

Shark mortality cannot be assessed by fishery overlap alone

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Many shark species worldwide are vulnerable to overexploitation due to fishing. Using only the horizontal spatial overlap between the space use of 23 satellite-tracked shark species and the fishing distribution of pelagic longline fisheries tracked using an automatic identification system, Queiroz et al.¹ concluded that sharks are at high risk when substantial horizontal overlap occurs. This approach to estimate fishing

susceptibility, coupled with limited tag-based shark distributions to estimate fishing exposure index (FEI) hotspots, severely limits their findings and, therefore, conclusions.

We challenge several assumptions made by the authors and argue that horizontal overlap alone is an unreliable indicator of susceptibility because other factors contribute considerably to catch risk, as shown

Table 1 | Linear regressions between North Atlantic annual shark landings and shark FEI

Change from original	Data	Annual average	Landings	Species	P value	F	d.f.	Adjusted R ²
Queiroz et al. ¹	2007–2016	Positive values only	log scale	Eight species, hammerhead sharks included <i>S. zygaena</i> , <i>S. mokarran</i> , <i>S. lewini</i>	0.0374 ^a	7.089	6	0.46
Landings averaged over the whole period	2007–2016	All time series	log scale	Same species as in Queiroz et al. ¹	0.0519	5.854	6	0.41
Landings computed for 2012–2016	2012–2016	Positive values only	log scale	Same as Queiroz et al. ¹	0.1883	2.318	5	0.18
Landings computed for 2012–2016 and averaged over the whole period	2012–2016	All time series	log scale	Same as Queiroz et al. ¹	0.2059	2.112	5	0.1563
Including not-identified hammerhead landings as hammerhead sharks	2007–2016	Positive values only	log scale	Including hammerhead sharks not identified as hammerhead sharks	0.1139	3.42	6	0.2569
Including not-identified hammerhead landings as hammerhead sharks and averaged over the whole period	2007–2016	All time series	log scale	Including hammerhead NEI as hammerhead sharks	0.1288	3.1	6	0.2308
Including not-identified hammerhead landings as hammerhead sharks and landings computed for 2012–2016	2012–2016	Positive values only	log scale	Including hammerhead NEI as hammerhead sharks	0.3605	1.013	5	0.0021
Including not-identified hammerhead landings as hammerhead sharks and landings computed for 2012–2016 averaged over the whole period	2012–2016	All time series	log scale	Including hammerhead NEI as hammerhead sharks	0.3782	0.9341	5	-0.0011
Absolute landings instead of in log scale	2007–2016	Positive values only	Absolute	Same as Queiroz et al. ¹	0.1676	2.463	6	0.1729
Absolute landings instead of in log scale and including not-identified hammerhead landings as hammerhead sharks	2007–2016	Positive values only	Absolute	Including hammerhead nei as hammerhead sharks	0.1812	2.287	6	0.1553

Landings from FAO total capture production ([http://www.fao.org/fishery/statistics/global-capture-production/query\(es\)](http://www.fao.org/fishery/statistics/global-capture-production/query(es))) and shark FEI were calculated as described in Queiroz et al.¹. 'Change from original' describes the changes from the original relationship in Queiroz et al.¹: (i) using all years to average the annual landings instead of only using the positive values as in Queiroz et al.¹, to account for zero catches; (ii) using data from 2012–2016 for which fishing effort data from the automatic identification system were available for estimating the average annual landings; and (iii) including *Sphyrna* spp. and/or hammerhead NEI in the hammerhead group because they may comprise *S. zygaena*, *S. mokarran* or *S. lewini*. NEI, not otherwise identified.

^aP value was statistically significant at the 5% level of significance.

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Table 2 | Contingency tables between FEI hotspots, fishing effort hotspots and shark-density hotspots for EEZ, ABNJ and globally

FEI hotspots	Fishing effort hotspots (EEZ data)			Fishing effort hotspots (ABNJ data)			Fishing effort hotspots (global scale)		
	Positive	Negative	Total	Positive	Negative	Total	Positive	Negative	Total
Positive	147	225	372	234	229	463	381	454	835
Negative	1,439	7,246	8,685	2,364	10,476	12,840	3,803	17,722	21,525
Total	1,586	7,471	9,057	2,598	10,705	13,303	4,184	18,176	22,360
Sensitivity or true-positive rate (95% CI)	9% (8–11%)			9% (8–10%)			9% (8–10%)		
Positive predictive value or precision (95% CI)	40% (35–45%)			51% (46–55%)			46% (42–49%)		
Statistical test	$\chi^2 = 128.46$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 291.49$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 411.32$, d.f. = 1, $P < 2.2 \times 10^{-16}$		
Shark-density hotspots	Fishing effort hotspots (EEZ data)			Fishing effort hotspots (ABNJ data)			Fishing effort hotspots (global scale)		
	Positive	Negative	Total	Positive	Negative	Total	Positive	Negative	Total
Positive	78	1,132	1,210	94	1,010	1,104	172	2,142	2,314
Negative	1,508	6,339	7,847	2,504	9,695	12,199	4,012	16,034	20,046
Total	1,586	7,471	9,057	2,598	10,705	13,303	4,184	18,176	22,360
Sensitivity or true-positive rate (95% CI)	5% (4–6%)			4% (3–4%)			4% (4–5%)		
Positive predictive value or precision (95% CI)	6% (5–8%)			9% (7–10%)			7% (6–9%)		
Statistical test	$\chi^2 = 117.49$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 92.183$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 215.05$, d.f. = 1, $P < 2.2 \times 10^{-16}$		
FEI hotspots	Shark-density hotspots (EEZ data)			Shark-density hotspots (ABNJ data)			Shark-density hotspots (global scale)		
	Positive	Negative	Total	Positive	Negative	Total	Positive	Negative	Total
Positive	238	134	372	211	252	463	449	386	835
Negative	972	7,713	8,685	893	11,947	12,840	1,865	19,660	21,525
Total	1,210	7,847	9,057	1,104	12,199	13,303	2,314	20,046	22,360
Sensitivity or true-positive rate (95% CI)	20% (17–22%)			19% (17–22%)			19% (18–21%)		
Positive predictive value or precision (95% CI)	64% (59–69%)			46% (41–50%)			54% (50–57%)		
Statistical test	$\chi^2 = 128.46$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 870.66$, d.f. = 1, $P < 2.2 \times 10^{-16}$			$\chi^2 = 1758$, d.f. = 1, $P < 2.2 \times 10^{-16}$		

