

## ECOLOGY

# Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the northeast Pacific

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Many species of sharks and some tunas are threatened by overexploitation, yet the degree of overlap between industrial fisheries and pelagic fishes remains poorly understood. Using satellite tracks from 933 industrial fishing vessels and predictive habitat models from 876 electronic tags deployed on seven shark and tuna species, we developed fishing effort maps across the northeast Pacific Ocean and assessed overlap with core habitats of pelagic fishes. Up to 35% of species' core habitats overlapped with fishing effort. We identified overlap hotspots along the North American shelf, the equatorial Pacific, and the subtropical gyre. Results indicate where species require international conservation efforts and effective management within national waters. Only five national fleets (Mexico, Taiwan, China, Japan, and the United States) account for >90% of overlap with core habitats of our focal sharks and tunas on the high seas. These results inform global negotiations to achieve sustainability on the high seas.

## INTRODUCTION

Approximately 75% of pelagic sharks and 30% of tunas are threatened by overexploitation, yet many are still subject to intense fishing pressure (1, 2). The movements and habitat preferences of many pelagic fishes include the use of the “high seas,” or the ~60% of global oceans that lie beyond any individual nation's control (3, 4). This exposes pelagic populations to multinational fishing fleets and diffuses accountability across dozens of nations that collectively fish these shared waters (4–6). In addition to jurisdictional challenges, many shark and tuna species are particularly susceptible to overfishing due to their relatively late ages at sexual maturity and tremendous commercial value; the global value of tuna and shark fisheries are estimated at \$42 billion and \$1 billion, respectively, which motivates ongoing overfishing of some species (1, 7–9).

Currently, high seas [also known as areas beyond national jurisdiction (ABNJs)] fisheries are primarily managed by regional fisheries management organizations (RFMOs). The effectiveness of high seas fisheries management has been debated (9); many high seas populations are depleted or overfished (5), and RFMO agreements only pertain to participating member nations (10). RFMOs have improved stock biomass when strong management measures such as quotas are adopted, yet 36% of RFMO-managed tuna populations and 61% of billfish populations globally have biomasses below target levels (11). The United Nations' recent commitment to create the world's first legally binding treaty on global high seas conservation (12) presents a historic opportunity to stabilize global pelagic fish populations (13). However, a better understanding of high seas fisheries and their effects on pelagic species is needed to inform the priorities of this treaty, which will be formally negotiated until 2020. Although fishing is the strongest

driver of declining population trends in sharks and tunas (14), the distributions and relative pressures of high seas and domestic fishing fleets on many migratory species remain poorly understood (15), making it unclear which species or regions may warrant prioritization in a high seas treaty.

Global understanding of industrial fishing activity has traditionally derived from the Food and Agriculture Organization of the United Nations (FAO) statistics or aggregated catch data (e.g., longlines are typically presented at 5° grid cell size, while purse seine data are often provided at 1° resolution) reported by RFMOs (16). A primary limitation of official datasets and finer-scale catch reconstructions from these data is that individual countries with competing national interests self-report data to international fisheries organizations, leading to misreporting that may compromise suitability for spatial management (17). For example, China's distant-water fleet, among the world's most active fleets, is estimated to underreport catch by one order of magnitude (0.4 million metric tons per year reported versus 4.6 million metric tons per year estimated in reconstructed catches) (18). There are typically no punishments for nations that do not self-report shark catch data, and the effectiveness of measures to penalize misreporting of shark and tuna catch data varies by RFMO (5, 19). As a result, some official datasets contain sparse reported shark catches from major fishing fleets including China, Taiwan, Japan, and South Korea (20). Fisheries observer programs, government-mandated vessel monitoring systems, and vessel logbooks have provided higher-quality data on industrial fishing, although these data are only available for a small fraction of fishing fleets and are typically kept private by individual nations (21). For example, over two-thirds of RFMO-managed fisheries lack regional observer programs, leading to continued uncertainties over the global impacts of pelagic fisheries in both national and international waters (22).

Recently, analysis of a publicly accessible, globally available vessel transmission system known as the Automatic Identification System (AIS) has provided maps of global fishing effort at unprecedented spatial and temporal resolution, allowing the direct observation of over 70,000 industrial fishing vessels (23–25). AIS can be used to observe 50 to 75% of all fishing vessels greater than 24 m despite known limitations (e.g., many smaller vessels do not transmit AIS detections and a

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small subset of vessels tamper with AIS devices), thus providing a high-resolution assessment of global fishing that is not reliant on self-reporting (25). This innovation facilitates novel investigation into the spatio-temporal dynamics of fishing effort, the influence of the physical environment in driving fisheries trends, and potential spatial overlaps with core habitats of commercially valuable and threatened pelagic species. Effectively quantifying overlap between marine predators and industrial fishing effort is essential for identifying regions of conservation concern (26, 27) and predicting bycatch hotspots for threatened species (21, 28). AIS analysis provides an opportunity to independently inform fisheries management practices and conservation initiatives, including efforts to better manage the overexploited and data-poor high seas (29).

Here, we used shipboard AIS signal analysis, electronic tagging datasets of pelagic species, and predictive habitat models to identify regions of overlap between commercial fishing effort and the core habitats [defined as the top quartile of monthly habitat model predictions following Hazen *et al.* (30) and Kappes *et al.* (31)] for seven species of pelagic sharks and tunas in the northeast Pacific Ocean. The northeast Pacific Ocean provides an ideal setting to investigate the interactions between pelagic fishes and fisheries due to the high commercial value of regional fisheries and the unprecedented amount of publicly available, fisheries-independent data available on habitat utilization by pelagic species; the Tagging of Pacific Predators (TOPP) program produced 876 tracks of our seven study species in this region (3). This biologging program also supported development of the predictive habitat models, which quantify relationships between animal movements and dynamic oceanographic variables and predict how species may respond to contemporaneous oceanographic conditions (30). Temporal differences between animal movement and fishing effort datasets (up to 5- to 10-year differences) are common in studies that examine overlap of fishing effort and species distributions (21, 28). AIS-derived maps of fishing effort are only available for recent years (25), so most animal tracking datasets predate observations of fishing (3). We used habitat models (30) to address this discrepancy by generating habitat predictions for the exact time period of our fishing effort observations.

