



Global spatial risk assessment of sharks under the footprint of fisheries.

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Global spatial risk assessment of sharks under the footprint of fisheries

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Supplementary Information

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1. Supplementary Tables and Figures

Supplementary Table 1. Habitat, distribution and body size data for 23 pelagic shark species tracked with electronic tags.

Taxonomic order	Family	Common name	Scientific name	¹ Habitat	¹ Distribution		¹ Maximum total length (m)
Carcharhiniformes	Carcharhinidae	Copper; bronze whaler	<i>Carcharhinus brachyurus</i>	Neritic -pelagic; Oceanic - epipelagic	Warm temperate; Subtropical	ATL, IND, PAC, MED	3.0
Carcharhiniformes	Carcharhinidae	Silky	<i>Carcharhinus falciformis</i>	Neritic -pelagic; Oceanic - epipelagic, mesopelagic	Tropical	ATL, IND, PAC, MED	3.7
Carcharhiniformes	Carcharhinidae	Galapagos	<i>Carcharhinus galapagensis</i>	Neritic -pelagic; Oceanic - epipelagic	Warm temperate; Tropical	ATL, IND, PAC	3.0
Carcharhiniformes	Carcharhinidae	Bull	<i>Carcharhinus leucas</i>	Rivers; Estuaries; Neritic -pelagic; Oceanic - epipelagic	Warm temperate; Tropical	ATL, IND, PAC	3.4
Carcharhiniformes	Carcharhinidae	Blacktip	<i>Carcharhinus limbatus</i>	Neritic -pelagic	Subtropical; Tropical	ATL, IND, PAC, MED	2.1
Carcharhiniformes	Carcharhinidae	Oceanic whitetip	<i>Carcharhinus longimanus</i>	Oceanic - epipelagic, mesopelagic	Subtropical; Tropical	ATL, IND, PAC	4.0
Carcharhiniformes	Carcharhinidae	Dusky	<i>Carcharhinus obscurus</i>	Neritic -pelagic; Oceanic - epipelagic, mesopelagic	Warm temperate; Tropical	ATL, IND, PAC, MED	3.6
Carcharhiniformes	Carcharhinidae	Sandbar	<i>Carcharhinus plumbeus</i>	Neritic -pelagic, estuaries	Temperate; Tropical	ATL, IND, PAC, MED	1.6
Carcharhiniformes	Carcharhinidae	Tiger	<i>Galeocerdo cuvier</i>	Neritic -pelagic; Oceanic - epipelagic, mesopelagic	Temperate; Tropical	ATL, IND, PAC	5.5

Taxonomic order	Family	Common name	Scientific name	Habitat	Distribution		Maximum total length (m)
Carcharhiniformes	Carcharhinidae	Blue	<i>Prionace glauca</i>	Oceanic - epipelagic, mesopelagic, bathypelagic; Neritic - pelagic	Temperate; Tropical	ATL, IND, PAC, MED	3.8
Carcharhiniformes	Sphyrnidae	Scalloped hammerhead	<i>Sphyrna lewini</i>	Neritic -pelagic; Oceanic - epipelagic, mesopelagic	Warm temperate; Tropical	ATL, IND, PAC, MED	3.5
Carcharhiniformes	Sphyrnidae	Great hammerhead	<i>Sphyrna mokarran</i>	Neritic -pelagic, reef, lagoon; Oceanic - epipelagic, mesopelagic	Tropical	ATL, IND, PAC, MED	5.5
Carcharhiniformes	Sphyrnidae	Smooth hammerhead	<i>Sphyrna zygaena</i>	Neritic -pelagic	Temperate; Tropical	ATL, IND, PAC, MED	4.0
Hexanchiformes	Hexanchidae	Broadnose sevengill	<i>Notorynchus cepedianus</i>	Neritic - benthopelagic	Temperate	ATL, IND, PAC	2.9
Lamniformes	Alopiidae	Pelagic thresher	<i>Alopias pelagicus</i>	Oceanic - epipelagic	Tropical	IND, PAC	4.6
Lamniformes	Alopiidae	Common thresher	<i>Alopias vulpinus</i>	Oceanic - epipelagic, mesopelagic. Neritic - pelagic	Temperate; Tropical	ATL, IND, PAC, MED	5.7
Lamniformes	Lamnidae	White	<i>Carcharodon carcharias</i>	Oceanic - epipelagic, mesopelagic. Neritic - pelagic	Cold and warm temperate; Tropical	ATL, IND, PAC, MED	6.4
Lamniformes	Lamnidae	Shortfin mako	<i>Isurus oxyrinchus</i>	Oceanic - epipelagic, mesopelagic, bathypelagic. Neritic - pelagic	Temperate; Tropical	ATL, IND, PAC, MED	4.0

Taxonomic order	Family	Common name	Scientific name	Habitat	Distribution		Maximum total length (m)
Lamniformes	Lamnidae	Longfin mako	<i>Isurus paucus</i>	Oceanic - epipelagic, mesopelagic	Warm temperate; Tropical	ATL, IND, PAC, MED	4.3
Lamniformes	Lamnidae	Salmon	<i>Lamna ditropis</i>	Oceanic - epipelagic, mesopelagic. Neritic - pelagic	Cold temperate; subtropical	N PAC	2.6
Lamniformes	Lamnidae	Porbeagle	<i>Lamna nasus</i>	Oceanic - epipelagic, mesopelagic. Neritic - pelagic	Cold temperate; subtropical	ATL, IND, PAC	3.6
Lamniformes	Odontaspidae	Smalltooth sandtiger	<i>Odontaspis ferox</i>	Neritic - benthopelagic	Warm temperate; Tropical	ATL, IND, PAC, MED	3.6
Orectolobiformes	Rhincodontidae	Whale	<i>Rhincodon typus</i>	Oceanic - epipelagic, mesopelagic, bathypelagic. Neritic - pelagic	Warm temperate; Tropical	ATL, IND, PAC	18.0

¹Habitat, distribution and body size information were accessed from the website of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (<<http://www.iucnredlist.org/>>; accessed 4 May 2018).

Supplementary Table 2. Conservation and management information for the 23 pelagic shark species tracked in this study. CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora; CMS: Convention of the Conservation of Migratory Species of Wild Animals. CITES or CMS ‘II’ denotes Appendix II listing with the year it was effective from. Data were accessed from the website of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (<<http://www.iucnredlist.org/>>; accessed 4 May 2018; *Isurus* entries updated 25 March 2019).

Scientific name	Global/ Regional IUCN assessments	IUCN Red List classification	Year of IUCN assessment	Population trend	Management measures	CITES listing effective from	CMS listing effective from
<i>Carcharhinus brachyurus</i>	Global	Near Threatened	2003	Unknown	No species-specific management or conservation measures known to be in place		
	Europe	Data Deficient	2015	Unknown	No species-specific management or conservation measures known to be in place		
	Mediterranean	Data Deficient	2016	Unknown	No species-specific management or conservation measures known to be in place		
<i>Carcharhinus falciformis</i>	Global	Vulnerable A2bd	2017	Decreasing	Retention bans and live release are in place for all vessels operating under ICCAT and WCPFC management. IATTC and IOTC has prohibited retention of Silky Sharks on purse seine vessels, limited longline vessel bycatch.	II (2017)	II (2015)
	Europe	Data Deficient	2015	Unknown	No management known to be in place.		
<i>Carcharhinus galapagensis</i>	Global	Near Threatened	2003	Unknown	No management known to be in place.		
<i>Carcharhinus leucas</i>	Global	Near Threatened	2009	Unknown	No specific management programmes known. Managed in the U.S. east coast shark fisheries		

					as part of the "large coastal" groups of species.		
<i>Carcharhinus limbatus</i>	Global	Near Threatened	2009	Unknown	Management in EEZs of Australia and USA.		
	Europe	Data Deficient	2015	Unknown	No species-specific management or conservation measures known to be in place		
	Mediterranean	Data Deficient	2016	Unknown	No species-specific management or conservation measures known to be in place		
<i>Carcharhinus longimanus</i>	Global	Vulnerable A2ad+3d+4ad (assessed as Critically Endangered in NW and W Central Atlantic)	2015	Decreasing	Subject to protections under all the world's tuna-focused Regional Fishery Management Organisations (RFMOs). EEZs: Listed on U.S. Endangered Species Act. Protected in New Zealand.	II (2013)	
	Europe	Endangered A2b	2015	Decreasing	EU: No retention, transshipment or landing allowed in any fishery.		
<i>Carcharhinus obscurus</i>	Global	Vulnerable A2bd	2009	Decreasing	EEZs: Prohibited species in U.S. Atlantic waters; management in Australia, e.g. a maximum size limit.		II (2018)
	Europe	Data Deficient	2015	Unknown	No species-specific management or conservation measures known to be in place within EU.		
	Mediterranean	Data Deficient	2016		No species-specific management measures in place in Mediterranean		
<i>Carcharhinus plumbeus</i>	Global	Vulnerable A2bd+4bd	2009	Decreasing	EEZs: Management plans in Australia, Canada and USA.		