Hotspots are defined by cells with ≥ 75 th percentile of FEI, shark relative density or fishing effort as described in Queiroz et al.¹. Data were obtained from (<https://github.com/GlobalSharkMovement/GlobalSpatialRisk>). Top, FEI hotspots match with fishing effort hotspots in only 40%, 51% and 46% of cases in EEZs, ABNJs and at the global scale, respectively; whereas the true-positive rate for which FEI correctly identifies a fishing effort hotspot is 9% in all cases. Middle, shark relative density hotspots match with fishing effort hotspots in only 6%, 9% and 7% of the cases in EEZs, ABNJs and at the global scale, respectively, whereas the true-positive rate is about 5%. Bottom, FEI hotspots match shark relative density hotspots in 64%, 46% and 54% of cases in EEZs, ABNJs and at the global scale, respectively; whereas the true-positive rate is around 20%. 95% CI, 95% confidence interval.

by well-established ecological risk assessment methods^{2,3}. Moreover, we consider that the locations of FEI hotspots are biased towards areas for which tagging data are available. These limitations may misdirect urgent management actions that are needed to mitigate—globally and holistically—true fishing risks for sharks in all ocean regions. Our criticisms comprise the four main points below.

First, horizontal overlap does not provide a robust risk estimate. The two-dimensional horizontal overlap between the distribution of a species and fishing effort (that is, ‘availability’) is only one component of susceptibility explaining risk⁴, which also includes encounterability, selectivity and post-capture mortality. Encounterability is the potential for a species to interact with fishing gear within its depth range. Selectivity is the propensity for an organism to be caught once it encounters the fishing gear⁴. For example, even with 100% horizontal overlap between the distribution of a mesopelagic shark and a surface pole-and-line fishery, encounterability and selectivity are negligible, and thus the species would have low catchability and risk. The species assessed by Queiroz et al.¹ occupy different depth ranges and undergo diel vertical migrations^{5,6} that result in different encounterability⁷; however, this was not considered. Furthermore, shark species have different life-history traits, behaviours and mouth morphologies that differentially affect their selectivity to baited longline hooks^{8,9}, which should also be included in risk assessments.

Current handling and release practices can reduce at-vessel and post-release mortality¹⁰. For example, at-vessel and post-release survival of pelagic sharks—including the great hammerhead and tiger shark species analysed by Queiroz et al.¹—ranges from 33% to 100%^{6,11}; information that was also omitted from the risk estimation of Queiroz et al.¹.

Widely used ecological risk assessments^{2,3} include all susceptibility (and productivity) components³ to estimate risk. Therefore, risk may not necessarily be high with high horizontal overlap if encounterability, selectivity and/or post-capture mortality is low (for example, for tiger sharks^{7,9}).

Second, the fishing exposure index (FEI) developed by Queiroz et al.¹—relative shark density multiplied by fishing effort—is not a robust proxy for fishing-induced shark mortality as it is fundamentally another measure of geospatial overlap. The authors claim that FEI “reflects fishing-induced shark mortality” based on a linear relationship between FAO landings data for the North Atlantic and FEI values for eight shark species (extended data figure 5 of Queiroz et al.¹). We accessed the FAO statistics, following the authors’ description of the data used, to calculate the relationship between shark landings and FEI. We tested different options of (1) landing periods; (2) all versus positive years; and (3) including non-identified hammerhead landings as hammerhead landings, and found no significant relationships ($P > 0.1$) in all combinations, except the single case cited by Queiroz et al.¹ (Table 1). Moreover, the relationship between FEI and catch including all species does not reflect fishing mortality, unless the abundance of each species is the same (catch = fishing mortality \times abundance), which is not the case. For example, if abundance is low—as for white sharks—even low catches could reflect high fishing mortality and, vice versa, high catches could indicate higher shark abundance but not necessarily higher fishing mortality. Thus, FEI is not a reliable proxy for fishing-induced shark mortality. Because the conclusions of Queiroz et al.¹ hinge on FEI representing risk and fishing mortality, their conclusions lack support.