To inform how national and international management actions may address the impacts of fishing on these species, our primary objectives were to (i) map commercial fishing effort by tracking all fishing vessels that transmitted AIS signals in the northeast Pacific Ocean in 2015–2017, (ii) calculate fisheries overlap with the predicted core habitats of pelagic sharks and tunas using habitat models (3, 30), (iii) determine which species may require an international approach to conservation and management due to fisheries overlap in the high seas, and (iv) identify which nations' fisheries most frequently overlap with these pelagic species. These analyses may be used to identify regions of concern for ongoing United Nations negotiations on the conservation and sustainable use of the high seas and to evaluate fisheries self-reporting by identifying where countries may be targeting or landing species that are not reported to management agencies.

## RESULTS

### Patterns of fishing effort

Using 80 million detections of AIS transmissions, 933 industrial fishing vessels flagged to 12 different nations were tracked in the northeast Pacific study region (10°N to 60°N, 110°W to 180°W) from 1 January

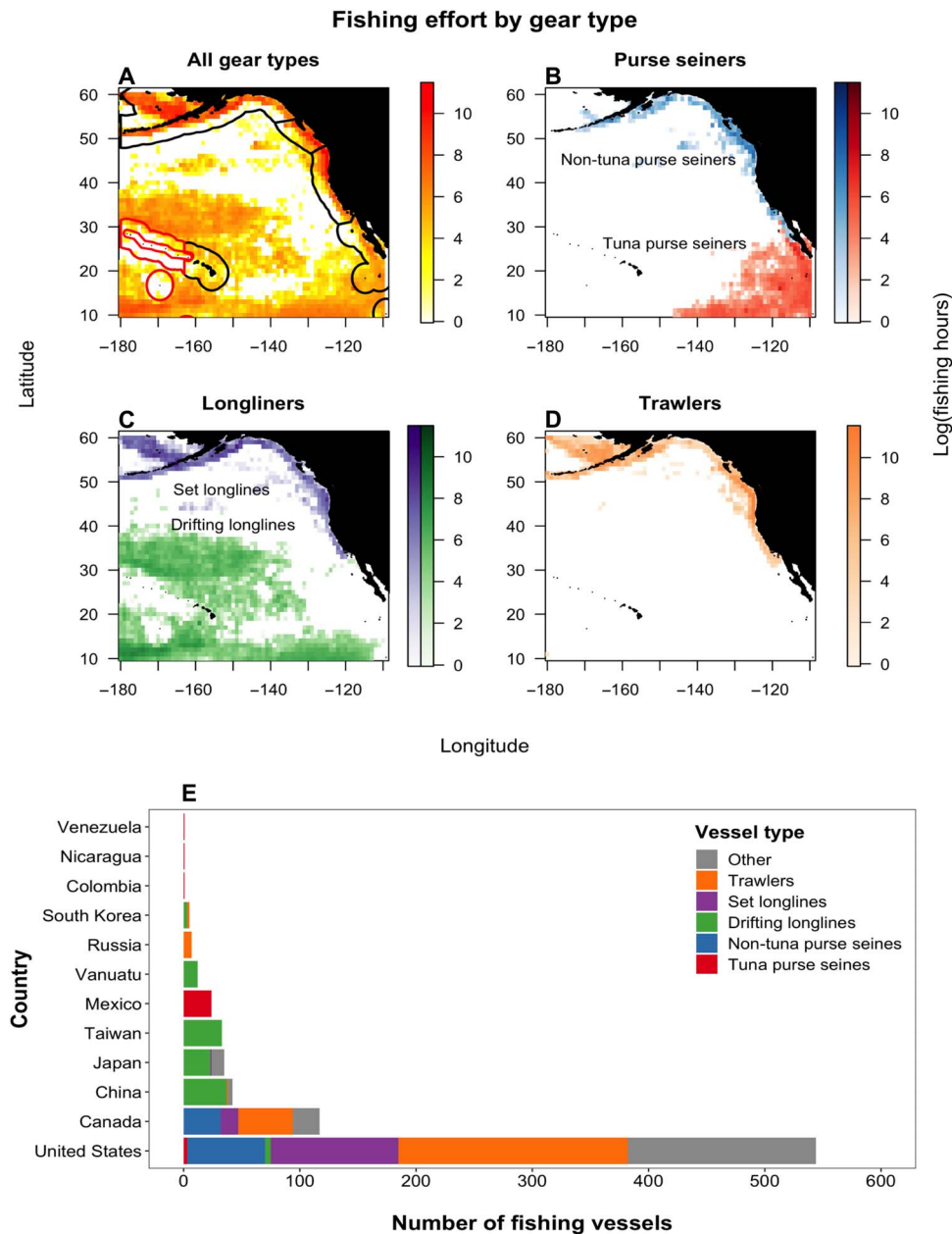
2015 to 31 December 2017. These vessels produced 1.7 million total hours of fishing effort across diverse gear types including drifting longlines, bottom-set longlines, tuna purse seines, non-tuna purse seines, trawlers, trollers, pot/trap vessels, and squid jiggers (Fig. 1 and fig. S1). The gear type used by 111 fishing vessels (12%) could not be identified due to their absence from international vessel registries and vessel information websites (table S2). These vessels accounted for <3% of total fishing hours in the region (44,529 hours; fig. S1) and thus were omitted from the overlap analyses. The United States accounted for 63% of fishing vessels and 68% of fishing effort detected via AIS, largely due to activity within the U.S. exclusive economic zone (EEZ; Table 1). The high seas were primarily fished by vessels flagged to Taiwan (29% of fishing hours), China (24%), Japan (19%), Vanuatu (12%), Mexico (7%), and the United States (7%) (Table 1). The three North American EEZs within our study region (Canada, United States, and Mexico) were almost exclusively fished by vessels flagged to that same EEZ (91 to 99% of total fishing hours within each EEZ).

