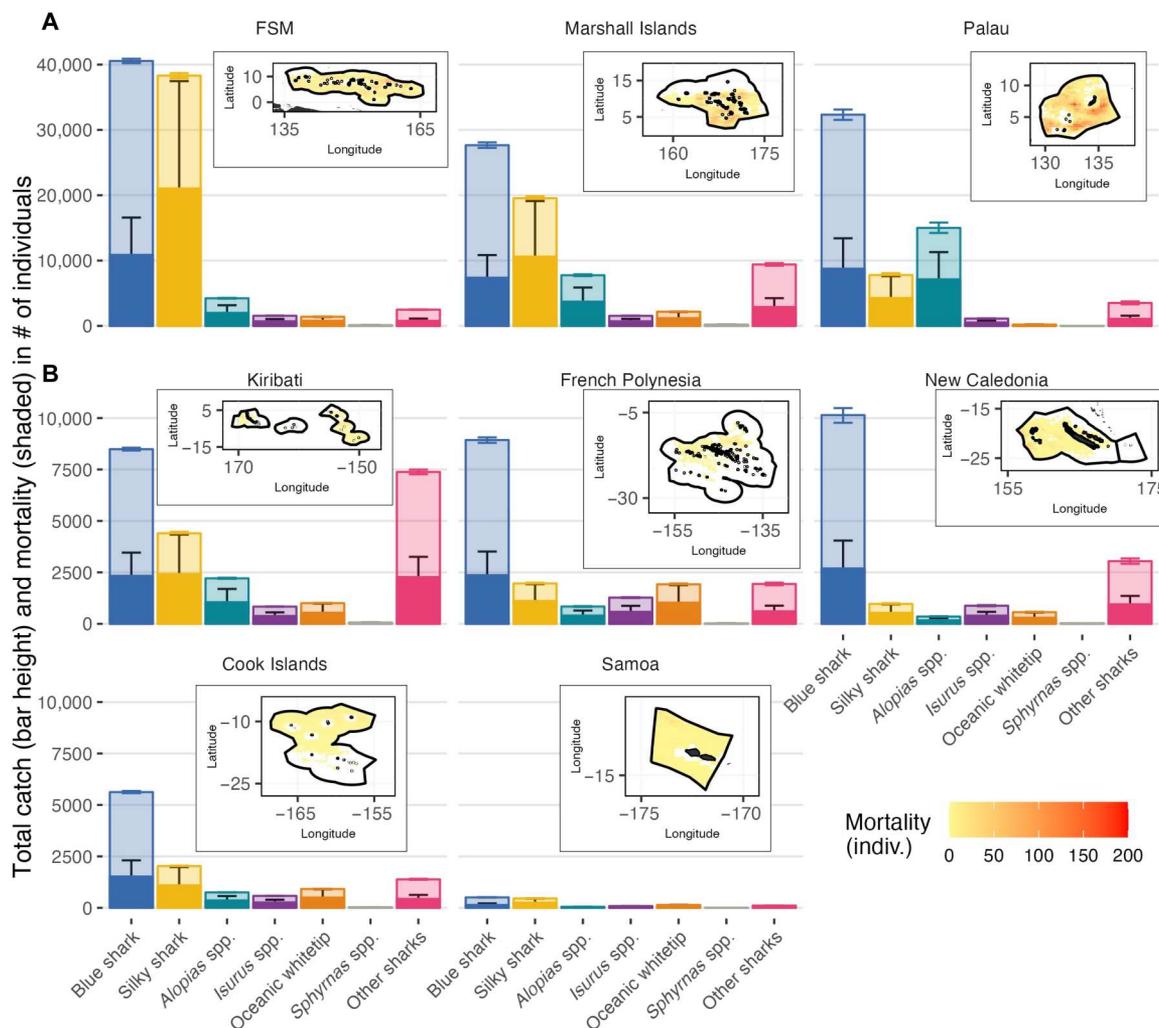
Our modeling approach to standardizing CPUE revealed heterogeneous distributions of catch rates (i.e., species abundance) across the WCPO. Blue sharks were generally associated with the highest catch rates of all species or groups across the WCPO (figs. S2 and S3), with sanctuary-wide medians ranging from approximately 0.2 to >1.5 individuals per 1000 hooks, although there was a noticeable decrease in blue shark CPUE near the equator (fig. S2). Silky sharks were also associated with relatively high CPUEs (>0.1 individuals per 1000 hooks) in most sanctuaries, particularly near the equator, while CPUEs for other species were generally lower and highly variable between sanctuaries. Plotted landscapes of CPUEs across the WCPO revealed a high degree of heterogeneity and variation for all species and groups (fig. S3).