	Europe	Endangered A4d	2015	Decreasing	EEZs: Sandbar Shark fisheries are currently prohibited in Turkey		
	Mediterranean	Endangered A4d	2016	Decreasing	No species-specific measures in place in the Mediterranean Sea. EEZs: Sandbar Shark fisheries are currently prohibited in Turkey		
<i>Galeocerdo cuvier</i>	Global	Near Threatened	2009	Unknown	No specific conservation or management measures in place. EEZs: US Atlantic and Gulf of Mexico this species is managed under a Fisheries Management Program.		
<i>Prionace glauca</i>	Global	Near Threatened	2009	Unknown	No species-specific catch limits or other protections in place in international waters for this species. Managed in EEZs of Canada, Mexico, USA (Atlantic, Gulf of Mexico) and New Zealand waters		
	Europe	Near Threatened	2015	Decreasing	No species-specific catch limits or other protections in place in European waters for this species		
	Mediterranean	Critically Endangered A2bd	2016	Decreasing	No species-specific catch limits or other protections in place in the Mediterranean Sea		
<i>Sphyrna lewini</i>	Global	Endangered A2bd+4bd	2007	Unknown	EEZs: Included in U.S. Large Coastal Shark complex management unit.	II (2014)	II (2015)
<i>Sphyrna mokarran</i>	Global	Endangered A2bd+4bd	2007	Decreasing	No known species specific conservation measures in place. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)	II (2015)

<i>Sphyrna zygaena</i>	Global	Vulnerable A2bd+3bd+4bd	2005	Decreasing	ICCAT region: Banned retention, transshipment, landing, storage, and sale of species in the family Sphyrnidae. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)	
	Europe	Data Deficient	2015	Decreasing	ICCAT region: Banned retention, transshipment, landing, storage, and sale of species in the family Sphyrnidae.		
	Mediterranean	Critically Endangered A2bd	2016	Decreasing	ICCAT region: Banned retention, transshipment, landing, storage, and sale of species in the family Sphyrnidae.		
<i>Notorynchus cepedianus</i>			<i>Not yet assessed by IUCN</i>				
<i>Alopias pelagicus</i>	Global	Vulnerable A2d+4d	2009	Decreasing	IND: Prohibited to retain, tranship or land in IOTC waters	II (2017)	II (2015)
<i>Alopias vulpinus</i>	Global	Vulnerable A2bd+3bd+4bd	2009	Decreasing	ATL: Prohibited to target in ICCAT waters. IND: Prohibited to retain, tranship or land in IOTC waters	II (2017)	II (2015)
	Europe	Endangered A2bd	2015	Decreasing	Article 23 of European Commission (EC) Regulation Number 43/2014 prohibits European vessels having a directed fishery for thresher sharks in the ICCAT convention area		
	Mediterranean	Endangered A2bd	2016	Decreasing	Article 23 of European Commission (EC) Regulation Number 43/2014 prohibits European vessels having a directed		

					fishery for thresher sharks in the ICCAT convention area		
<i>Carcharodon carcharias</i>	Global	Vulnerable A2cd+3cd	2009	Unknown	EEZs: Protection in waters of Australia, EU, South Africa, Namibia, Israel, New Zealand, Malta and USA.	II (2005)	II (2002)
	Europe	Critically Endangered C2a(ii)	2015	Decreasing	NE ATL: European Commission Regulation No 43/2009 prohibits Community vessels to fish for, to retain on board, to transship and to land Great White Shark in all Community and non-Community waters; and also prohibits third country fishing vessels to fish for, to retain on board, to transship and to land this species in all Community waters		
	Mediterranean	Critically Endangered A2d	2016	Decreasing	MED: European Commission Regulation No 43/2009 prohibits Community vessels to fish for, to retain on board, to transship and to land Great White Shark in all Community and non-Community waters; and also prohibits third country fishing vessels to fish for, to retain on board, to transship and to land this species in all Community waters.		

<i>Isurus oxyrinchus</i>	Global	Endangered A2bd	2019	Decreasing	N ATL: ICCAT 2017 Shortfin Mako Stock Assessment concludes "overfished and experiencing overfishing" and recommends zero TAC. Starting 2018 in N ATL ICCAT waters can only retain if brought alongside dead (hence 'live release'). MED: Retention, transshipment, landing, display or sale prohibited. EEZs: Management in Australia, Canada, Chile, EU, New Zealand, USA		II (2009)
	Europe	Data Deficient	2015	Unknown	NE ATL: Starting 2018 in ICCAT waters can only retain if brought alongside dead (hence 'live release').		
	Mediterranean	Critically Endangered A2bd	2016	Decreasing	MED: Retention, transshipment, landing, display or sale prohibited.		
<i>Isurus paucus</i>	Global	Endangered A2d	2019	Decreasing	No management measures in place for this species.		II (2009)
	Europe	Data Deficient	2015	Unknown	No management measures in place for this species.		
	Mediterranean	Data Deficient	2016	Unknown	No management measures in place for this species.		
<i>Lamna ditropis</i>	Global	Least Concern	2009	Stable	NE PAC: Included in the commercial bycatch TAC (Total Allowable Catch) for Alaska Federal waters. Commercial fishing for all shark species in Alaska State waters has been illegal since 1997.		
<i>Lamna nasus</i>	Global	Endangered A1abd	2006	Decreasing	EEZs: Management plans in waters of Canada and USA.	II (2014)	II (2009)

					Managed by quotas in New Zealand.		
	Europe	Critically Endangered A2bd	2015	Decreasing	NE ATL: Prohibited species for all EU and third country vessels in EU waters and to all EU vessels in non-EU waters		
	Mediterranean	Critically Endangered A2bd	2016	Decreasing	MED: Prohibited species for all EU and third country vessels in EU waters and to all EU vessels in non-EU waters		
<i>Odontaspis ferox</i>	Global	Vulnerable A2bd	2016	Decreasing	New Zealand Wildlife Act 1953 making it illegal to hunt, kill or harm them within New Zealand's territorial sea and Exclusive Economic Zone. Australia: NSW protected species list. Malpelo Fauna and Flora Sanctuary marine park provides protection (no fishing) in its range.		
	Europe	Critically Endangered A2bcd	2015	Decreasing	MED: Protected in waters of Spain, Malta and Croatia.		
	Mediterranean	Critically Endangered A2bcd	2016	Decreasing	MED: Protected in waters of Spain, Malta and Croatia.		
<i>Rhincodon typus</i>	Global	Endangered A2bd+4bd	2016	Decreasing	IND, PAC: Regional Fisheries Management Organisations (RFMOs) have banned the intentional setting of purse-seine nets around Whale Shark; not yet in the ATL. EEZs: Protected in New Zealand and throughout much of its range within EEZs.	II (2003)	II (2000)

Supplementary Table 3. Summary data of individual sharks tagged with satellite transmitters. See Methods for tag type information.