Matters arising

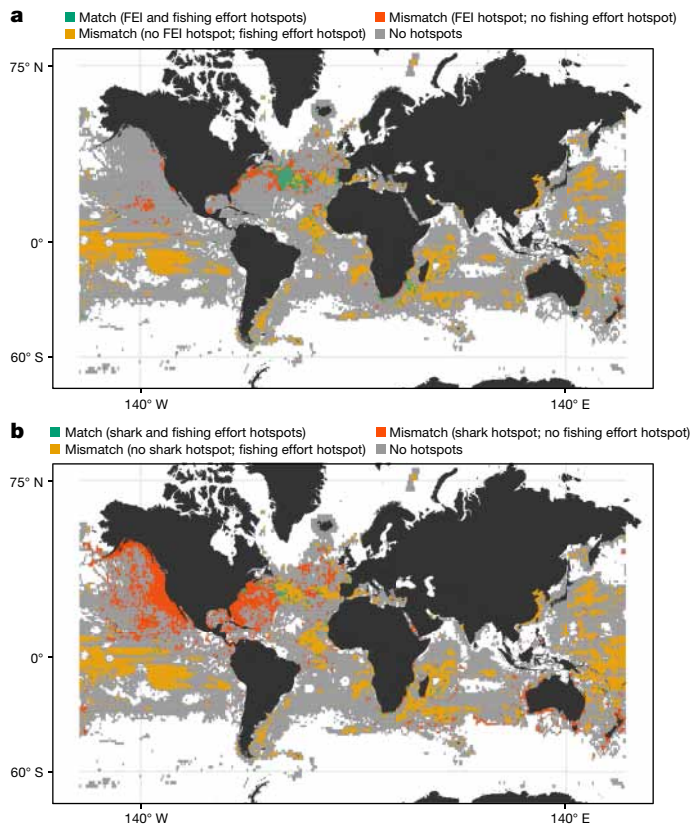


Fig. 1 | Match or mismatch between FEI hotspots or shark density hotspots, and fishing effort hotspots. a, b, Match or mismatch between FEI hotspots and fishing effort hotspots (a) and match or mismatch between shark relative density hotspots and fishing effort hotspots (b). Green points indicate that there is a match between FEI or shark relative density hotspots and fishing effort hotspots grids. Red points indicate mismatched grids of FEI or shark relative density hotspots with no fishing effort hotspots. Orange points indicate mismatched grids of fishing effort hotspots with no FEI or shark relative density hotspots. Grey points indicate grids with no hotspots for both FEI or shark relative density and fishing effort. The figure was created using R software¹⁶.

Third, the use of ‘exposure risk plots’ between spatial overlap and FEI by species using the mean overlap and mean FEI across all species in a region as a reference point to delineate risk is misleading. High risk (red quadrants in figure 3 of Queiroz et al.¹) means that the risk of a species is above average, which may occur when exposure risk is low (for example, blue shark (*Prionace glauca*), eastern Pacific; great white shark (*Carcharodon carcharias*), Oceania). Worryingly, high-risk species can be considered low risk in a region if most sharks show high overlap and FEI.

Moreover, based on FEI hotspots, Queiroz et al.¹ concluded that “high fishing effort is focused on extensive shark hotspots globally”. We disagree as there is a significant mismatch between FEI hotspots and shark density hotspots and fishing effort hotspots (Table 2), revealing that shark hotspots are not related to main fishing effort areas (Fig. 1b). For example, the true-positive rate when FEI hotspots correctly identifies a fishing effort hotspot is 9% (Table 2). Furthermore, using their methodology, FEI hotspots cannot be identified in regions for which no fishing data from the automatic identification system are available (for example, neritic regions within Exclusive Economic Zones (EEZs)) or in areas with no shark tagging information (Fig. 1).

Finally, although the size of grid cells did not affect species risk exposure plots and species occurrence within the high- or low-risk zones, the absolute values of overlap and FEI are greatly affected by grid cell size. Supplementary table 9 of Queiroz et al.¹ shows that the mean overlap

decreased from 21.6% at a resolution of $1^\circ \times 1^\circ$ to 5.03% overlap using a resolution of $0.10^\circ \times 0.10^\circ$, whereas FEI decreased from 3.0×10^{-5} to 3.9×10^{-8} , respectively. The concomitantly large decrease in overlap and FEI may therefore affect FEI hotspots and, thus, compromise the results of Queiroz et al.¹

Queiroz et al.¹ concluded that limited spatial refuges for sharks exist in Areas Beyond National Jurisdictions (ABNJs). Of the total FEIs in their data (<https://github.com/GlobalSharkMovement/GlobalSpatialRisk>), 36% and 64% lie in ABNJs and EEZs, respectively. Furthermore, 56% of ABNJs (7,856 km²) and 67% of EEZs (8,325 km²) have FEI values of zero, thus clearly identifying possible refuge areas (Fig. 1). Although Queiroz et al.¹ underestimate refugia due to limited tagging, their results do not support the conclusion of “limited spatial refuge” in ABNJs.