### Estimated catch and mortality

Across all eight sanctuaries, our modeling suggested that 286,820 (95% confidence interval, 281,391 to 292,341) large pelagic sharks were captured as bycatch in shark sanctuaries in 2019 (Fig. 3), of

which we estimate that 109,729 (64,819 to 178,846) succumbed to either CM or PRM. Blue and silky sharks combined represented more than 73% of the projected catch [blue, 134,244 (132,052 to 136,396); silky, 75,445 (74,334 to 76,588)], with the bulk of the remainder representing thresher species and “other” sharks. Similarly, blue and silky sharks represented approximately 70.5% of all projected mortalities, including an estimated 41,302 (23,229 to 73,849) silky sharks and 36,061 (22,014 to 54,377) blue sharks. We also estimate the projected number of hook deployments to have resulted in substantial losses of thresher [14,836 (9162 to 23,545)], oceanic whitetip [4497 (2607 to 8171)], and “other” sharks [9024 (5665 to 13,102)].

To better contextualize the estimated losses of large sharks, we compared area-standardized mortality rates within shark sanctuaries with reference points gleaned from regional stock assessments. For the species presently considered, there are stock assessments available for blue, silky, shortfin mako (*Isurus oxyrinchus*), and oceanic whitetip sharks; however, blue and shortfin mako sharks each comprise two distinct stocks in the Western Pacific (northern and southern), and no stock assessment for the southern stock of



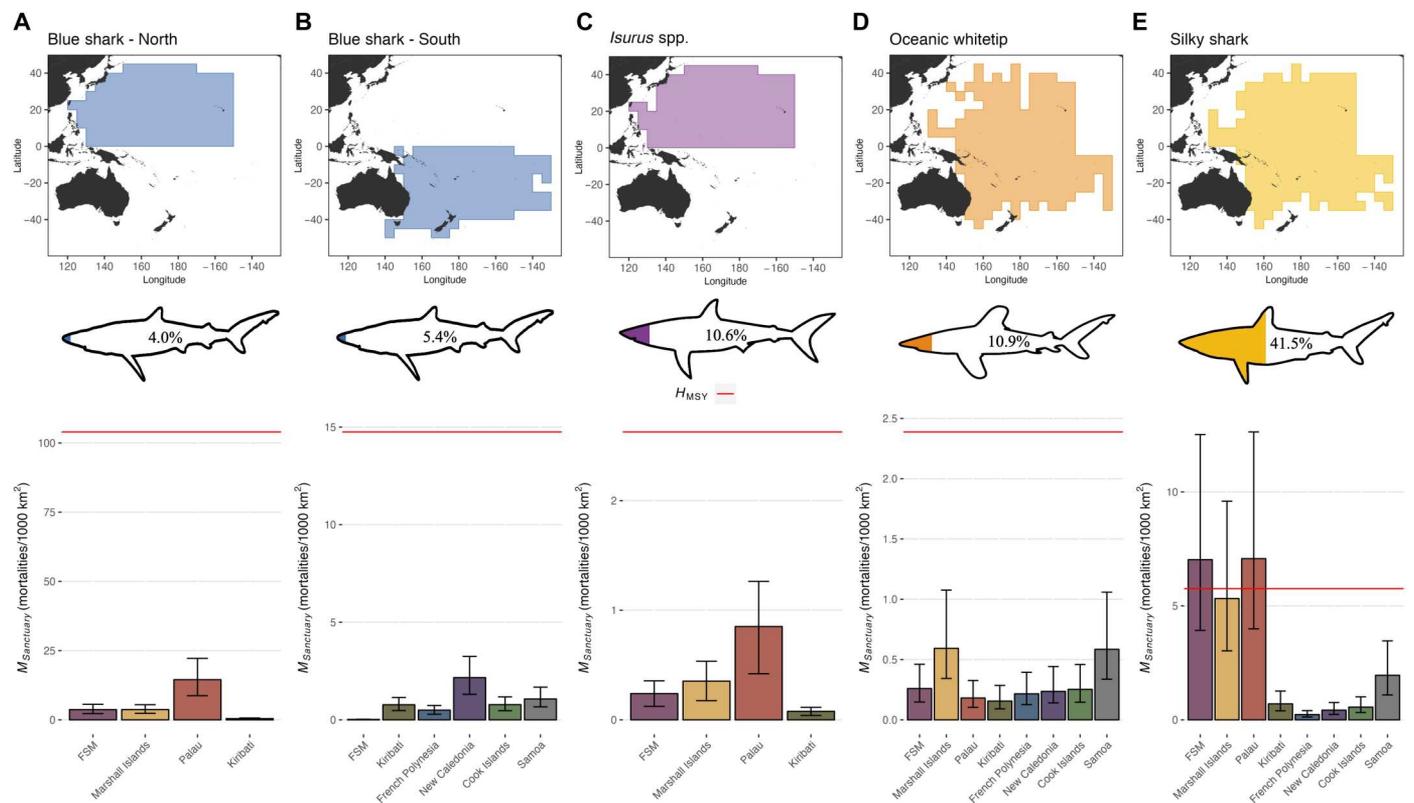
**Fig. 3. In-sanctuary bycatch mortality.** Total pelagic shark catches (bar height) and mortality by species (filled portion bars) and heatmaps of pooled mortality (insets, number of individuals). Sanctuaries divided into (A) “high catch” and (B) “low catch” to better facilitate comparisons.