Family	Common name	Scientific name	Tagging region(s)	ARGOS	PSAT	Total tags	Tracking days
Carcharhinidae	Copper	<i>Carcharhinus brachyurus</i>	IND	0	4	4	359
Carcharhinidae	Silky	<i>Carcharhinus falciformis</i>	ATL, IND, PAC	20	31	51	3,180
Carcharhinidae	Galapagos	<i>Carcharhinus galapagensis</i>	ATL, PAC	9	12	21	1,133
Carcharhinidae	Bull	<i>Carcharhinus leucas</i>	ATL, IND	37	4	41	3,425
Carcharhinidae	Blacktip	<i>Carcharhinus limbatus</i>	ATL, PAC	19	0	19	2,176
Carcharhinidae	Oceanic whitetip	<i>Carcharhinus longimanus</i>	ATL, PAC	20	85	105	17,687
Carcharhinidae	Dusky	<i>Carcharhinus obscurus</i>	ATL	1	1	2	116
Carcharhinidae	Sandbar	<i>Carcharhinus plumbeus</i>	PAC	1	0	1	20
Carcharhinidae	Tiger	<i>Galeocerdo cuvier</i>	ATL, IND, PAC	221	33	254	43,910
Carcharhinidae	Blue	<i>Prionace glauca</i>	ATL, IND, PAC	176	104	280	28,597
Sphyrnidae	Scalloped hammerhead	<i>Sphyrna lewini</i>	ATL, PAC	23	8	31	1,040
Sphyrnidae	Great hammerhead	<i>Sphyrna mokarran</i>	ATL	31	3	34	1,056
Sphyrnidae	Smooth hammerhead	<i>Sphyrna zygaena</i>	ATL	1	0	1	39
Hexanchidae	Broadnose sevengill	<i>Notorynchus cepedianus</i>	IND	0	2	2	118
Alopiidae	Pelagic thresher	<i>Alopias pelagicus</i>	PAC	0	5	5	305
Alopiidae	Common thresher	<i>Alopias vulpinus</i>	IND, PAC	0	11	11	1,498
Lamnidae	White	<i>Carcharodon carcharias</i>	ATL, IND, PAC	54	106	160	41,870
Lamnidae	Shortfin mako	<i>Isurus oxyrinchus</i>	ATL, IND, PAC	190	71	261	56,071
Lamnidae	Longfin mako	<i>Isurus paucus</i>	ATL	0	1	1	49
Lamnidae	Salmon	<i>Lamna ditropis</i>	PAC	134	38	172	57,037
Lamnidae	Porbeagle	<i>Lamna nasus</i>	ATL, PAC	0	56	56	8,863
Odontaspidae	Smalltooth sandtiger	<i>Odontaspis ferox</i>	PAC	0	5	5	341
Rhincodontidae	Whale	<i>Rhincodon typus</i>	ATL, IND, PAC	129	35	164	12,834
			Total	1,066	615	1,681	281,724

Supplementary Table 4. Summary of tag deployments per year for those tags reporting usable location data.

Year	N tags	Cumulative frequency	Cumulative %
2002	19	19	1.13
2003	30	49	2.91
2004	76	125	7.44
2005	90	215	12.79
2006	160	375	22.31
2007	126	501	29.80
2008	75	576	34.27
2009	93	669	39.80
2010	174	843	50.15
2011	196	1039	61.81
2012	167	1206	71.74
2013	122	1328	79.00
2014	134	1462	86.97
2015	120	1582	94.11
2016	75	1657	98.57
2017	24	1681	100.00

Supplementary Table 5. Summary data of the spatial coverage of pelagic shark tracks in each ocean region.

	Ocean region			
	North Atlantic	East Pacific	South Indian	Oceania
Total no. grid cells	5607	5118	3345	6263
No. of cells not occupied by sharks	3113	2433	2348	4723
No. cells occupied by sharks	2494	2685	997	1540
% cells occupied by sharks	44.5	52.5	29.8	24.6
Total area of grid cells (million km ²)	65.244	61.476	39.189	73.906
Total area of grid cells occupied by sharks (million km ²)	29.020	32.251	11.680	18.172

Supplementary Table 6. Space use hotspots of tracked pelagic sharks estimated from the relative density distribution ($\geq 75^{\text{th}}$ percentile of the weighted daily location density).

Ocean	Hotspot
North & Central Atlantic	Gulf Stream and western approaches (extending to convergence with Labrador Current and eastward to Azores) North Atlantic Current (incl Charlie Gibbs Fracture Zone) Western European shelf edge & Bay of Biscay Caribbean Sea Gulf of Mexico West African upwelling Oceanic Islands: Bermuda, Azores, Ascension
Pacific	Aleutian Islands/Alaska Current California Current (incl white shark Café) Baja California North Equatorial current (westward to Hawaiian Islands) Eastern Equatorial Counter Current (incl islands: Galapagos, Malpelo, Clipperton) Great Barrier Reef (Papua New Guinea – Australia) South Australian Basin (incl Great Australian Bight; Bass Strait) New Zealand (North and South Island, Chatham Rise/Is., Kermadec Is.)
Indian	Red Sea Agulhas Current (Mozambique Channel, South Africa) Agulhas Return Current (incl southern Madagascar) Oceanic islands: Seychelles, north of Crozet Is., east of Amsterdam Is. Northwest and southwest Australia

Supplementary Table 7. Set of generalised additive models (GAM) used to explain the log-transformed relative density of all 23 shark species, the fishing effort of all vessels, and fishing effort of longlines only. Smooth terms considered in our GAM models are indicated by ‘ti’ for the tensor product representing interaction terms with main effects considered separately (e.g., ti(a) + ti(b) + ti(a,b)), and ‘s’ represents the spline functions for each environmental variable considered. The dimension basis for all terms was limited to 5 (i.e., $k = 5$) to assist controlling for overfitting. A null, intercept-only model was also included in the model set. See Methods for abbreviations used for the environmental variables.

Model	Variables included
1 Hypothesis 1	ti(MLD_0m) + ti(TGR_0m) + ti(MLD_0m, TGR_0m) + s(SSH_0m) + s(CHL_0m) + s(SAL_100m) Observed shark density is explained mostly by their relationship with habitat types characterised by surface temperature gradients (fronts; thermoclines) and their interaction
2 H2	ti(CHL_100m) + ti(TGR_100m) + ti(CHL_100m, TGR_100m) + s(MLD_0m) + s(PHY_0m) + s(DO_0m) Observed shark density is explained mostly by their relationships with habitat types characterised by subsurface temperature gradients (fronts; thermoclines) and their interactions
3 H3	ti(CHL_100m) + ti(TEM_100m) + ti(CHL_100m, TEM_100m) Observed shark density is explained mostly by the interaction between subsurface temperature and chlorophyll-a as a proxy for productivity
4 H4	s(NPP_0m) + s(PHY_100m)

	Observed shark density is explained mostly by variables that are co-linear with those commonly perceived as important for shark occurrence
5 H5	s(NPP_100m) + s(DO_100m) Observed shark density is explained mostly by variables that are co-linear with those commonly perceived as important for shark occurrence
6 H6	ti(TEM_100m) + ti(SAL_100m) + ti(TEM_100m, SAL_100m) + s(MLD_0m) Observed shark density is explained mostly by the interaction between subsurface temperature and salinity and affected by surface thermocline
7 H7	s(SST_0m) + s(SAL_0m) Observed shark density is explained mostly by the interaction between surface temperature and salinity only
8	<i>D_{it}</i> Null model added for model comparison using an information-theoretic approach

Supplementary Table 8. Summary of fitted generalised additive models (GAM) relating the log-transformed weighted relative density of all sharks (D_{it}) and the fishing effort of all vessels and of longlines only to environmental variables. Environmental variables included in each model are detailed in Supplementary Table 7. $wAIC$ indicates the weight of the Akaike’s information criteria for each model in the model set with bold highlighting the highest ranked model. The percentage of deviance explained (%DE) by each model is given and the highest and second highest values for each response variable are highlighted in bold.

Model	D_{it}		Fishing effort (all vessels)		Longline fishing effort	
	$wAIC$	%DE	$wAIC$	%DE	$wAIC$	%DE
1	1.000	36.31	1.000	29.88	1.000	16.12
2	0.000	25.69	0.000	16.12	0.000	12.90
3	0.000	14.91	0.000	14.52	0.000	14.62
4	0.000	7.09	0.000	9.49	0.000	5.73
5	0.000	7.49	0.000	7.20	0.000	11.14
6	0.000	33.79	0.000	24.89	0.000	14.99
7	0.000	20.76	0.000	17.72	0.000	6.21
8	0.000	0.00	0.000	0.00	0.000	0.00

Supplementary Table 9. Effect of different grid cell size on the mean monthly spatial overlap of all sharks and fishing vessels (%) and fishing exposure index (FEI). Values were calculated for all ARGOS transmitter tracked sharks ($n = 1066$) and longline vessels. ARGOS tracked sharks were used in the analysis as spatial accuracy of locations estimated from SSMs fit to ARGOS observation was $<0.1^\circ$ (see Methods).