To conclude, we agree with Queiroz et al.¹ about the need for improved conservation and management measures for sharks as mounting evidence suggests that their populations are being subjected to increasing pressure globally by fishing¹². We also agree that ‘industrial’ pelagic fisheries have an important role in these impacts, but note that regional fishery management organizations for tuna have made some progress by adopting several shark non-retention and mitigation management measures¹³. There is also growing evidence¹⁴ that the fleet size and impact of the often less regulated and monitored artisanal coastal fisheries—which primarily use longlines and gillnets—can be as large as those of industrial fleets that fish the ABNJs¹⁵. The magnitude of total shark catches by these fisheries must be better understood to determine the true global risk for sharks.

The analysis by Queiroz et al.¹ defines risk based only on horizontal overlap, equates FEI to fishing mortality and estimates FEI only on the basis of areas for which shark tagging data are available. It therefore identifies FEI hotspots that are not necessarily the areas in which sharks are at greatest risk from fishing. Therefore, using the hotspots identified by Queiroz et al.¹ to define spatial management measures may not only focus protection in sub-optimal areas, but could also detract from management efforts across 100% of shark distributions to mitigate mortality by reducing fishery encounterability, selectivity and post-capture mortality. Such management approaches, in collaboration with regional fishery management organizations for tuna and small-scale fleets, are essential to achieving meaningful reductions in risks from fishing for sharks.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

To prepare Table 1 and linear regressions between North Atlantic annual shark landings (FAO total capture production) and shark FEI as calculated by Queiroz et al.¹, FAO statistics available from <http://www.fao.org/fishery/statistics/global-capture-production/query/es> were used following the description of the data by Queiroz et al.¹. To produce Table 2 and Fig. 1, data from Queiroz et al.¹ were used from <https://github.com/GlobalSharkMovement/GlobalSpatialRisk>.

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Additional information

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REPLYING TO H. Murua et al. *Nature* <https://doi.org/10.1038/s41586-021-03396-4> (2021)

Our previously published paper¹ provided global fine-scale spatiotemporal estimates ($1^\circ \times 1^\circ$; monthly) of overlap and fishing exposure risk (FEI) between satellite-tracked shark space use and automatic identification system (AIS) longline fishing effort. We did not assess shark mortality directly, but in addition to replying to the Comment by Murua et al.², we confirm—using regression analysis of spatially matched data—that fishing-induced pelagic shark mortality (catch per unit effort (CPUE)) is greater where FEI is higher.

We focused on assessing shark horizontal spatiotemporal overlap and exposure risk with fisheries because spatial overlap is a major driver of fishing capture susceptibility and previous shark ecological risk assessments (ERAs) assumed a homogenous shark density within species-range distributions^{3–5} or used coarse-scale modelled

occurrence data, rather than more ecologically realistic risk estimates in heterogeneous habitats that were selected by sharks over time. Furthermore, our shark spatial exposure risk implicitly accounts for other susceptibility factors with equal or similar probabilities to those commonly used in shark ERAs^{3,5}.

First, actual depth distributions are seldom incorporated in shark ERAs and full vertical overlap with an encounterability probability of one is often applied^{3,5}. This is an implicit assumption in our FEI as the pelagic species that we tracked exhibit vertical movements that overlap with depths of pelagic longlines (for example, 18–267 m)⁶ during both the day and night⁷. Second, we account for selectivity by focusing our fisheries-independent spatial estimates directly on individuals that were actually caught by the focal fisheries.

A list of affiliations appears at the end of the paper.

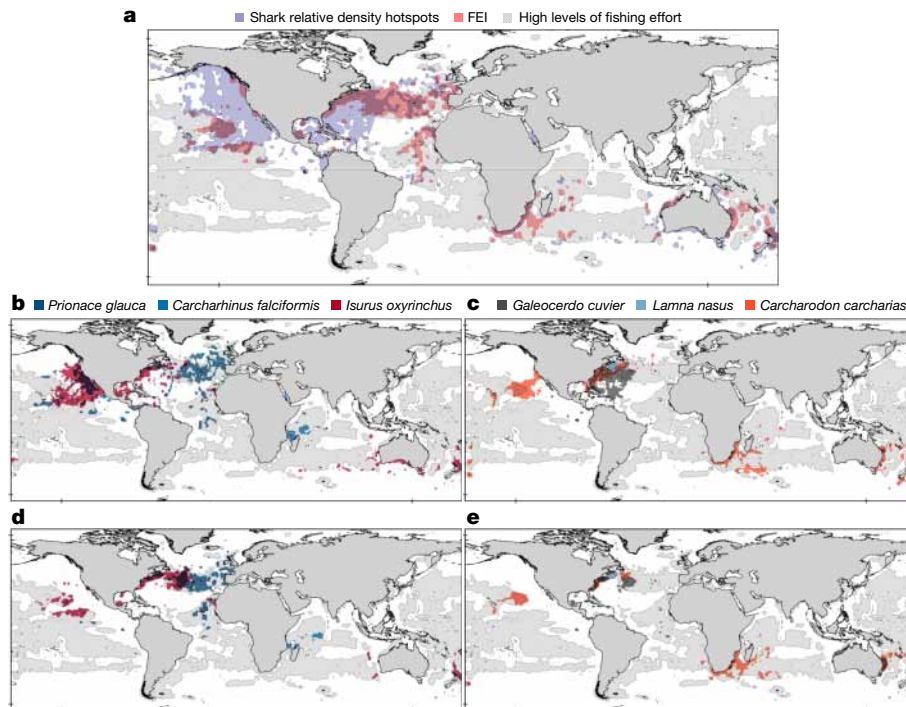


Fig. 1 | Spatial distributions and overlap of sharks and longline fishing vessels. **a**, Shark relative density hotspots (>75th percentile) and FEI hotspots (>75th percentile) overlaid on high longline fishing effort (higher than average; >50th percentile) at the $1^\circ \times 1^\circ$ grid size to illustrate the degree of overlap between the different drivers of FEI hotspots. Higher than average fishing