either species has been accepted by the WCPFC Scientific Committee. A preliminary assessment for the South Pacific has been completed for blue sharks, however (41). We considered all mako sharks to be shortfin mako as there is a paucity of data available for its congener, the longfin mako (*Isurus paucus*) in the Pacific (42), and additionally because where mako sharks were identified to the species level within WCPFC observer data, the nominal catch rate for shortfin mako was more than five times greater than that of longfin mako. The WCPFC has not established target and limit reference points for pelagic sharks in the Pacific. Hence, stock status is reported in relation to maximum sustainable yield (MSY), which represents the harvest rate at which a population can be fished to maximize harvest while still able to fully replenish its losses from fishing each year. It should be emphasized, however, that MSY-level harvest is not an objective of shark sanctuaries, whose goal is to conserve shark populations, not maximize their sustainable harvest—MSY is just used here to contextualize results with available reference points.

To create an area-standardized benchmark for characterizing longline mortality rates in sanctuaries, we standardized MSY estimates from available stock assessments using the total area of each species' stock in the WCPO to establish the hypothetical reference point  $H_{MSY}$ .  $H_{MSY}$  represents the annual harvest rate per unit area that would result in MSY-level harvest if the allotted harvest were equally distributed across the species' stock area within the WCPFC fishing area for all gears. Stock areas were delineated by creating a species-specific polygon encompassing all 5° by 5° cells with any catches reported to the WCPFC since 1950 (Fig. 4). We

then standardized our in-sanctuary bycatch mortality estimates by the area of the sanctuaries to generate sanctuary-level and pooled estimates of the standardized bycatch mortality  $M_{Sanctuary}$  ( $M_{Sanctuary} = \text{bycatch mortality}/\text{sanctuary area}$ ) for longlines. We compared  $M_{Sanctuary}$  with  $H_{MSY}$  to provide a basis for evaluating the performance of shark sanctuaries against a fishing-at-MSY scenario.