		Grid cell size											
		$2 \times 2^\circ$		$1 \times 1^\circ$		$0.75 \times 0.75^\circ$		$0.50 \times 0.50^\circ$		$0.25 \times 0.25^\circ$		$0.10 \times 0.10^\circ$	
		Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Global	%	29.66	9.73	21.62	1.56	19.66	1.06	15.51	0.00	10.25	0.00	5.03	0.00
	FEI	4.6×10^{-5}	1.6×10^{-6}	3.0×10^{-5}	1.1×10^{-6}	3.3×10^{-6}	1.9×10^{-8}	8.2×10^{-6}	0.00	2.7×10^{-6}	0.00	3.9×10^{-8}	0.00
N. Atlantic Ocean	%	39.01	20.00	32.79	7.41	30.64	5.56	26.10	3.24	19.22	1.09	10.23	0.00
	FEI	4.5×10^{-5}	1.4×10^{-5}	3.7×10^{-5}	1.0×10^{-5}	4.5×10^{-6}	4.4×10^{-7}	1.1×10^{-5}	1.8×10^{-6}	3.9×10^{-6}	4.5×10^{-7}	7.0×10^{-8}	0.00
E. Pacific Ocean	%	11.70	0.00	7.14	0.00	6.00	0.00	4.28	0.00	2.39	0.00	0.84	0.00
	FEI	5.3×10^{-6}	0.00	6.6×10^{-6}	0.00	4.2×10^{-7}	0.00	1.9×10^{-6}	0.00	5.0×10^{-7}	0.00	5.1×10^{-9}	0.00
S. Indian Ocean	%	76.62	92.14	50.33	58.33	45.36	45.93	32.77	31.07	17.24	11.25	7.78	2.47
	FEI	2.7×10^{-4}	4.4×10^{-5}	1.1×10^{-4}	5.8×10^{-5}	1.2×10^{-5}	5.1×10^{-6}	2.6×10^{-5}	1.2×10^{-5}	9.1×10^{-6}	3.3×10^{-6}	9.4×10^{-8}	1.4×10^{-8}
Oceania	%	38.02	30.66	22.56	14.64	19.81	10.44	12.83	4.28	6.75	0.28	2.77	0.00
	FEI	4.5×10^{-5}	1.7×10^{-5}	4.2×10^{-5}	1.3×10^{-5}	4.3×10^{-6}	9.1×10^{-7}	1.1×10^{-5}	2.2×10^{-6}	2.8×10^{-6}	5.5×10^{-8}	3.7×10^{-8}	0.00

Supplementary Table 10. Calculated mean monthly spatial overlap and fishing exposure index for ocean regions and species. Mean fishing effort index is the mean monthly fishing effort sharks were exposed to within areas they occupied (see Methods). S.D., \pm one standard deviation of the mean; S.E., \pm one standard error of the mean. Ocean regions were selected based upon FAO fishing regions (see Extended Data Fig. 1c). There were 70 individual sharks that did not fall into FAO regions and these were not included in this analysis.

(a) Global. Calculated mean monthly spatial overlap and longline fishing exposure index for the 11 most data-rich species/taxa groups.

Species	N tags	Mean monthly spatial overlap (%)	Median	S.D.	S.E.	Mean monthly fishing exposure index	Median	S.D.	S.E.
<i>Prionace glauca</i>	280	48.69	48.73	39.46	2.36	2.0×10^{-4}	9.7×10^{-5}	2.8×10^{-4}	1.7×10^{-5}
<i>Carcharhinus leucas</i>	41	7.22	0.00	24.84	3.88	2.0×10^{-4}	0.00	1.1×10^{-3}	1.7×10^{-4}
<i>Isurus oxyrinchus</i>	262	36.84	22.11	35.84	2.21	1.6×10^{-4}	5.4×10^{-5}	3.0×10^{-4}	1.8×10^{-5}
<i>Carcharhinus longimanus</i>	105	1.60	0.00	5.19	0.51	4.0×10^{-6}	0.00	1.6×10^{-5}	1.6×10^{-6}
<i>Lamna nasus</i>	56	47.29	48.43	28.58	3.82	3.5×10^{-4}	1.6×10^{-4}	4.3×10^{-4}	5.7×10^{-5}
<i>Lamna ditropis</i>	172	1.33	0.00	4.28	0.33	4.0×10^{-6}	0.00	9.8×10^{-6}	7.5×10^{-7}
<i>Carcharhinus falciformis</i>	51	14.59	0.00	22.52	3.15	4.6×10^{-5}	0.00	1.1×10^{-4}	1.6×10^{-5}
Sphyrna spp.	66	7.13	0.00	19.23	2.37	1.8×10^{-5}	0.00	6.8×10^{-5}	8.3×10^{-6}
<i>Galeocerdo cuvier</i>	254	15.62	3.78	24.81	1.56	7.3×10^{-5}	2.5×10^{-6}	1.6×10^{-4}	9.7×10^{-6}
<i>Rhincodon typus</i>	164	12.32	0.00	27.90	2.18	3.0×10^{-5}	0.00	9.6×10^{-5}	7.5×10^{-6}
<i>Carcharodon carcharias</i>	160	33.90	27.28	26.09	2.06	3.6×10^{-4}	1.1×10^{-4}	6.7×10^{-4}	5.3×10^{-5}
Total tags or mean/median	1611	24.37	5.00	33.08	0.82	1.3×10^{-4}	6.1×10^{-6}	3.5×10^{-4}	8.8×10^{-6}

(b) North Atlantic. Calculated mean monthly spatial overlap and longline fishing exposure index for the 11 most data-rich species/taxa groups.

Species	N tags	Mean monthly spatial overlap (%)	Median	S.D.	S.E.	Mean monthly fishing exposure index	Median	S.D.	S.E.
<i>Prionace glauca</i>	152	75.59	81.21	25.94	2.10	3.4×10^{-4}	2.4×10^{-4}	2.9×10^{-4}	2.3×10^{-5}
<i>Carcharhinus leucas</i>	38	0.39	0.00	2.43	0.39	2.3×10^{-7}	0.00	1.4×10^{-6}	2.3×10^{-7}
<i>Isurus oxyrinchus</i>	120	62.44	70.69	34.16	3.12	3.0×10^{-4}	2.1×10^{-4}	3.8×10^{-4}	3.5×10^{-5}
<i>Carcharhinus longimanus</i>	99	1.52	0.00	5.27	0.53	4.0×10^{-6}	0.00	1.6×10^{-5}	1.6×10^{-6}
<i>Lamna nasus</i>	46	52.21	51.61	26.77	3.95	3.9×10^{-4}	2.3×10^{-4}	4.6×10^{-4}	6.7×10^{-5}
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>	1*								
Sphyrna spp.	40	7.77	0.00	17.86	2.82	2.8×10^{-5}	0.00	8.6×10^{-5}	1.4×10^{-5}
<i>Galeocerdo cuvier</i>	124	7.97	0.24	15.10	1.36	5.0×10^{-5}	9.8×10^{-9}	1.2×10^{-4}	1.1×10^{-5}
<i>Rhincodon typus</i>	3	25.89	21.43	22.21	12.83	3.5×10^{-5}	1.2×10^{-5}	4.9×10^{-5}	2.8×10^{-5}
<i>Carcharodon carcharias</i>	26	50.59	47.44	22.83	4.48	1.6×10^{-4}	1.2×10^{-4}	1.3×10^{-4}	2.6×10^{-5}
Total tags or mean/median	649	37.41	25.12	38.60	1.52	1.8×10^{-4}	5.3×10^{-5}	3.0×10^{-4}	1.2×10^{-5}

*The single tag was not included in the mean/median overlap or effort values shown.

(c) **East Pacific.** Calculated mean monthly spatial overlap and longline fishing exposure index for the 11 most data-rich species/taxa groups.