We identified substantial hotspots of fishing effort that could affect pelagic fishes along the North American continental shelf, the subtropical gyre, and the equatorial Pacific (Fig. 1). In contrast, the temperate waters of the northeast Pacific were largely devoid of pelagic fishing effort in 2015–2017. We detected minimal pelagic fishing effort in large marine protected areas (MPAs) within our study region, including the Papahānaumokuākea Marine National Monument and Johnston Atoll of the Pacific Remote Islands Marine National Monument (Fig. 1). In contrast, we detected some of the northeast Pacific's most intense hotspots of longline fishing effort in the regions outside the boundaries of these protected areas. These regional patterns were present across all 3 years of vessel tracking analyses (figs. S2 to S4). In addition, the annual total of fishing effort varied only slightly (3.6 to 9.6% annual change) across 2015 (572,939 fishing hours), 2016 (593,499 hours), and 2017 (538,128 hours).

### Fishing effort and core habitat overlap

By combining species-specific habitat modeling with AIS-detected fishing effort, we identified regions of overlap in the northeast Pacific between predicted core habitats (top 25% of habitat predictions) and fishing effort (Figs. 2 to 4). The core habitats of all seven shark and tuna species overlapped with industrial fisheries, with the percent of core habitats fished ranging from 4 to 35% across species (Fig. 2C). Although all seven species used both coastal and offshore habitats, there was considerable variation across species as to where fisheries overlap occurred. For example, 94% of salmon shark overlap occurred within EEZs of the United States and Canada, and 74% of yellowfin tuna overlap occurred in Mexico's EEZ. In contrast, 87% of blue shark overlap occurred in international waters, while Pacific bluefin tuna and albacore tuna overlap (50 and 46% in high seas, respectively) were more evenly distributed across international and domestic waters. Regional hotspots of overlap were generally consistent across years, although the relative intensity displayed interannual variability (figs. S6 to S8).

Vessels flagged to seven nations were detected overlapping with the core habitats of pelagic fishes (Fig. 2D). These nations span North America, Central America, Asia, and Oceania, while globally active European fleets (e.g., Spain) were not detected in this study region. The vast majority of high seas overlap in this region (94%) was driven by just five nations: Mexico (30.4%), Taiwan (22.7%), China (14.4%), Japan (13.3%), and the United States (13.3%). The core habitats of individual species in the high seas overlapped with an average of six different national fleets (Fig. 2D).



**Fig. 1. Fishing effort by fishing gear type.** Fishing activity detected by AIS for (A) all vessels, (B) purse seiners, (C) longliners, and (D) trawlers. (E) Registered nationality and primary fishing gear type for fishing vessels active in the northeast Pacific Ocean in 2015–2017. Color scales represent unique gear types in (A) to (D) and unique nations in (E). Vessels from 12 nations were detected in our study region (10°N to 60°N, 110°W to 180°W). Purse seiners and longliners are subdivided into two classes (tuna and non-tuna) based on permits from RFMOs. In (A), black lines denote EEZs and red lines show two large MPAs: Papahānaumokuākea Marine National Monument (north; boundaries expanded from the inner line to the outer line in 2016) and Johnston Atoll of the Pacific Remote Islands Marine National Monument (south). In (E), “Other” vessel types include trollers, squid jiggers, pole-and-line, and pot or trap vessels.

## DISCUSSION

Interactions between industrial fishing fleets and highly migratory species are directly relevant to international agreements pertaining to the management of the high seas and EEZs. We demonstrate how combining predictive habitat models for pelagic fishes with novel datasets on fishing vessel activity can better resolve these key interactions. Our results highlight regions and national fishing fleets that drive overlap between fishing activity and the core habitats of pelagic sharks and tunas (4 to 35% overlap across seven species). Six of our seven study species

are listed as Near Threatened or Vulnerable on the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species, although salmon sharks are classified as a species of Least Concern and albacore and blue shark populations are above target population thresholds in the north Pacific Ocean (32). Strategically reducing overlap between threatened species’ most crucial habitats and industrial fishing effort may be an important step toward their global population recoveries. However, “overlap” carries different significance for sustainably caught species; overlap for a sustainably fished population may

**Table 1. Industrial fishing activity in the northeast Pacific Ocean by nation and jurisdiction in 2015–2017.** Values are in units of fishing hours. The values listed in parentheses are the percentage of fishing hours in each jurisdictional column that are attributed to vessels flagged to a given nation.

Nation	Total hours	High seas	Mexico EEZ	U.S. EEZ	Canada EEZ	Clipperton EEZ
United States	1,181,281 (68%)	23,489 (7%)	1,046 (4%)	1,154,246 (98%)	2,500 (1%)	0
Canada	206,058 (12%)	3,504 (1%)	1,294 (5%)	12,729 (1%)	188,530 (99%)	0
Taiwan	98,680 (6%)	98,378 (29)	0	303 (<1%)	0	0
China	81,004 (5%)	81,004 (24%)	0	0	0	0
Japan	71,824 (4%)	66,256 (19%)	0	5,568 (<1%)	0	0
Mexico	49,753 (3%)	24,952 (7%)	23,831 (91%)	0	0	970 (100%)
Vanuatu	41,560 (2%)	41,536 (12%)	0	24 (<1%)	0	0
South Korea	3,906 (<1%)	3,906 (1%)	0	0	0	0
Nicaragua	108 (<1%)	108 (<1%)	0	0	0	0
Venezuela	106 (<1%)	106 (<1%)	0	0	0	0
Colombia	62 (<1%)	62 (<1%)	0	0	0	0
Russia	26 (<1%)	21 (<1%)	0	5 (<1%)	0	0
Sum	1,734,369	343,323	26,172	1,172,875	191,030	970

indicate efficient fishing activity, while overlap for a threatened population may indicate a conservation concern.