Although  $M_{Sanctuary}$  rates were generally much lower than  $H_{MSY}$  rates per unit area, there was substantial variation among species and sanctuaries. Pooled across sanctuaries,  $M_{Sanctuary}$  for blue sharks was approximately 95% lower than  $H_{MSY}$  (northern stock:  $H_{MSY} = 104.0$  mortalities/1000 km<sup>2</sup>,  $M_{Sanctuary} = 4.2$  mortalities/1000 km<sup>2</sup>; southern stock:  $H_{MSY} = 14.8$  mortalities/1000 km<sup>2</sup>,  $M_{Sanctuary} = 0.8$  mortalities/1000 km<sup>2</sup>; Fig. 4, A and B). For oceanic whitetip sharks, we estimated bycatch interactions to result in mortality equivalent to approximately 279.7 metric tons (mt) of harvest; this corresponds to an  $M_{Sanctuary}$  of 0.26 mortalities/1000 km<sup>2</sup>, 89.1% lower than  $H_{MSY}$  (Fig. 4C). Similarly, our estimated mortality of approximately 62.63 mt of Mako sharks from the northern stock corresponded to an  $M_{Sanctuary}$  rate 89.4% below  $H_{MSY}$  (Fig. 4D); however, for mako sharks, an additional 49.2 mt estimated to be lost from the southern stock cannot be contextualized because of a lack of stock assessment data. Spatial protections were least effective for silky sharks, for which  $M_{Sanctuary}$  was 41.5% of  $H_{MSY}$  overall across all sanctuaries, and our sanctuary-level estimates for  $M_{Sanctuary}$  exceeded  $H_{MSY}$  in the FSM and Palau (Fig. 4E).



**Fig. 4. Mortality in context.** Stock domains and harvest rate reference points for (A) blue shark (northern stock), (B) blue shark (southern stock), (C) *Isurus* spp., (D) oceanic whitetip, and (E) silky shark. Top row: Stock delineations. Middle row: Pooled effect of all WCPO sanctuaries with  $M_{Sanctuary}$  as a percentage of  $H_{MSY}$ . Bottom row:  $M_{Sanctuary}$  in number of individuals killed/1000 km<sup>2</sup>, compared to  $H_{MSY}$  (red line).

**DISCUSSION**

Spatial protections have long been championed as an effective tool in threatened species conservation, including for sharks. However, any permitted fishing is likely to result in a nonnegligible level of bycatch mortality, particularly in the case of longline fishing. Although we show here that properly enforced spatial protections can generally restrict longline-induced pelagic shark mortality to levels below hypothetical reference points (i.e., MSY-based harvest rates per unit area), it is important to consider that MSY-based reference points represent targets or limits relative to maximum sustainable exploitation, and the conservation goals of shark sanctuaries are designed to minimize the loss of sharks, not maximize their sustainable take. A true “shark sanctuary” likely entails the prohibition of all longline fishing effort, but this may not be feasible, given the economic and food security role of longline fishing in many remote island nations. In the absence of outright longline bans, managers of shark sanctuaries wishing to further mitigate shark losses within these protected areas should consider adoption of targeted bycatch reduction measures (e.g., gear modifications, effort restrictions, and/or temporary or permanent area closures of key habitat).

Acknowledging the economic role of commercial fishing in many sanctuaries, our analyses could be used to estimate how much long-lining effort could be allowed in a specific sanctuary to ensure a by-catch level within reference points deemed acceptable by sanctuary managers. For example, in the Marshall Islands, our estimate would suggest that reducing overall longlining by 6.6% could reduce silky shark mortality to meet harvest-at-MSY levels (Fig. 4E), although we would recommend substantially stronger reductions for more ambitious targets, given that the goal of sanctuary designation is shark conservation and not their sustainable take. Furthermore, since silky shark CPUE varies spatially (similar to other sharks), these reductions may be prescribed only in specific sectors of the sanctuary to limit negative impacts on fishery operations. To this end, the performance metrics of a sanctuary should be clearly defined. As any commercial fishing will inevitably result in bycatch mortality, establishing “permissible” levels of bycatch mortality [for example, in terms of shark mortalities per unit weight of longline fishery production, or the total longline revenue gained by the sanctuary, either via domestic production or byin revenue generated through allocation of fishing rights, per shark mortality] would allow for quantitative assessment of progress toward conservation goals while balancing against the economic and food-security role of commercial fishing regionally.