Species	N tags	Mean monthly spatial overlap (%)	Median	S.D.	S.E.	Mean monthly fishing exposure index	Median	S.D.	S.E.
<i>Prionace glauca</i>	112	14.33	4.01	24.66	2.33	3.5×10^{-5}	1.5×10^{-6}	1.4×10^{-4}	1.4×10^{-5}
<i>Carcharhinus leucas</i>									
<i>Isurus oxyrinchus</i>	113	12.75	7.83	16.15	1.52	3.4×10^{-5}	1.4×10^{-5}	4.7×10^{-5}	4.4×10^{-6}
<i>Carcharhinus longimanus</i>	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lamna nasus</i>									
<i>Lamna ditropis</i>	172	1.33	0.00	4.28	0.33	4.0×10^{-6}	0.00	9.8×10^{-6}	7.5×10^{-7}
<i>Carcharhinus falciformis</i>	17	3.32	0.00	13.21	3.20	2.6×10^{-6}	0.00	1.0×10^{-5}	2.5×10^{-6}
Sphyrna spp.	21	0.48	0.00	1.50	0.33	1.0×10^{-7}	0.00	3.9×10^{-7}	8.5×10^{-8}
<i>Galeocerdo cuvier</i>	15	12.75	0.00	29.30	7.56	1.7×10^{-5}	0.00	3.9×10^{-5}	1.0×10^{-5}
<i>Rhincodon typus</i>	77	2.21	0.00	6.09	0.69	3.5×10^{-6}	0.00	1.3×10^{-5}	1.4×10^{-6}
<i>Carcharodon carcharias</i>	59	15.01	13.31	13.34	1.74	1.2×10^{-4}	5.7×10^{-5}	2.1×10^{-4}	2.7×10^{-5}
Total tags or mean/median	588	7.80	0.00	15.99	0.66	2.7×10^{-5}	0.00	1.0×10^{-4}	4.1×10^{-6}

(d) Indian Ocean. Calculated mean monthly spatial overlap and longline fishing exposure index for the 11 most data-rich species/taxa groups.

Species	N tags	Mean monthly spatial overlap (%)	Median	S.D.	S.E.	Mean monthly fishing exposure index	Median	S.D.	S.E.
<i>Prionace glauca</i>	5	46.67	33.33	43.14	19.29	3.1×10^{-5}	2.1×10^{-5}	2.7×10^{-5}	1.2×10^{-5}
<i>Carcharhinus leucas</i>	3	93.74	100.00	10.84	6.26	2.8×10^{-3}	1.5×10^{-3}	3.4×10^{-3}	2.0×10^{-3}
<i>Isurus oxyrinchus</i>									
<i>Carcharhinus longimanus</i>									
<i>Lamna nasus</i>									
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>	33	19.32	11.71	23.99	4.18	6.2×10^{-5}	8.0×10^{-6}	1.3×10^{-4}	2.2×10^{-5}
Sphyrna spp.									
<i>Galeocerdo cuvier</i>	30	31.78	26.74	24.11	4.40	8.6×10^{-5}	7.0×10^{-5}	8.9×10^{-5}	1.6×10^{-5}
<i>Rhincodon typus</i>	48	32.71	0.00	43.59	6.29	8.7×10^{-5}	0.00	1.6×10^{-4}	2.3×10^{-5}
<i>Carcharodon carcharias</i>	34	64.29	65.36	17.43	2.99	1.1×10^{-3}	7.5×10^{-4}	1.1×10^{-3}	1.8×10^{-4}
Total tags or mean/median	153	38.31	33.33	35.31	2.85	3.7×10^{-4}	5.1×10^{-5}	8.6×10^{-4}	6.9×10^{-5}

(e) **Oceania.** Calculated mean monthly spatial overlap and longline fishing exposure index for the 11 most data-rich species/taxa groups.

Species	N tags	Mean monthly spatial overlap (%)	Median	S.D.	S.E.	Mean monthly fishing exposure index	Median	S.D.	S.E.
<i>Prionace glauca</i>	11	27.79	15.00	32.75	9.87	1.2×10^{-4}	1.5×10^{-5}	2.0×10^{-4}	6.1×10^{-5}
<i>Carcharhinus leucas</i>									
<i>Isurus oxyrinchus</i>	15	17.64	11.35	20.38	5.26	2.1×10^{-4}	7.2×10^{-5}	3.2×10^{-4}	8.2×10^{-5}
<i>Carcharhinus longimanus</i>									
<i>Lamna nasus</i>	10	24.66	14.28	26.80	8.47	1.5×10^{-4}	4.5×10^{-5}	1.8×10^{-4}	5.6×10^{-5}
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>									
Sphyrna spp.									
<i>Galeocerdo cuvier</i>	58	28.24	13.01	34.87	4.58	1.5×10^{-4}	3.5×10^{-5}	2.5×10^{-4}	3.2×10^{-5}
<i>Rhincodon typus</i>	16	12.15	8.56	12.94	3.23	2.2×10^{-5}	5.7×10^{-6}	4.1×10^{-5}	1.0×10^{-5}
<i>Carcharodon carcharias</i>	41	25.28	23.29	17.42	2.72	1.6×10^{-4}	7.1×10^{-5}	2.5×10^{-4}	4.0×10^{-5}
Total tags or mean/median	151	24.41	16.33	27.21	2.21	1.5×10^{-4}	3.9×10^{-5}	2.4×10^{-4}	1.9×10^{-5}

Supplementary Table 11. Correlations of monthly mean and median spatial overlap and fishing exposure index (FEI) of shark species and longline fishing effort. The Kendall rank correlation method was used. Results show significant correlations between means and medians of overlap and FEI for individual species globally and within oceans. This indicates that although we use monthly means in the main overlap-FEI analyses (e.g. Fig. 3), similar risk exposure results are found when monthly medians were used. ‘na’ denotes where correlation values were not computed due to ties. * denotes $p < 0.05$.

	Global			N Atl			E Pac			S Ind			Oceania		
	N tags	%	FEI	N tags	%	FEI	N tags	%	FEI	N tags	%	FEI	N tags	%	FEI
<i>Prionace glauca</i>	280	0.87*	0.72*	152	0.81*	0.64*	112	0.66*	0.31*	5	0.84	0.84	11	0.79*	0.69*
<i>Carcharhinus leucas</i>	41	0.87*	0.87*	38	na	na	0			3	1.00	1.00	0		
<i>Isurus oxyrinchus</i>	262	0.86*	0.59*	120	0.87*	0.54*	113	0.67*	0.18*	0			15	0.81*	0.52*
<i>Carcharhinus longimanus</i>	105	0.45*	0.21*	99	0.43*	0.22*	2			0			0		
<i>Lamna nasus</i>	56	0.85*	0.54*	46	0.82*	0.54*	0			0			10	0.89*	0.25
<i>Lamna ditropis</i>	172	0.22*	na	0			172	0.22*		0			0		
<i>Carcharhinus falciformis</i>	51	0.84*	0.53*	1			17	0.72*	0.72*	33	0.78*	0.50*	0		
<i>Sphyrna</i> spp.	66	0.89*	0.50*	40	0.85*	0.46*	21	1.00*	na	0			0		
<i>Galeocerdo cuvier</i>	254	0.71*	0.41*	124	0.61*	0.30*	15	0.88*	0.57*	30	0.86*	0.28	58	0.73*	0.49*
<i>Rhincodon typus</i>	164	0.91*	0.65*	3	1.00	0.82	77	0.76*	na	48	0.98*	0.89*	16	0.81*	na
<i>Carcharodon carcharias</i>	160	0.83*	0.47*	26	0.87*	0.22	59	0.59*	0.16	34	0.80*	0.63*	41	0.75*	0.18
Total tags or mean/median	1611	0.83*	0.58*	649	0.88*	0.67*	588	0.62*	0.20*	153	0.91*	0.65*	151	0.75*	0.40*

Supplementary Table 12. Hotspots of shark spatial density overlapping with exposure to longline fishing effort estimated by the mean fishing exposure index (FEI). Hotspots were defined as grid cells with $\geq 75\%$ percentile of mean FEI for all individuals. Geographical positions of named hotspots are given in Extended Data Fig. 1.