effort is used here to reflect a major driver of FEI hotspots as FEI hotspots do not arise solely as a result of shark density hotspots overlapping with fishing effort hotspots (>75th percentile), the metric used by Murua et al.². **b–e**, Relative density hotspots (**b, c**) and FEI hotspots (**d, e**) for six shark species overlaid on high longline fishing effort. Data are from our original paper¹.

The majority of the 1,804 sharks tagged were caught on commercial-type longline hooks before release. This is equivalent to a selectivity probability of around one as used in shark ERAs⁵. Third, the commercially valuable sharks that we tracked are seldom discarded by major high-seas longlining fleets⁸, indicating that an implicit assumption of a fishing mortality probability of one does not substantially overestimate the mortality that occurs. Murua et al.² overlook that fact that although some species with fishing prohibitions (such as silky and great hammerhead sharks) may be released alive, reported hooking mortalities are high (for example, 56% for silky sharks and 96% for great hammerhead sharks)^{9,10} in addition to at least around 50% post-release mortality^{11,12}. Collectively, this indicates 78–98% total mortality even of prohibited species. The similar assumptions between our analyses and previous assessments result in comparable susceptibility estimates that will not alter our FEI. For example, we estimated that shortfin mako, blue and porbeagle sharks as the highest exposure risk species in the North Atlantic, which were also the shark species with the highest estimated susceptibilities to longline fishing in a recent Atlantic shark ERA⁴.

Regarding FEI being related to fishing-induced shark mortality, we stated¹ that the significant positive relationship between Food and Agriculture Organization (FAO) fishery landings data and individual-species mean FEI “implies that the index reflects fishing-induced shark mortality”. Our conclusion was appropriately cautious because we recognized that FAO landings data were limited in quality, aggregated at regional scales and subject to high levels of unreported or underreported data¹³, and are potentially unrelated to shark relative abundances. Murua et al.² confirm the result presented in our paper and also show nine further data combinations that we did not test resulting in eight non-significant positive relationships. However, having few data points ($n = 8$ species per test) when comparing the spatial complexity of FEI ($1^\circ \times 1^\circ$ grid) to non-spatially explicit FAO datasets—given the high variability in the quality of landings data—biases results towards non-significance. To address this, we tested linear-regression models for spatially matched

data, including longline CPUE (a relative measure of abundance) of pelagic sharks as the response variable and FEI, fishing effort and number of longline sets as explanatory variables, including interactions with year or month (Supplementary Information). The best model when testing interactions with month was for fishing effort (Akaike information criterion weights (wAIC) = 1), but the deviance explained was similar between this model (46%) and those models that included FEI (42%) or the number of sets (43%). When testing interactions with year, the best model was FEI (wAIC = 0.89), showing a significant and positive relationship with CPUE ($n = 523$, $r^2 = 0.11$, $F_{9,513} = 7.17$, $P < 0.0001$). Bootstrapping tests randomly by removing 1–25% of data confirmed that the best model alternates between fishing effort and FEI as an explanatory variable of shark CPUE. For spatially matched data, therefore, pelagic shark CPUE is significantly greater in areas in which FEI is higher and is as good an explanatory variable of CPUE as fishing effort itself, corroborating our previously published result¹ that FEI reflects fishing-induced shark mortality.

Using spatial exposure risk plots between overlap and FEI to indicate higher or lower than average exposure risk (that is, potential capture susceptibility) is not misleading because the categorization relates specifically to areas in which shark species were tracked and overlap with fishing effort occurred. We previously showed¹ the FEI maps alongside the exposure risk plots to make this point clear. Higher exposure risk can be driven by high FEI when it occurs in specific space-use areas, even if spatial overlap appears relatively low in a region (for example, for white sharks in Oceania). Correct interpretation of our exposure risk estimates requires reference to the areas over which shark hotspots and fishing effort occurred.

FEI hotspots driven by shark hotspots in large-scale ocean ecosystems (for example, the Gulf Stream) led us to conclude that high levels of fishing effort are focused on extensive hotspots of shark space use¹. Murua et al.² generate a new metric (fishing effort hotspots, >75th percentile) to conclude that shark hotspots are not related to main fishing