Any metrics should be defined at the species level where possible to account for the species-specific vulnerability to bycatch mortality found here. Although it has been shown previously that marine protected areas may disproportionately protect reef-associated species (35) as compared to those inhabiting the pelagic, here, we also show substantial variation in the effects of spatial protection even among pelagic sharks. In particular, silky sharks appear especially vulnerable to longline-associated bycatch mortality, with higher catch rates than all species other than blue shark, as well as comparably high CM and PRM rates; however, the effect of this variability on different species cannot be fully contextualized because of a lack of pelagic shark stock assessments regionally. Thresher sharks, for example, represent some of the more common shark bycatch in the region and may be particularly vulnerable to overexploitation due to

low reproductive rates (43). However, there are no stock assessments available for either bigeye thresher (*Alopias superciliosus*) or pelagic thresher (*Alopias pelagicus*), the more frequently encountered thresher species in the WCPO. While catch rates are comparably lower for thresher sharks than for species for which there are stock assessments available, the effect of these bycatch losses on populations is unknown, particularly as the rate at which thresher sharks encountered by fishers in the WCPO outside sanctuaries are retained is not known. Efforts to complete stock assessments for pelagic shark stocks in the WCPO should be prioritized, particularly as in our workflow, approximately 70% of the stock areas for most species lie outside of protected waters where bycatch retention is generally not prohibited—although silky and oceanic whitetip sharks are now subject to WCPFC-wide retention bans (44)—and sharks are targeted to support the increasing global demand for shark products (45).

The variation among sanctuaries stems from differing levels of fishing effort as well as CPUEs and, by proxy, shark abundance. The sanctuaries with the greatest catch and mortality estimates—FSM, Marshall Islands, and Palau—are all located in the tropics in areas that overlap with high CPUE estimates for silky sharks (fig. S3), a commonly occurring bycatch species with high bycatch mortality rates (table S1). This increased pressure on silky sharks in the tropics is particularly relevant when considering other sources of bycatch mortality, such as purse seine fisheries. Although our workflow focuses on longlines, data from GFW suggest that there is also substantial purse seine fishing effort within more tropical sanctuaries, particularly Kiribati and the FSM, which together contributed nearly 20% of the AIS-detected fishing effort by purse seines in the WCPFC in 2019. An estimated 92,165 (91,579 to 92,801) silky sharks were captured as bycatch across WCPFC purse seine fisheries in 2019 (46), although this number may be an underestimate, and the total bycatch mortality (combined capture and post-release) rate for silky sharks caught in this fishery has been estimated at ~86% (47). Assuming this mortality rate and distributing mortality evenly by effort, this would suggest substantial additional in-sanctuary bycatch mortality of silky sharks in both Kiribati (~10,000 individuals) and FSM (~5000). Although there is currently a WCPFC-wide retention ban on silky sharks, our study suggests that additional management measures may be required beyond a retention ban to reduce silky shark mortality levels and rebuild the stock, particularly within shark sanctuaries where conservation is a stated goal. As longline fishing has increased in recent years in the FSM (fig. S1), a silky shark bycatch hotspot, these management measures are likely needed sooner rather than later.

Although we focus on shark sanctuaries and longlines, our approach is highly generalizable across ocean sectors, species, and fishing gears. Data integration workflows such as ours can be refined and scaled as complementary and potentially transformative tools for fisheries managers on a global scale. By cross-validating disparate streams of fishing effort data, we can better understand the space use of fishing vessels and more accurately estimate catch, particularly for nontarget or discard species (or mandatory discards, in the case of shark sanctuaries). Our pipeline relies only on publicly available data and, by relying on observer data to generate CPUEs, minimizes potential data failures associated with misreporting or underreporting of traditional catch statistics (27, 38). Using public data, our CPUE estimates are consistent with other published CPUEs from the region (20), although, here, we

provide greater taxonomic resolution. This approach can be further refined by expanding to additional gear types and integrating species distribution maps, habitat maps, and/or environmental and oceanographic variables, which may also inform estimates of a species' catchability at a given place and time and improve the spatiotemporal resolution of CPUE modeling, particularly for data-poor species.