Ocean	Hotspot
North & Central Atlantic	Gulf Stream and western approaches extending east to the Labrador Current Current Convergence Zone & Azores Islands North Atlantic Current Western European continental shelf edge Iberian Peninsula West Africa upwelling Caribbean Sea & Gulf of Mexico South Africa
Pacific	West Canadian shelf California Current (incl white shark Café) North Equatorial Current Southern Great Barrier Reef New Zealand (North Island & Chatham Islands)
Indian	Mozambique Channel South Africa Agulhas Current & Agulhas Return Current (incl. north of Prince Edward Islands and Crozet Islands) Mauritius and Réunion Islands Northwest Australia

Supplementary Table 13. Tag recapture data for the most data-rich species studied.

Shark species	Global			North Atlantic			Eastern Pacific			Indian Ocean			Oceania		
	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%
Silky	51	4	7.84	1	0	0	17	2	11.76	28	2	7.14			
Tiger	254	7	2.76	131	5	3.82	12	0	0	26	0	0	58	0	0
Blue	280	17	6.07	152	12	7.89	112	5	4.46	5	0	0	11	0	0
White	160	2	1.25	26	0	0	59	0	0	34	2*	5.88	41	0	0
Mako	261	30	11.49	119	23	19.3	113	5	4.42				15	1	6.67
Salmon	172	1	0.58				172	1	0.58						
Porbeagle	56	3	5.36	46	3	6.52							10	0	0
Whale	134	1	0.61	3	0	0	77	0	0	18	0	0	16	1	6.25
	<i>1398</i>	<i>65</i>	<i>4.65</i>	<i>478</i>	<i>43</i>	<i>9.00</i>	<i>562</i>	<i>13</i>	<i>2.31</i>	<i>111</i>	<i>4</i>	<i>3.60</i>	<i>151</i>	<i>2</i>	<i>1.32</i>

*The two white sharks were caught in nets: one from South Africa in KwaZulu-Natal shark nets, and one from Mozambique in the artisanal coastal gill nets.

Supplementary Table 14. Number of tags deployed of the most frequently tagged species within the defined general oceanic regions. These species account for 96% of individuals tagged.

Species	Oceanic region			
	N. Atlantic Ocean	E. Pacific Ocean	S. Indian Ocean	Oceania
<i>Prionace glauca</i>	152	112	5	11
<i>Isurus</i> spp.	120	113	0	15
<i>Galeocerdo cuvier</i>	131	12	26	58
<i>Lamna ditropis</i>	0	172	0	0
<i>Rhincodon typus</i>	3	77	18	16
<i>Carcharodon carcharias</i>	26	59	34	41
<i>Carcharhinus longimanus</i>	99	2	0	0
<i>Lamna nasus</i>	46	0	0	10
<i>Carcharhinus falciformis</i>	1	17	28	0
<i>Carcharhinus leucas</i>	38	0	3	0
<i>Sphyrna</i> spp.	40	21	0	0

Supplementary Table 15. Proportion of temporal gaps of a given length per track for the different species and tag types.

Species	Tag type	Frequency of gaps; mean (\pm SD)			
		$\leq 5d$	$> 5 - \leq 10d$	$> 10 - \leq 20d$	$> 20d$
<i>Prionace glauca</i>	PSAT	0.86 (0.15)	0.08 (0.09)	0.05 (0.11)	0.01 (0.03)
	ARGOS	0.95 (0.08)	0.04 (0.06)	0.01 (0.04)	0.00 (0.01)
<i>Isurus oxyrinchus</i>	PSAT	0.90 (0.13)	0.06 (0.08)	0.03 (0.06)	0.01 (0.03)
	ARGOS	0.97 (0.06)	0.02 (0.04)	0.01 (0.01)	0.00 (0.01)
<i>Galeocerdo cuvier</i>	PSAT	0.78 (0.18)	0.11 (0.13)	0.10 (0.14)	0.01 (0.03)
	ARGOS	0.88 (0.15)	0.07 (0.09)	0.04 (0.09)	0.01 (0.02)
<i>Lamna ditropis</i>	PSAT	0.99 (0.01)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
	ARGOS	0.93 (0.09)	0.05 (0.06)	0.01 (0.03)	0.01 (0.02)
<i>Rhincodon typus</i>	PSAT	0.74 (0.29)	0.10 (0.15)	0.15 (0.23)	0.01 (0.03)
	ARGOS	0.92 (0.14)	0.05 (0.11)	0.02 (0.05)	0.01 (0.03)
<i>Carcharodon carcharias</i>	PSAT	0.86 (0.21)	0.07 (0.12)	0.05 (0.08)	0.02 (0.04)
	ARGOS	0.89 (0.09)	0.06 (0.05)	0.03 (0.03)	0.02 (0.03)
<i>Carcharhinus longimanus</i>	PSAT	0.96 (0.09)	0.02 (0.05)	0.01 (0.04)	0.00 (0.01)
	ARGOS	0.78 (0.16)	0.11 (0.1)	0.07 (0.07)	0.04 (0.05)
<i>Lamna nasus</i>	PSAT	0.68 (0.19)	0.17 (0.11)	0.10 (0.09)	0.05 (0.05)
<i>Carcharhinus falciformis</i>	PSAT	0.91 (0.13)	0.04 (0.05)	0.04 (0.09)	–
	ARGOS	0.81 (0.15)	0.15 (0.16)	0.04 (0.05)	0.01 (0.02)
<i>Carcharhinus leucas</i>	PSAT	0.82 (0.19)	0.07 (0.03)	0.09 (0.13)	0.02 (0.05)
	ARGOS	0.81 (0.20)	0.11 (0.12)	0.06 (0.11)	0.02 (0.04)
<i>Sphyrna mokarran</i>	PSAT	0.90 (0.17)	0.03 (0.06)	0.07 (0.12)	–
	ARGOS	0.77 (0.31)	0.14 (0.24)	0.08 (0.15)	0.01 (0.05)
<i>Sphyrna lewini</i>	PSAT	0.92 (0.15)	0.02 (0.06)	0.04 (0.07)	0.02 (0.04)
	ARGOS	0.87 (0.15)	0.09 (0.12)	0.04 (0.09)	0.00 (0.01)
<i>Carcharhinus galapagensis</i>	PSAT	0.79 (0.23)	0.08 (0.12)	0.10 (0.11)	0.03 (0.06)
	ARGOS	0.84 (0.21)	0.11 (0.12)	0.04 (0.08)	0.01 (0.04)
<i>Carcharhinus limbatus</i>	ARGOS	0.92 (0.08)	0.04 (0.06)	0.04 (0.06)	0.00 (0.01)
<i>Alopias vulpinus</i>	PSAT	0.99 (0.04)	0.01 (0.04)	0.00 (0.00)	–
<i>Alopias pelagicus</i>	PSAT	0.78 (0.20)	0.16 (0.18)	0.06 (0.07)	–
<i>Odontaspis ferox</i>	PSAT	0.70 (0.30)	0.07 (0.08)	0.18 (0.24)	0.05 (0.09)
<i>Carcharhinus brachyurus</i>	PSAT	0.44 (0.51)	0.24 (0.35)	0.28 (0.48)	0.03 (0.06)
<i>Carcharhinus obscurus</i>	PSAT	1.00 (0.00)	–	–	–
	ARGOS	0.60 (0.00)	0.20 (0.00)	0.07 (0.00)	0.13 (0.00)
<i>Notorynchus cepedianus</i>	PSAT	0.38 (0.06)	0.54 (0.18)	0.04 (0.06)	0.04 (0.06)
<i>Isurus paucus</i>	PSAT	0.44 (0.00)	0.44 (0.00)	0.11 (0.00)	–
<i>Sphyrna zygaena</i>	ARGOS	1.00 (0.00)	–	–	–
<i>Carcharhinus plumbeus</i>	ARGOS	0.89 (0.00)	0.11 (0.00)	–	–

Supplementary Table 16. Mean daily movement distances of the most frequently tagged species across all oceans.