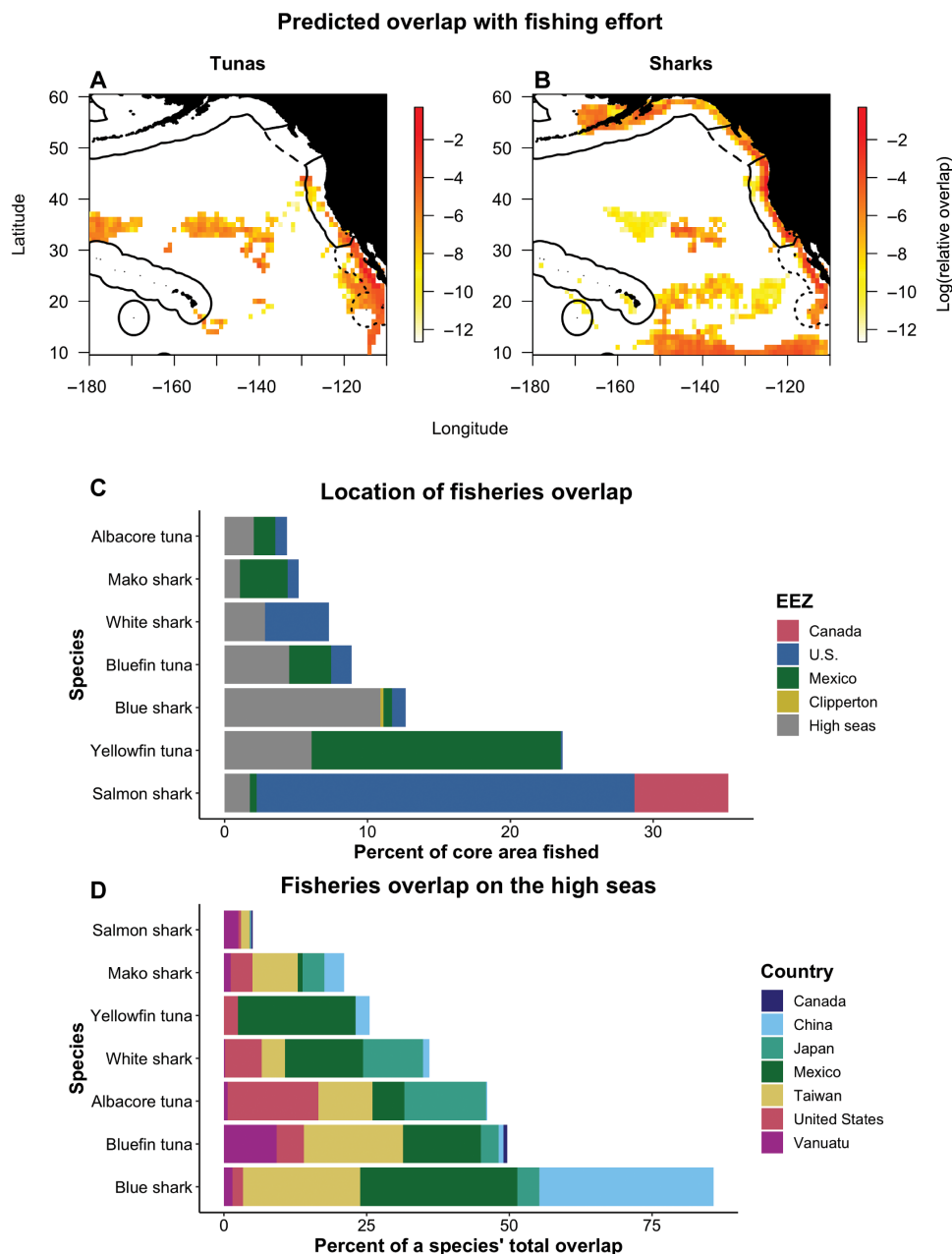
The seven study species vary greatly in their location of overlap with industrial fisheries, indicating which jurisdiction (national or international) may be most appropriate for a species' management. For example, although salmon sharks regularly undertake migrations to the high seas, 94% of their predicted overlap with commercial fisheries occurs in coastal waters of the United States and Canada, suggesting that these two nations can implement meaningful conservation measures for this species without commitments from other nations. In contrast to patterns of domestic fisheries overlap, 87% of blue shark overlap and 46% of albacore tuna overlap occur in international waters. These results suggest that high seas conservation measures are crucially important if domestic efforts to manage these pelagic fishes are to be successful.

Pacific bluefin tuna and the eastern Pacific population of yellowfin tuna are overfished (11), and high seas quotas do not exist for any pelagic sharks despite the efficacy of quotas for increasing biomass of pelagic fishes (11, 19). International catch restrictions for pelagic sharks remain globally scarce, although the Inter-American Tropical Tuna Commission (IATTC), the international body that manages pelagic populations in the eastern Pacific Ocean, recently adopted promising measures that aim to reduce catch of silky sharks (19, 33). The degree of international overlap presented here further suggests that a legally binding high seas treaty could include language to improve management of these species. Large MPAs in national and international waters have been proposed as an additional tool for managing overfished populations of pelagic fishes, although their effectiveness for highly migratory species is debated (13, 34). We observe minimal fishing effort in two large MPAs in our study region (the Papahānaumokuākea and Pacific Remote Islands Marine National Monuments within the U.S. EEZ), while we detect high rates of fishing effort in the regions beyond their boundaries, suggesting that well-enforced MPAs may help reduce overlap between pelagic fishes and fisheries. Further studies are necessary to better

resolve the population-level impacts of large MPAs on mobile species, including potential edge effects related to those management zones.