Our approach makes several assumptions that are, if anything, conservative estimates of mortality, notably including the assumption of 100% compliance with sanctuary regulations (i.e., it makes no allowances for illegal retention of sharks captured either alive or dead). Enforcement is a notable challenge in remote protected areas such as these (11, 48), and this assumption is unlikely to always be valid. This may be particularly true for the Marshall Islands and FSM, two sanctuaries that do not include outright possession bans as part of their legislation (11, 49) and are associated with high rates of longline effort and estimated catch (Figs. 1B and 3A). The lack of a possession ban allows fishers to potentially flaunt the sanctuaries' prohibition on the retention of sharks captured as bycatch, as fishers, in theory, could keep any sharks encountered as bycatch and later claim that those animals were brought into the sanctuary after legal capture in other waters. Given the volume of sharks that we demonstrate are likely to be encountered as bycatch, closing the loophole on possession bans is essential to better facilitate the already challenging issue of enforcement (49). Similarly, our models do not consider the potential (perhaps even likelihood) for illegal, unreported, and unregulated fishing to occur within sanctuaries, which may substantially contribute to pelagic shark mortality through targeted shark fishing as well as bycatch. Additional bycatch mortality is likely to occur in subsistence fisheries as well, although at a smaller scale. Last, our CPUE models are based purely on observer data, and there is some evidence that observer data may underestimate shark catches in WCPFC fisheries (47); furthermore, there is inherent uncertainty in scaling data to a higher spatial resolution. Nonetheless, here, we provide a realistic estimate of considerable shark mortality that persists in areas purportedly offering full protection for sharks, which managers can use to quantitatively assess the performance of shark sanctuaries with respect to conservation of shark populations.

Establishing shark sanctuaries is an important milestone in the journey toward shark conservation, as they codify the intent of nations to actively work to preserve their important shark populations. Our analysis suggests that species-specific spatial closures alone reduce area-standardized mortality below area-standardized, MSY-based reference points, but more stringent and/or alternative reference points should be established so that sanctuary performance can be assessed quantitatively and weighed against the economics of allowing in-sanctuary commercial fishing. Integrating additional management techniques, such as gear modifications, effort restrictions, and/or temporary or permanent area closures within EEZs, is likely to further mitigate the impacts of ongoing fishing operations on large shark populations. Here, we show an original approach to estimating catch and mortality that can be applied to different species and regions and be used to evaluate and refine current regulations with minimal data requirements. For longlines, this can be applied to other common bycatch and data-poor species, as well as target species, as our workflow only requires an index of catchability (e.g., CPUEs) and RFMO-level effort

reporting and can substantially improve the spatial resolution of indices of fishing catch and mortality, making it a valuable tool for remote fisheries monitoring. An improved understanding of the complex relationship between catch and effort for other gears will allow the expansion of this workflow beyond longlines. In this sense, data integration workflows that harness and leverage big data have the potential to reshape fisheries management, particularly for remote ocean regions.

## MATERIALS AND METHODS

Our analysis consisted of three primary stages. First, we modeled the relationship between AIS-detected apparent fishing effort in hours (obtained from GFW) (50) and the declared number of longline hooks deployed (obtained from global tuna RFMOs) at the global scale using a GAMM. RFMO effort data (hooks) are generally reported at a relatively coarse resolution (5° by 5°), which makes quantifying the number of longline hooks deployed within a given sanctuary or EEZ challenging, as 5° by 5° cells near sanctuaries often include large areas of other territorial waters or the high seas (e.g., Fig. 2A). We used our GAMM model and remotely sensed apparent fishing effort (in hours) from GFW aggregated at a finer, 0.25° by 0.25° resolution (Fig. 2B) to generate estimates of longline hook deployments within WCPO shark sanctuaries for the year 2019 (Fig. 2C). Next, we used fisheries observer data and GAMs to generate landscapes of standardized catch rates for seven species or genera of pelagic sharks across the WCPO. Last, using the location-specific hook deployment estimates and catch rates calculated previously, we estimated the number of sharks (at the group level) caught annually as bycatch in longline fisheries operating within sanctuary limits and, in turn, quantified the expected mortality of captured sharks using CM rates and PRM rates gleaned from the literature. All analyses were run using R version 4.1.1 (51) and RStudio version 1.4.1717 (52), with GAMs and GAMMs fit using the R package mgcv v.1.8-40 (53–56), and further analyzed with the package gratia v0.7.3 (57). Model diagnostics plots are included as figs. S4 to S10.