	Mean daily movement distance (km)	S.D.	Upper 95% confidence interval	N tracks
<i>Prionace glauca</i>	33.19	20.28	39.91	280
<i>Isurus</i> spp.	37.57	28.80	56.71	262
<i>Galeocerdo cuvier</i>	28.25	33.14	65.25	254
<i>Lamna ditropis</i>	41.17	36.31	71.68	172
<i>Rhincodon typus</i>	24.28	26.83	52.99	164
<i>Carcharodon carcharias</i>	30.94	39.10	77.22	160
<i>Carcharhinus longimanus</i>	26.04	26.59	52.73	105
<i>Carcharhinus falciformis</i>	11.16	15.07	30.28	51
<i>Carcharhinus leucas</i>	4.29	10.03	20.26	41
<i>Sphyrna</i> spp.	17.67	23.27	46.47	66

Supplementary Table 17. The number and total hours fished by flag state of the AIS longline fleets analysed in this study and arranged by the largest twenty values (totals for 2012 – 2016). In (a) total the number of unique Maritime Mobile Safety Identity (MMSI) codes per flag state present in the dataset in 2012 – 2016. In (b), the total longline hours fished is the total during 2012 – 2016.

(a)

Flag state	No. unique MMSI codes	% total
China	2,646	47.55
Taiwan	791	14.21
Japan	460	8.27
Korea	248	4.46
Spain	227	4.08
USA	187	3.36
Portugal	67	1.20
Canada	65	1.17
Vanuatu	63	1.13
Fiji	46	0.83
Australia	43	0.77
India	39	0.70
Russia	35	0.63
South Africa	33	0.59
Seychelles	28	0.50
Argentina	27	0.49
Greece	22	0.40
Italy	22	0.40
New Caledonia	21	0.38
France	20	0.36

(b)

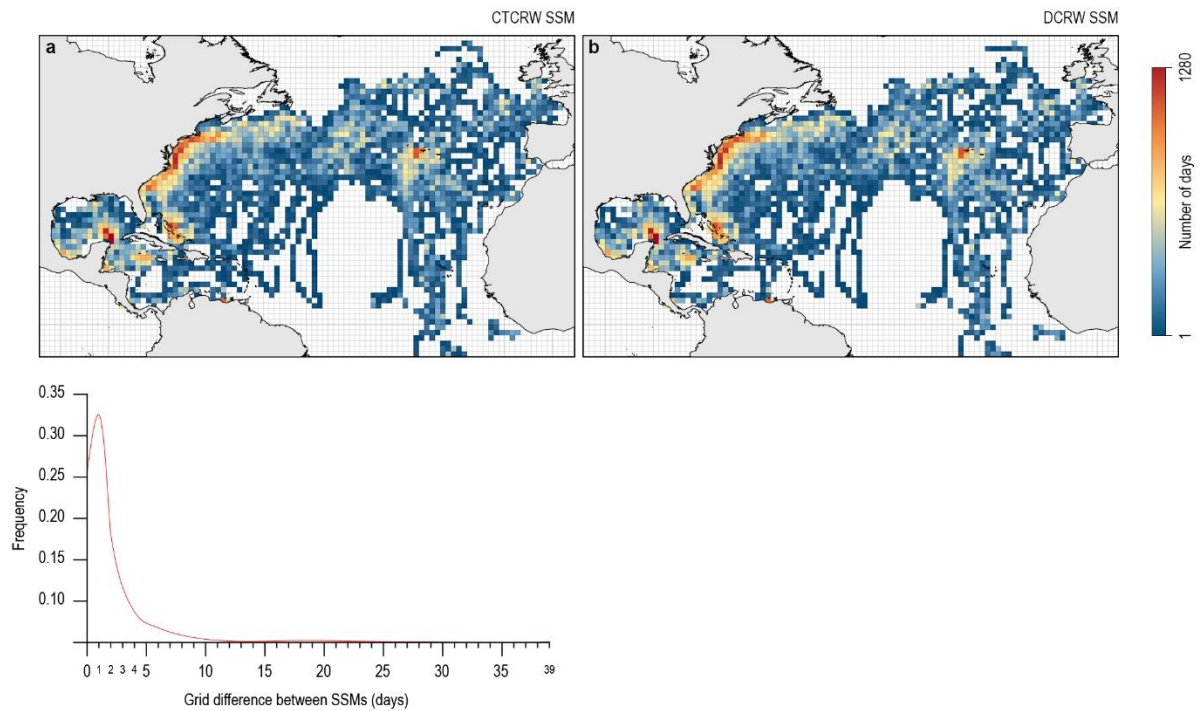
Flag state	Estimated total longline hours fished	% total
China	5,227,295	20.81
Taiwan	4,476,896	17.82
Korea	4,292,482	17.09
Japan	3,996,883	15.91
Spain	2,972,677	11.83
Portugal	630,843	2.51
Vanuatu	425,445	1.69
Fiji	284,558	1.13
USA	278,485	1.11
Australia	191,313	0.76
New Caledonia	187,137	0.74
Russia	168,067	0.67
Reunion Islands	164,682	0.66
Chile	164,423	0.65
Argentina	159,235	0.63
South Africa	157,890	0.63
Seychelles	135,016	0.54
France	129,678	0.52
Malaysia	104,742	0.42
Canada	86,943	0.35

Supplementary Table 18. Statistical differences between North Atlantic species risk exposure scores. Full statistical details given in Methods. Red cells represent the percentage between 75 and 100% and purple cells between 50 and 75% of significant tests (at $\alpha < 0.05$ level of significance) from 1000 tests in total, and white cells <50% of tests. Species codes are those given in Fig. 1.

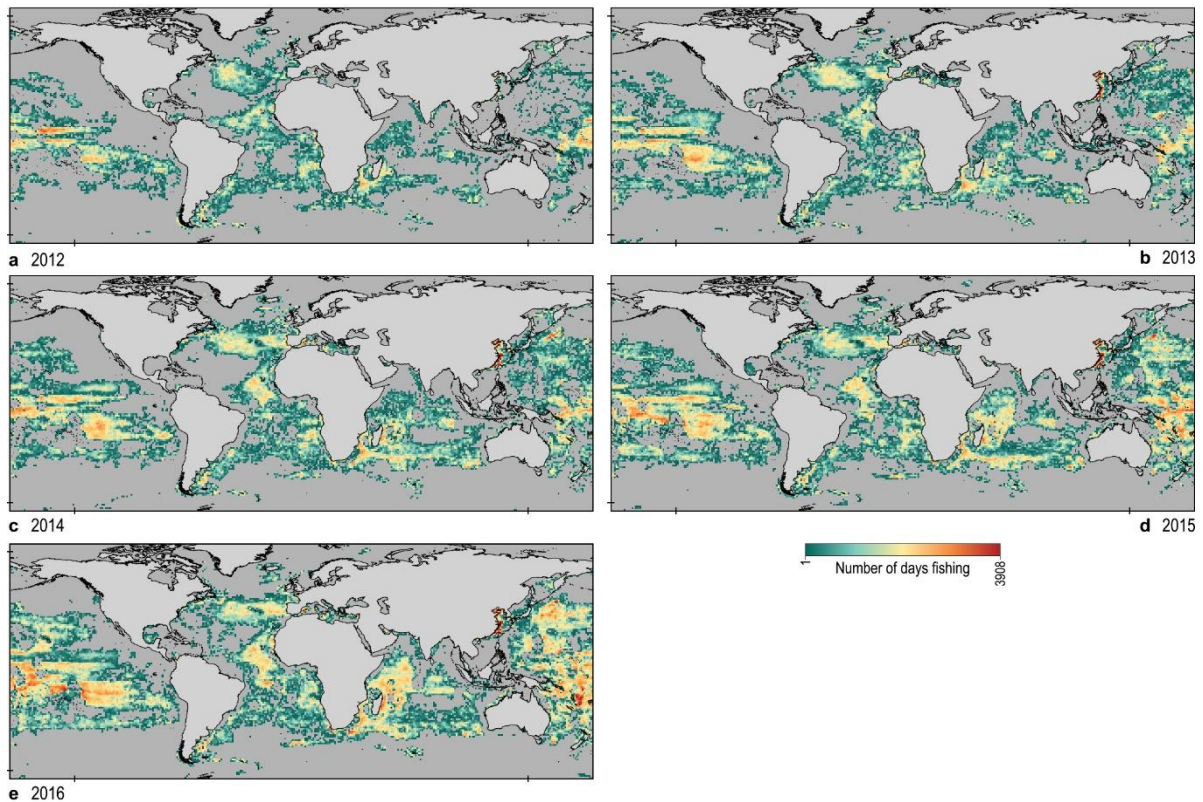
	PGL	CLE	IOX	CLO	LNA	SPH	GCU	CCA
PGL		100.0	7.8	100.0	1.4	100.0	100.0	44.4
CLE	100.0		100.0	1.7	100.0	2.8	78.3	100.0
IOX	7.8	100.0		100.0	11.1	99.9	99.4	10.3
CLO	100.0	1.7	100.0		100.0	-	26.0	100.0
LNA	1.4	100.0	11.1	100.0		100.0	100.0	3.0
SPH	100.0	2.8	99.9	-	100.0		6.7	100.0
GCU	100.0	78.3	99.4	26.0	100.0	6.7		99.8
CCA	44.4	100.0	10.3	100.0	3.0	100.0	99.8	

Supplementary Table 19. Statistical differences between Northeast Pacific species risk exposure scores. Full statistical details given in Methods. Red cells represent the percentage between 75 and 100% and purple cells between 50 and 75% of significant tests (at $\alpha < 0.05$ level of significance) from 1000 tests in total, and white cells <50% of tests. Species codes are those given in Fig. 1.