Our results suggest that observing and potentially modifying the fishing activities of a limited number of nations can bring substantial improvements to the sustainability of fishing on the high seas. Although dozens of nations fish the high seas (25, 35), just five nations from North America (Mexico and United States) and East Asia (China, Taiwan, and Japan) account for 94% of predicted overlap with core habitats of pelagic fishes in the high seas of the northeast Pacific Ocean. In the absence of a legally binding high seas treaty, the economic benefits of fishing on the high seas (36) and the resulting impacts on pelagic fishes will likely continue to be disproportionately driven by a relatively small number of nations with the capacity and interests to fish these global commons. Identifying nations that contribute to patterns of overlap with pelagic fishes may reveal which national interests must be considered if international protected areas or other management strategies are to be cooperatively established in the high seas. In addition, given persistent underreporting of catch in self-reported datasets (17), AIS-derived patterns of overlap may be useful in detecting potential instances of national underreporting. For example, while China is estimated to underreport catch data to some RFMOs, particularly for sharks (18, 20), we find that Chinese fisheries account for the highest national overlap (36%) with core habitats of blue sharks in the high seas.

We emphasize, however, that the overlap patterns we present pertain specifically to our study populations that were tracked extensively throughout the northeast Pacific Ocean (3). Populations in other oceanic regions may display different overlap patterns, and important hotspots of catch or bycatch overlap may fall outside the geographic scope of this study if our tagged populations did not occupy those areas (e.g., potential bycatch of white sharks in coastal Mexico) (37). Our analyses demonstrate how dynamic tools like predictive habitat modeling and high-resolution vessel tracking may be used to identify overlap patterns in these places where predictions are not currently available (38). The