## Quantifying fishing effort

We first obtained apparent fishing effort in each shark sanctuary studied using the GFW database (50). GFW uses vessel positioning information broadcast by AIS from equipped fishing vessels to estimate the apparent fishing effort (in hours or days) by a given vessel (30). We selected AIS broadcasts associated with longlining vessels for the year 2019, aggregated to a 0.25° by 0.25° resolution to summarize apparent fishing hours by flag, year, and position (latitude and longitude), and then filtered the data using EEZ-specific shapefiles (58) to obtain the annual apparent longline fishing effort within 17 designated shark sanctuaries: the Bahamas, Bonaire, British Virgin Islands, Cayman Islands, Cook Islands, Dominican Republic, the FSM, French Polynesia, Honduras, Kiribati, Maldives, Marshall Islands, New Caledonia, Palau, Saba, Samoa, and Sint Maarten. After applying these spatial filters, we removed the data from the eight shark sanctuaries in the Greater Caribbean region, as poor satellite coverage and low rates of AIS deployment in the area (30) resulted in high degrees of uncertainty. Furthermore, we excluded the Maldives due to the nationwide ban on longlining (59) and instead focused only on WCPO sanctuaries: Cook Islands,

FSM, French Polynesia, Kiribati, Marshall Islands, New Caledonia, Palau, and Samoa (Fig. 1A).

We then transformed the detected apparent fishing effort (in hours) in WCPO sanctuaries into the annual number of hooks likely deployed within each sanctuary using a GAMM model (family = scaled-t, link = identity). First, we extracted the total number of longline hooks deployed globally in 2019 from catch and effort statistics published online by global tuna RFMOs, aggregated to a 5° by 5° resolution. Next, we aggregated GFW global longline apparent fishing effort to the same resolution and fit a GAMM model to the number of hooks deployed as a function of AIS apparent fishing hours detected, in each cell, using the following equation,

$$\log(\text{Hooks}) \sim \log(\text{Hours}) + s(\text{Latitude}) + s(\text{Longitude}) + (1 | \text{Fleet})$$

where  $s$  represents a smoothing spline parameter that varies over the range of the covariate. Splines allow for nonlinear patterns between the individual predictors and the dependent variable—in the present example, fishing effort, both in terms of time and intensity (number of hooks), is not expected to follow a linear relationship with respect to latitude and longitude. We used a random effect for the flag nation of the fishing vessel to account for potential fleet-wide targeting strategies that may influence the number of hooks set on a given length of line (60). After fitting the model at a resolution of 5° by 5°, we then used the 0.25° by 0.25° AIS dataset and sanctuary-specific spatial filters (58) to project the number of longline hooks deployed within shark sanctuary boundaries at 0.25° by 0.25° resolution. Where the flag state of the fishing vessel could not be determined (either due to incomplete AIS transmission or deliberate tampering) or if a fishing vessel flag did not occur in the model training dataset, a median-level random effect representative of all fleets operating in that sanctuary was used for those flags.

### CPUE rates

We estimated species- or genus-specific CPUEs via standardization of fisheries observer data from the WCPFC (downloaded 24 October 2022). We used GAMs (family = negative binomial; link = log) to standardize CPUEs by first modeling captures (in number of individuals) using the following equation

$$\begin{aligned} \text{Captures} \sim & s(\text{Latitude}) + s(\text{Longitude}) \\ & + ti(\text{Longitude} * \text{Latitude}) + s(\text{Year}) \\ & + \text{offset}[\log(\# \text{ of hooks})] \end{aligned}$$

This model structure allows for each of the three smoothing splines (latitude, longitude, and their tensor interaction) to be fit with a different smoothing parameter (i.e., the number of permitted knots in the smooth or kernels in the covariate's range), allowing the model to reflect the heterogeneity of the WCPO fishing area while restricting the variability of splines where possible to prevent overfitting (i.e., latitude is generally more heterogeneous than longitude). The number of knots  $k$  for each covariate was checked to ensure that  $k$  was sufficiently large to illustrate underlying patterns. We then used the fitted model to predict CPUE values (in terms of number of sharks captured per 1000 hooks deployed) across the WCPO at 0.25° by 0.25° resolution for the year 2019.