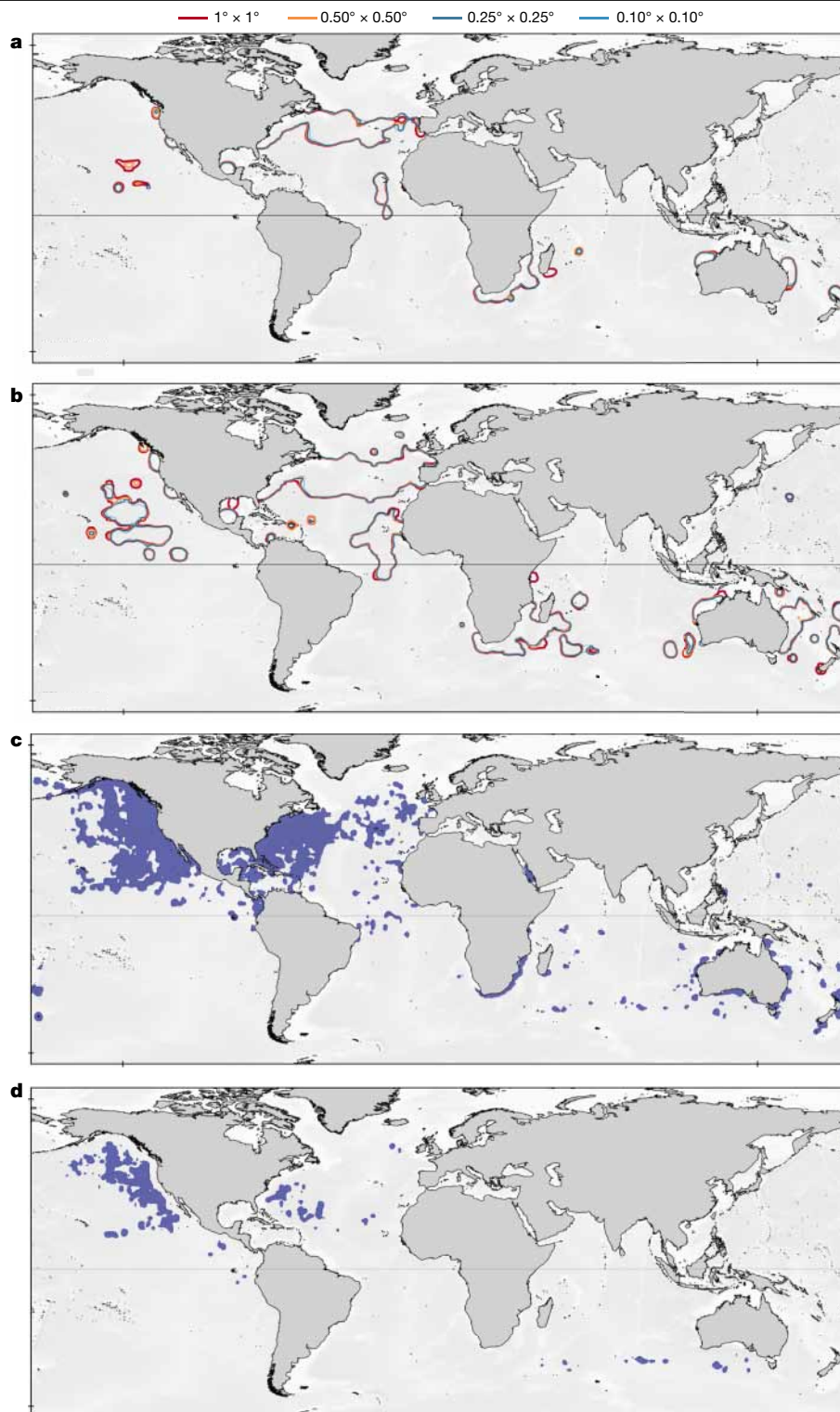


Fig. 2 | Effect of scale on the position and extent of FEI hotspots and areas free from AIS longline fishing effort. **a, b**, The position and extent of FEI hotspots at the >90th percentile (**a**) and >75th percentile (**b**) of the mean FEI do not substantially change across four grid cell sizes from $1^\circ \times 1^\circ$ to $0.1^\circ \times 0.1^\circ$. **c, d**, Global distribution of the shark relative density hotspots estimated from

satellite locations (**c**) and the shark hotspots where there was no recorded AIS longline fishing effort (2012–2016) in ABNJs, the high seas (**d**). **d**, Data from Global Fishing Watch (<https://globalfishingwatch.org/>). This supports our original conclusion that pelagic sharks have limited spatial refuge from the current levels of fishing effort in ABNJs.

effort areas. However, we did not calculate fishing effort hotspots nor relate them to shark density hotspots or FEI hotspots because this approach ignores key drivers of FEI hotspots (see below) and is selective of available data. We did not equate high levels of fishing effort solely to fishing effort hotspots because sharks are often caught and retained by

fishing vessels that did not specifically target sharks, so shark relative density or FEI hotspots should not be expected to correctly predict fishing effort hotspots in the majority of cases. Rather, we showed that FEI hotspots arise from shark relative density hotspots, high fishing effort levels (not only the highest fishing effort levels considered by

Murua et al.²), a combination of both, and some (<2%) are driven by lower shark densities or fishing intensities (Extended Data Table 1).

Consistent with our conclusion, vast areas with higher-than-average fishing effort extend across major shark density and FEI hotspots (Fig. 1). For example, FEI hotspots overlap with shark density hotspots in 56% of grid cells globally, and overlap with higher-than-average fishing effort in 81% of grid cells (Fig. 1). That shark density hotspots and higher-than-average fishing effort together drive 39% of FEI hotspots supports our original conclusion. This is even more clearly seen for individual species (Fig. 1b–e and Extended Data Table 2). For example, globally, blue shark hotspots and high fishing effort together drive 50% of blue shark FEI hotspots (Fig. 1b, d) and, regionally, white shark hotspots and high fishing effort in the northeast Pacific together drive 67% of FEI hotspots (Fig. 1c, e). The claim by Murua et al.² that shark hotspots are not related to main fishing effort areas is not supported when all drivers of FEI hotspots are considered.