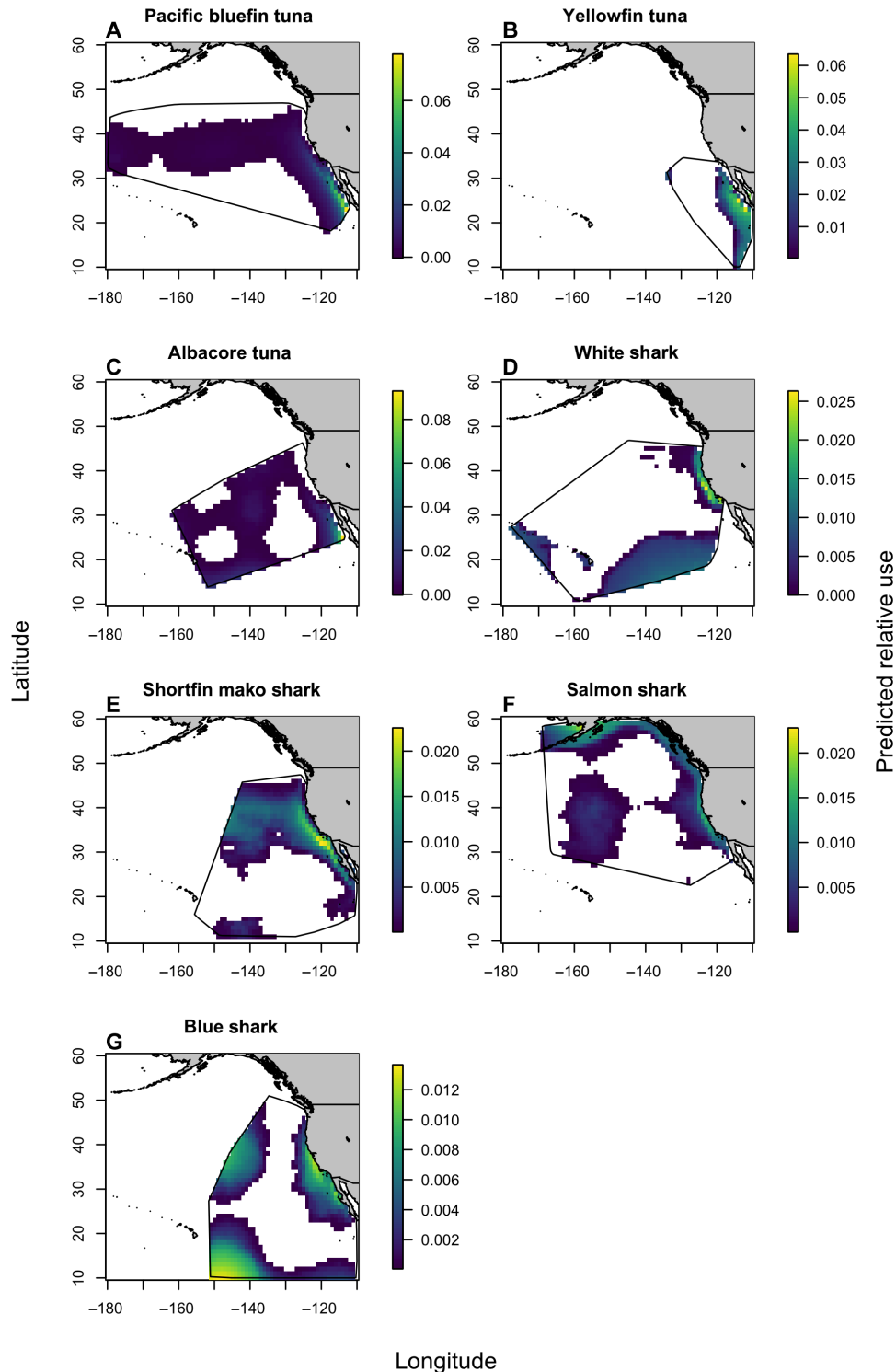


**Fig. 2. Location, jurisdiction, and vessel nationality of fish/ fisheries overlap.** The predicted overlap between industrial fishing effort and core habitats for seven species of (A) tunas (Pacific bluefin, yellowfin, and albacore tunas) and (B) pelagic sharks (white, shortfin mako, salmon, and blue shark). The scale in (A) and (B) indicates the log-transformed relative overlap values, which sum to 1 for each species and are summed across species in these multispecies plots. Solid lines on the maps denote the U.S. EEZ, and dashed lines indicate the EEZs of Canada and Mexico. (C) Jurisdiction of fisheries overlap (within an EEZ or on the high seas). (D) National contributions to high seas overlap: Bar length is equivalent to the percent of each species' total fisheries overlap that occurs in the high seas [i.e., gray bar in (C)].

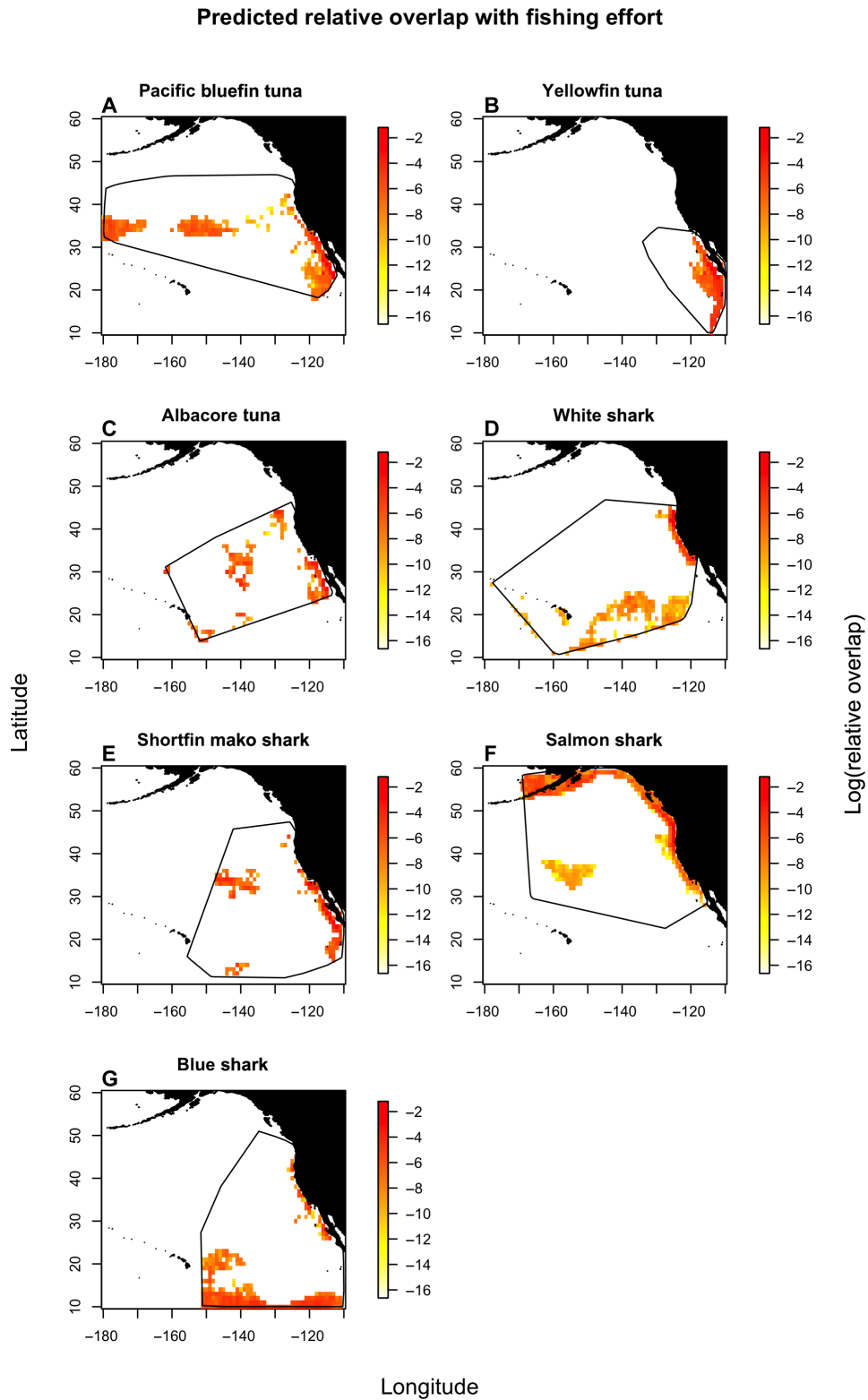
potential spatial bias caused by the initial tagging location was reduced in the synthesis analyses of tracks of Block *et al.* (3) by implementing a weighting scheme that assigned a higher weight to tracks of longer duration and to location estimates that occur later in a given track (3). Despite the application of this weighting scheme, our results may still be influenced by the coastal location of most tag deployments (3), so our assessment of fisheries overlap on the high seas may be minimum estimates of potential overlap. We also note that mapping overlap is crucial

for understanding which regions may warrant finite conservation attention (e.g., present efforts to manage salmon sharks should prioritize Alaskan waters over international waters, and white sharks may require more attention in international waters where hotspots of overlap are located), although our findings are best interpreted at a regional scale as opposed to the scale of individual pixels. As is often the case with broad-scale studies, predictions for individual cells may differ from more localized and geographically limited data collection. We further

Predicted core habitats, 2015–2017



**Fig. 3. Core habitat predictions for seven species of pelagic sharks and tunas.** (A to G) Core habitats are defined as the top 25% of predicted habitat use values (30, 31). Black lines denote minimum convex polygons (MCPs) constructed around position data available from Block *et al.* (3) for an individual species; to avoid spatial extrapolation, habitat model predictions pertain only to these regions. The color scale indicates the predicted relative use of cells (i.e., probability that a cell contains core habitat relative to other cells) from 1 January 2015 to 31 December 2017.