### Projected catches and mortalities

We estimated total catch, CM, and PRM for each group using our standardized CPUEs as well as CM and PRM rates gleaned from published literature (see table S1). This was performed by running Monte Carlo simulations along a four-step analytical workflow a total of 1000 times. This workflow was applied at the sanctuary level for each group considered. In preparation for our Monte Carlo simulations, we first generated 1000-hook deployment estimates for each 0.25° by 0.25° cell in a sanctuary by drawing from log-normal distributions produced by our GAMM predictions. These hook deployments were then used as the starting point for each set of 1000 group-specific runs for the sanctuary. In addition, 1000 group-specific CM rates were drawn from a uniform distribution between minimum and maximum CM rates gleaned from the literature (23–25), while 1000 group-specific PRM rates were drawn from a logit-normal distribution of PRM rates from a published meta-analysis of 33 PRM studies covering seven pelagic shark species (22) to encapsulate the variability around these previous estimates. After generating hook deployments and group-specific CM and PRM values, we initiated the set of 1000 runs of our workflow for each group for that sanctuary.

In the first step of the analysis, a group-specific CPUE for each cell was drawn from a log-normal distribution generated by our GAM modeling of CPUEs and then multiplied by the hook deployment total in that cell (for that run) to generate an estimate of total catch. Next, the total catch was multiplied by the run-specific CM rate to estimate the level of at-vessel mortality (or total CM) for each cell. In shark sanctuaries, all sharks are mandated to be released, so in the third step, we used the difference between total catch and total CM to estimate the number of sharks released alive. The number of live releases was then multiplied by the run-specific PRM rate to estimate total PRM, and in the fifth and final step, total CM and total PRM were then summed to quantify total mortality. We summed the total catch, CM, and PRM for each run and took the means and generated a mean estimate and error range for each group in each cell. Reported sanctuary level estimates are from the mean of the summed run totals, with confidence intervals generated using 5 and 95% quantiles for catch and mortality for each species.

In two instances (Palau and French Polynesia), fishing effort occurred beyond the domain of WCPFC observer coverage, and CPUEs for those areas could not be directly predicted by our GAM models. In this circumstance, we assigned each 0.25° cell the species- or genus-specific CPUEs from the nearest cell within the WCPFC observer domain.

### Stock delineation and sanctuary performance assessment

After calculating total mortality, we compared our estimates to available stock assessment data (for species with an assessment available) from the WCPFC to assess how sanctuaries are performing compared to available MSY-based reference points (no target or threshold limits exist for pelagic sharks in the WCPFC, so MSY-based reference points are used instead). We delineated stock areas by reviewing historical catch data from the WCPFC dating back to 1950 and considered the stock area to include all 5° by 5° cells where any catch of the species has occurred historically (i.e., binary—either catch has occurred, or it has not). Although it is possible or even likely that the stock boundaries for some species, notably blue sharks, extend beyond WCPFC boundaries, this nonetheless allows us to compare bycatch mortality within WCPFC

shark sanctuaries to the estimated level of sustainable take for the stock by WCPFC fishing vessels. The stock area was considered to comprise all positive cells (i.e., catch had occurred) and any negative cells that were surrounded by positive cells—That is to say, the stock area of positive cells was interpolated across negative cells but never extrapolated.

For all species, we standardized MSY by the stock area and calculated a harvest rate at MSY per unit area ( $H_{MSY}$ ). We then standardized our estimated in-sanctuary bycatch per unit area ( $M_{Sanctuary}$ ) and compared these rates to  $H_{MSY}$ . While it is unlikely that pelagic shark mortality is evenly distributed across the WCPO, even outside sanctuary borders, this provided a benchmark by which to assess the performance of the sanctuaries and their relative contribution to the conservation of each species.

## Supplementary Materials

This PDF file includes:

Supplementary Text  
Figs. S1 to S12  
Tables S1 and S2

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## Quantifying longline bycatch mortality for pelagic sharks in western Pacific shark sanctuaries

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