Furthermore, large reductions in grid cell size do not affect FEI hotspots. We previously provided results showing, as expected, that reductions from $2 \times 2^\circ$ to $0.1 \times 0.1^\circ$ lowers absolute overlap and FEI values but relative exposure–risk plots remain unchanged (extended data figure 4 and supplementary figure 4 of ref.¹). It is possible that our results and conclusions could be affected if the spatial positions and extent of FEI hotspots—indicating potential changes in relative drivers that affect overlap and FEI estimates (see above)—were substantially altered as the size of the grid cells decreases. However, the position and extent of FEI hotspots remain largely unchanged as grid size decreases (Fig. 2a, b), indicating that the results and conclusions concerning FEI hotspots are highly unlikely to be affected.

Lastly, we disagree that our analyses do not support our conclusion of limited spatial refuge for pelagic sharks from current levels of fishing effort in Areas Beyond National Jurisdictions (ABNJs). Globally, only about one third of ABNJ shark hotspot grid cells were free from AIS-tracked longline fishing effort, indicating that fishing effort overlapped with the majority of shark hotspots (Fig. 2c, d and Extended Data Table 3). Some heavily fished regions showed even lower levels of spatial refuge, only 13% and 20% of Indian Ocean and North Atlantic shark hotspot grid cells, respectively, were free from fishing effort. Hotspots are areas of preferred habitat where sharks spent most time¹, thus it was justified to conclude that for the results presented there was limited spatial refuge in ABNJs. The percentage of spatial refuge for sharks in ABNJs decreases to <25% of shark relative density hotspots when additional AIS data that were not previously available are included (Extended Data Table 4), indicating that our original spatial refuges were actually overestimated.

In summary, we think that the arguments presented neither call into question our results and conclusions nor misdirect management efforts as our exposure risk estimates are spatially and temporally explicit. We do not dispute that regional fishery management organizations for tuna have put management measures in place; these were described in our paper¹. Nevertheless, pelagic sharks have declined globally over many decades^{13–15}, strongly indicating that additional measures are still required to conserve populations effectively, including more complete data reporting, catch quotas and greater enforcement^{13,15}. The data and analyses in our paper¹ contribute to this goal. Indeed, regional fishery management organizations for tuna state that data on biologically important areas, spatiotemporal distributions of shark stocks and interactions with fishing fleets⁸ are needed to aid management. We have provided a first step by making available fishery-independent data¹ on shark spatial density and hotspot locations to complement current assessment approaches.

Reporting summary

Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Data used in linear-regression modelling are available on GitHub (https://github.com/GlobalSharkMovement/GlobalSpatialRisk/tree/master/derived_data). Data used to prepare the maps (shark relative spatial density, longline-fishing effort and shark–longline-fishing overlap and FEI) are available on GitHub (<https://github.com/GlobalSharkMovement/GlobalSpatialRisk>).

Code availability

Code used to prepare the maps (shark relative spatial density, longline-fishing effort and shark–longline-fishing overlap and FEI) is available on GitHub (<https://github.com/GlobalSharkMovement/GlobalSpatialRisk>).

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Additional information

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Matters arising

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Extended Data Table 1 | Global and regional drivers of FEI hotspots

Ocean	Shark hotspots in FEI hotspots (%)	High fishing effort in FEI hotspots (%)	Shark hotspots & High fishing effort in FEI hotspots (%)	Neither shark hotspots nor high fishing effort in FEI hotspots (%)	FEI hotspots overlap shark hotspots (%)	FEI hotspots overlap high fishing effort (%)
Global	17.2	42.1	38.8	1.9	56.0	80.9
N Atlantic	16.7	43.9	37.6	1.8	54.3	81.5
Oceania	8.8	52.7	37.4	1.1	46.2	90.1
SW Indian	11.7	53.2	34.2	0.9	45.9	87.4
NE Pacific	31.0	18.6	46.5	3.9	77.5	65.1

Values given in the first four columns are the percentages of grid cells of shark hotspots (>75th percentile of relative density) and/or high fishing effort (>50th percentile of mean fishing days) that contribute to FEI hotspots (>75th percentile of mean monthly FEI). The last two columns show the percentage of FEI hotspots that overlap shark hotspots and high fishing effort hotspots.

Matters arising

Extended Data Table 2 | Examples of global and regional drivers of FEI hotspots for individual shark species

Species	Ocean	Shark hotspots in FEI hotspots (%)	High fishing effort in FEI hotspots (%)	Shark hotspots & high fishing effort in FEI hotspots (%)	Neither shark hotspots nor high fishing effort in FEI hotspots (%)	FEI hotspots overlap shark hotspots (%)	FEI hotspots overlap high fishing effort (%)
Blue	Global	8.6	38.8	50.2	2.4	58.7	89.0
	N Atlantic	7.6	40.4	49.7	2.3	57.3	90.1
	Oceania	0.0	66.7	33.3	0.0	33.3	100.0
	SW Indian	-	-	-	-	-	-
	NE Pacific	33.3	6.7	53.3	6.7	86.7	60.0
White	Global	17.0	28.6	53.3	1.2	70.3	81.9
	N Atlantic	31.8	20.5	47.7	0.0	79.5	68.2
	Oceania	6.3	34.4	56.3	3.1	62.5	90.6
	SW Indian	11.8	41.8	45.5	0.9	57.3	87.3
	NE Pacific	20.5	11.0	67.1	1.4	87.7	78.1