**Fig. 4. Predicted fisheries overlap with the core habitats of seven shark and tuna species.** (A to G) Black lines denote MCPs formed around all location data available from Block *et al.* (3) for an individual species; to avoid spatial extrapolation, habitat model and fishing overlap predictions pertain only to these regions. The color scale indicates the relative intensity of predicted overlap.

acknowledge that a species' overlap with industrial fisheries is not necessarily equivalent to its catch rate or mortality, as different gear types may affect species to different extents. Reliable information on relative catchability, mortality, and post-release survival is unavailable for most species–gear type combinations (39), although future studies may better elucidate population-level impacts of overlap once this information is available.

Cross-evaluating maps of fishing effort derived from AIS alongside datasets released by management organizations (e.g., fisheries observer datasets, self-reported catch and effort datasets) may provide the clearest view of industrial fisheries, as both classes of datasets have strengths and limitations. While we focused on developing AIS analyses to identify regional patterns of overlap between fishes and fisheries, future efforts may build on this work by uniting insights from both vessel tracking and management organization datasets. For example, modeling the relationship between RFMO datasets and vessel tracking datasets may be used to generate predictions for time periods or regions for which only one dataset is available. Similarly, comparing overlap indices with reliable catch and effort data may improve estimates and predictions of catch rates for underreported species.

Both human and marine predators respond to a dynamic set of biotic and abiotic drivers (22). The recent expansion of vessel tracking data, combined with the increasing sophistication of species distribution and habitat models derived from biologging datasets, can facilitate dynamic approaches to fisheries management, such as high seas closures that directly account for variable ocean conditions and predicted hotspots of overlap. Our approach uses habitat models that consider the relationship between animal movements and the biophysical drivers of those movements (30, 40). Similar efforts to better understand the processes governing human behavior, including both biophysical and bioeconomic drivers, will further improve future predictions of overlap between fishes and fisheries. As climate change is predicted to redistribute species richness in the north Pacific Ocean (41), data-rich tools such as AIS analysis, telemetry, and dynamic habitat models may play a vital role in managing a changing ocean.

## MATERIALS AND METHODS

### Tracking fishing vessels

Vessels were remotely tracked using satellite and terrestrial detections of AIS vessel transmissions (23–25) provided by Global Fishing Watch. We accessed the raw detections used to analyze global fishing effort by Kroodsma *et al.* (25). Likely fishing events were identified using the convolutional neural network published by Kroodsma *et al.* (25) (code available at <https://github.com/GlobalFishingWatch/vessel-classification>). This algorithm identifies fishing events with >90% accuracy by comparing a vessel track's characteristics (e.g., speed, course, and distance to shore) to a training database of labeled fishing events from 503 vessels (25). The training dataset of labeled AIS tracks was originally produced through interviews with fishermen, former fisheries observers, and a literature review (25). Each AIS position is classified as fishing or not fishing based on this convolutional neural network. We analyzed the tracks of all identified fishing vessels that entered our study region (10°N to 60°N, 110°W to 180°W) from 1 January 2015 to 31 December 2017. We summed fishing hours, defined as hours of all positions identified as fishing (25), within 1° by 1° grid cells as this resolution is appropriate for longlines, which can span up to 100 km in length (nearly 1°) (21) and are the largest gear type considered. We note that overlap metrics would decrease at higher resolutions of input

data (42, 43). Our chosen resolution also matches our habitat models, which were limited by the accuracy of location estimates from light-based geolocation tags (3, 21).

A second convolutional neural network was developed in (25) to estimate the fishing gear classes of global fishing fleets. Those fishing gear classifications (including purse seiners, trawlers, drifting longliners, squid jiggers, and fixed gear) contain both vessels that catch pelagic fishes and those that do not (e.g., tuna-targeting purse seiners were not distinguishable from those targeting forage fish, vessels using set longlines were not separated from those setting crab pots, and maps of trollers were not available). As risks associated with different gear types vary in terms of potential catch and bycatch of pelagic sharks and tunas, we disaggregated these broader gear classifications and mapped fishing effort to the fishing gear type resolution needed to isolate effort relevant to our study species (table S1). Vessel gear types were primarily determined by matching identifying vessel information from AIS transmissions to official vessel registries (83% of identified vessels; table S2). For vessels that did not have gear type listed on a registry, we identified gear type using photographs from marine vessel websites (14% of identified vessels; table S2), and expert knowledge of fishery seasons was used to identify an additional 3% of vessels (i.e., coastal vessels fishing exclusively during crab season in the same region as other known crab vessels were labeled “pots and traps” vessels). We excluded vessels that could not be identified to gear type (12% of all vessels).

### Predicted core habitats

We assessed overlap between AIS-observed fishing effort and the predicted core habitats of seven shark and tuna species electronically tagged in the TOPP program (3). These species were Pacific bluefin tuna (*Thunnus orientalis*), yellowfin tuna (*Thunnus albacares*), albacore tuna (*Thunnus alalunga*), white shark (*Carcharodon carcharias*), shortfin mako shark (*Isurus oxyrinchus*), salmon shark (*Lamna ditropis*), and blue shark (*Prionace glauca*). All species, except for the salmon shark, are currently listed as Threatened or Near Threatened on the IUCN's Red List of Threatened Species, although the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC) has determined that albacore and blue shark populations are above target population thresholds in the north Pacific region (32). The animal movement dataset used for this study spans from October 2000 to September 2009 and consists of 876 tag events from which tracks were previously derived and modeled (table S3). Tracking data were produced from a combination of deployments that included Lotek 2310 and Wildlife Computer mk9 archival tags, Wildlife Computer pop-up satellite archival tags, and SPOT Argos satellite tags. Daily position estimates of tagged animals were obtained from a Bayesian state-space model that accounts for uncertainty and gaps in position estimates (3).

From this prior biologging dataset (3), we predicted core habitats for 2015–2017 at a monthly 1° resolution throughout the northeast Pacific Ocean through temporal extrapolation of habitat suitability predictions generated using generalized additive models (GAMs) by Hazen *et al.* (30). Because we used habitat models developed by Hazen *et al.* (30), we matched their study region boundaries (10°N to 60°N, 110°W to 180°W) for our analyses. These boundaries were originally selected to ensure adequate spatial and temporal coverage of the TOPP tagging dataset within the study region (30). The habitat models used a wide range of ocean conditions across years of species–environment relationships to align the time range of core habitats and fishing activity; the habitat models predict core habitats for the exact year of our fisheries



dataset (2015–2017) (3, 30). These single-species GAMs were fit using the tracking dataset generated from 876 satellite tags (table S3) and are used to predict animal space use as a function of sea surface temperature (SST), chlorophyll a (Chl-a), depth, latitude, and longitude at monthly temporal resolution. We downloaded monthly SST and Chl-a data from the National Oceanic and Atmospheric Administration (NOAA) Environmental Research Division's Data Access Program (ERDDAP) server [0.01° Multiscale Ultrahigh Resolution (MUR) and 0.025° Moderate Resolution Imaging Spectroradiometer (MODIS) datasets, respectively] and regrided the data at a common 1° resolution using bilinear interpolation functions from the “raster” and “ncdf4” packages in R statistical software version 3.3.1. A spatial resolution of 1° was used to account for positional uncertainty in location estimates from electronic tagging data (3, 21). To avoid unrealistic spatial extrapolations beyond species' observed movements (44, 45), we only generated model predictions within minimum convex polygons (MCPs) created from all electronic tagging data available for individual species (table S3). The deviance explained by these models ranges from 18.3 to 44.1% (30). Core habitats were identified by selecting the top quartile of distribution values, as predicted by habitat models, for a given species and month to ensure that infrequently used habitats would not bias results (30, 31). This previously identified threshold is chosen to represent the most critical habitat while excluding transitory habitat and to provide a more conservative overlap metric.

### Overlap with fishing effort

To investigate how the distributions of pelagic predators interact with spatiotemporal dynamics of industrial fishing fleets, we calculated the monthly relative overlap between fishing effort and species' core habitats in 2015–2017. For each grid cell, we summed the fishing hours of all vessels with primary gear types that capture a particular study species within a given year (table S1). To facilitate comparisons among months and different species, we then converted fishing hour sums and a given species' predicted distributions into probabilities that are relative to all other grid cells in all other months within that year for that species (28, 46). To calculate the probability that vessels and animals overlap in space and time (relative to their likelihood of overlapping in all other cells and months within that year), we applied the following equations modified from (28, 46), where  $i$  is an individual grid cell,  $n$  is the total number of all cells, and  $t$  is 1 month

$$P_{\text{rel}}(\text{species})_{it} = \frac{\text{density}_{it}}{\sum_{i=1}^n \sum_{t=1}^{12} \text{density}_{it}} \quad (1)$$

$$P_{\text{rel}}(\text{fishing})_{it} = \frac{\text{effort}_{it}}{\sum_{i=1}^n \sum_{t=1}^{12} \text{effort}_{it}} \quad (2)$$

$$P_{\text{rel}}(\text{overlap})_{it} = \frac{P_{\text{rel}}(\text{species})_{it} \times P_{\text{rel}}(\text{fishing})_{it}}{\sum_{i=1}^n \sum_{t=1}^{12} (P_{\text{rel}}(\text{species})_{it} \times P_{\text{rel}}(\text{fishing})_{it})} \quad (3)$$

We then averaged these standardized results across years to calculate species' mean predicted overlap throughout the study period.

We allocated core area/vessel overlap to an EEZ within our study region or to the high seas. To assess how overlap was distributed across waters of national jurisdictions and the high seas, we calculated the re-

lative proportions of overlap grid cells that fell either within a national EEZ or in the high seas. In addition, as AIS transmissions include a vessel's reported flag state and the majority of vessels were matched to registries with known flag states, we gridded high seas fishing effort by nation and calculated the relative proportions of overlapped cells attributed to national fishing fleets.

### SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/5/3/eaau3761/DC1>

Fig. S1. Fishing activity detected by AIS in 2015–2017 for additional gear types.

Fig. S2. Fishing activity detected by AIS in 2015.

Fig. S3. Fishing activity detected by AIS in 2016.

Fig. S4. Fishing activity detected by AIS in 2017.

Fig. S5. Tagging data for seven species of pelagic sharks and tunas.

Fig. S6. Predicted fisheries overlap with the core habitats of seven shark and tuna species, 2015.

Fig. S7. Predicted fisheries overlap with the core habitats of seven shark and tuna species, 2016.

Fig. S8. Predicted fisheries overlap with the core habitats of seven shark and tuna species, 2017.

Table S1. The gear types included in overlap analyses for each species and supporting references.

Table S2. Official vessel registries and online vessel photo repositories used to identify the primary fishing gear type used by vessels.

Table S3. The tagging datasets that supported the habitat models and MCPs for this study, modified from Block *et al.* (3).

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## Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the northeast Pacific

Timothy D. White, Francesco Ferretti, David A. Kroodsma, Elliott L. Hazen, Aaron B. Carlisle, Kylie L. Scales, Steven J. Bograd and Barbara A. Block

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