Values given in the first four columns are the percentages of grid cells of shark hotspots (>75th percentile of relative density) and/or high fishing effort (>50th percentile of mean fishing days) that contribute to FEI hotspots (>75th percentile of mean monthly FEI). The last two columns show the percentage of FEI hotspots that overlap shark hotspots and high fishing effort hotspots. Blue, blue shark (*Prionace glauca*); white, white shark (*Carcharodon carcharias*). No blue sharks were tracked in the southwest Indian Ocean.

Extended Data Table 3 | Spatial refuge of pelagic sharks in ABNJs

Areas Beyond National Jurisdiction (ABNJ)	No. of grid cells		Potential refuge
	Shark relative density hotspot	Shark relative density hotspot with no AIS longline fishing effort	Percentage of shark hotspots with no AIS longline fishing effort
Global	1187	437	36.8
N Atlantic	400	79	19.8
Oceania	57	24	42.1
SW Indian	61	8	13.1
NE Pacific	651	324	49.8

Matters arising

Extended Data Table 4 | Comparison of spatial refuge estimated with AIS data 2012–2016 and 2012–2018

Areas Beyond National Jurisdiction (ABNJ)	Refuge estimated with GFW 2012-16 AIS data	Refuge estimated with GFW 2012-18 AIS data	Difference (percentage refuge in 2012-18 minus 2012-16)
	Percentage of shark hotspots with no AIS longline fishing effort	Percentage of shark hotspots with no AIS longline fishing effort	
Global	36.8	23.1	-13.7
N Atlantic	19.8	5.8	-14.0
Oceania	42.1	37.5	-4.6
SW Indian	13.1	8.2	-4.9
NE Pacific	49.8	34.3	-15.5

The Global Fishing Watch 2012–2016 AIS longline fishing effort data we used in our paper¹ have been further developed to include additional years (2017 and 2018) with a higher number of AIS satellites operating and vessels reporting, resulting in substantially more vessel locations for analysis (<https://globalfishingwatch.org/>). The percentage spatial refuge for sharks in ABNJs decreased to less than a quarter of shark relative density hotspots when more recent fishing effort data were included.

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Data used in linear regression modelling are available on GitHub (https://github.com/GlobalSharkMovement/GlobalSpatialRisk/derived_data/). Data and source code used for preparing figure maps (shark relative spatial density, longline-fishing effort and shark-longline-fishing overlap and FEI) are available on GitHub (<https://github.com/GlobalSharkMovement/GlobalSpatialRisk>).

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Study description	This study is a Reply to a Matters Arising comment on our original paper. To answer the points raised we re-plotted some of the original data from our paper which are fully described in figure and table legends and in our original paper. We carried out new analyses using general linear regression modelling to examine relationships between shark catch per unit effort and fishing exposure risk (FEI), number of longline sets and fishing effort.
Research sample	In this Reply, pelagic shark catch in biomass (kg) retained (recorded in skipper's logbooks) by the Spanish pelagic longline fleet in the North Atlantic was used. Catch data were available and were included for the following tracked sharks: blue shark (<i>Prionace glauca</i>), shortfin mako (<i>Isurus oxyrinchus</i>), longfin mako (<i>I. paucus</i>), tiger shark (<i>Galeocerdo cuiver</i>), white shark (<i>Carcharodon carcharias</i>), porbeagle shark (<i>Lamna nasus</i>), silky shark (<i>Carcharhinus falciformis</i>), smooth hammerhead shark (<i>Sphyrna zygaena</i>), bigeye thresher shark (<i>Alopias superciliosus</i>), copper shark (<i>Carcharhinus brachyurus</i>) and the sandbar shark (<i>C. plumbeus</i>).
Sampling strategy	Shark catch data recorded by the Spanish longline fleet in the North Atlantic were made available by the Spanish authorities after data collection so we had no control over the sampling strategy.
Data collection	Shark catch data recorded by the Spanish longline fishing fleet in the North Atlantic were made available by the Spanish authorities.
Timing and spatial scale	Shark catch data were available from the Spanish longline fishing fleet in the North Atlantic between January 2013 and November 2017.
Data exclusions	In this Reply, no data were excluded except when running sensitivity analysis for linear regression modelling. Here, models were compared using the Akaike and Bayesian information criterion (AIC) and the models strength of evidence assessed using the AIC weights (wAIC). We then used r^2 to quantify the models goodness of fit, and repeated the same procedure when randomly removing 1, 5, 10 and 25 % of the data.
Reproducibility	No experiments as such were conducted, rather our data are based on satellite tracked movements of individual pelagic sharks and fishing vessels, and shark catch data from fisheries.
Randomization	Randomization procedures were used when removing 1, 5, 10 and 25 % of the data for sensitivity analysis using linear regression modelling. Methods are fully described in the Reply and Supplementary Information files.
Blinding	Blinding is not relevant to this type of study because our original data were based on movements of wild animals and fishing vessels.
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

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