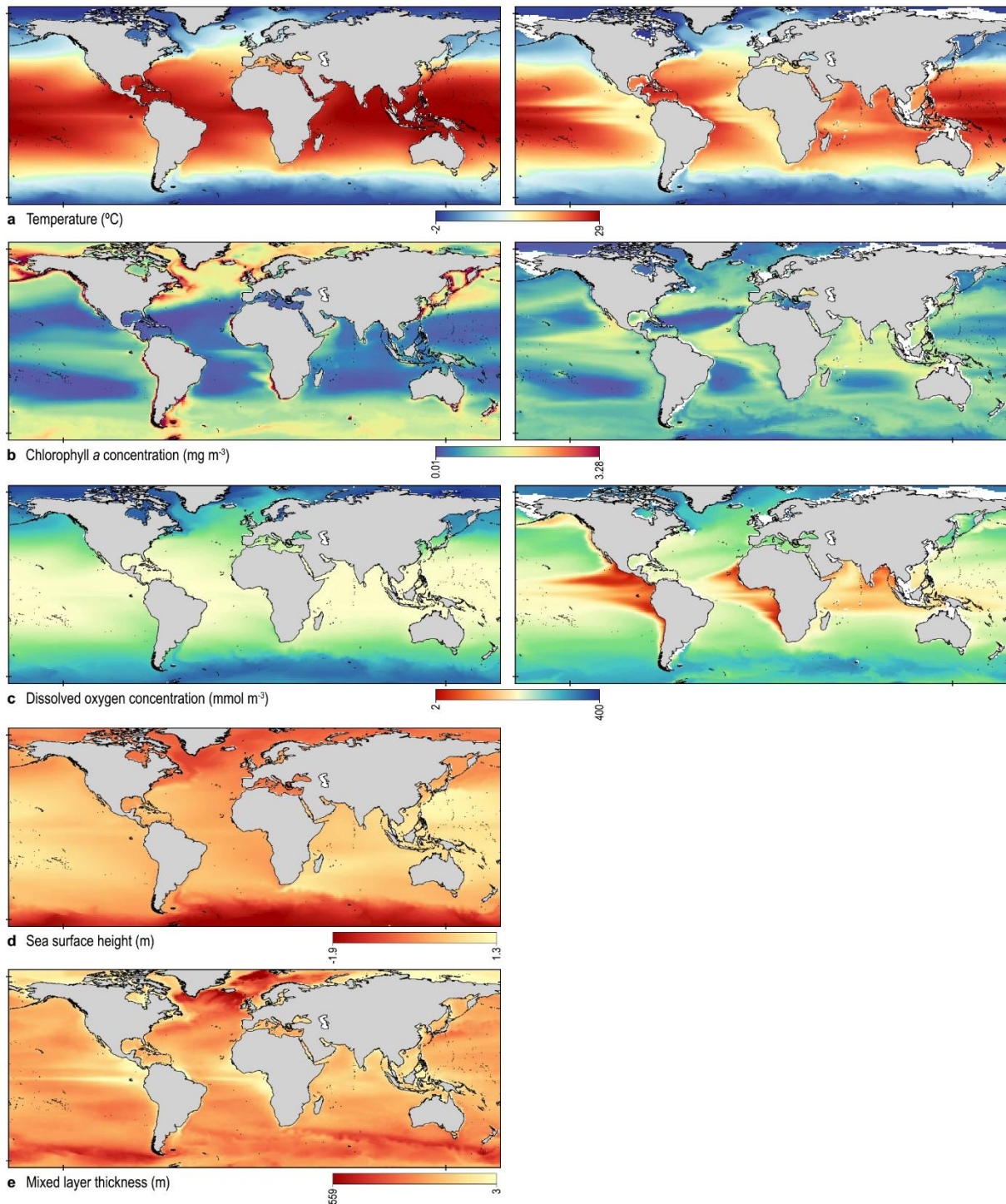
	PGL	IOX	LDI	RTY	CCA
PGL		13.7	38.3	60.9	40.8
IOX	13.7		90.9	96.6	12.8
LDI	38.3	90.9		13.1	99.6
RTY	60.9	96.6	13.1		100.0
CCA	40.8	12.8	99.6	100.0	



Supplementary Fig. 1. Gridded shark relative density maps for the same subset of ARGOS tracks filtered using different state-space models (SSMs). Relative density maps computed from locations estimated with the (a) CTCRW SSM and the (b) DCRW SSM. The plot (below the map panels) shows that the daily differences in gridded relative density were low.

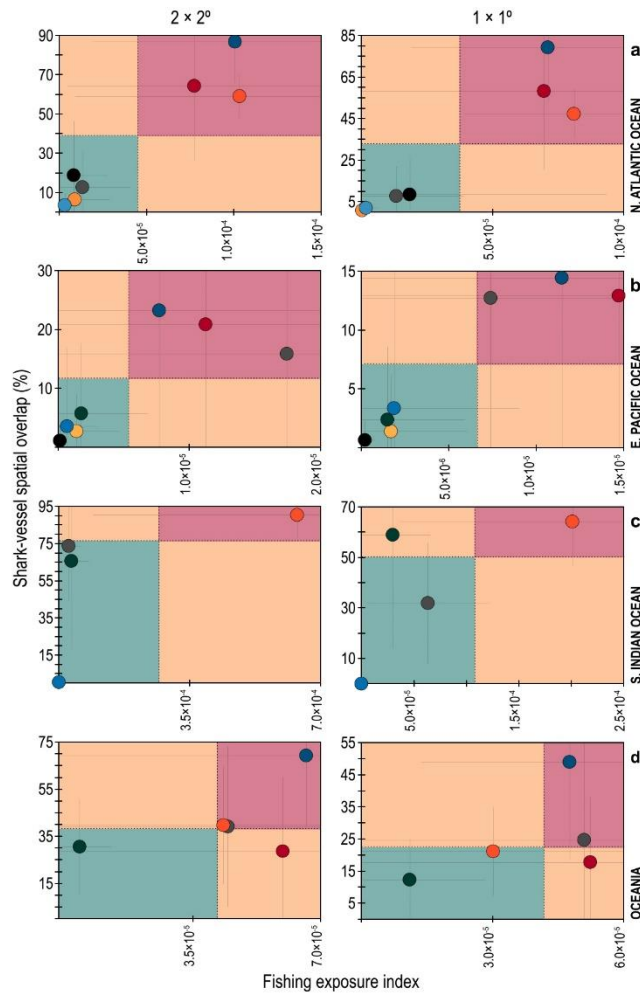


Supplementary Fig. 2. Annual spatial distribution of AIS longline fishing effort, 2012–2016. The global distribution of AIS monitored longline fishing effort varied across years as new AIS satellite receivers became operational which increases global coverage, from (a) 2012 to (e) 2016 (for details see ref. 19). However, we calculated the mean annual fishing effort distribution across the 5 year period since the global spatial extent was broadly similar between years but also overlapped temporally with more years for which we had shark track data (2002–2017). The maximum fishing effort value observed per grid cell showed no increasing trend through time (max. value: 2012 = 291 fishing effort days; 2013 = 2337 d; 2014 = 1860 d; 2015 = 1749 d; 2016 = 3908 d) indicating a mean value taken across the 5 years was conservative and unlikely to lead to overestimates of fishing effort sharks were exposed to in overlapped areas (see Methods).

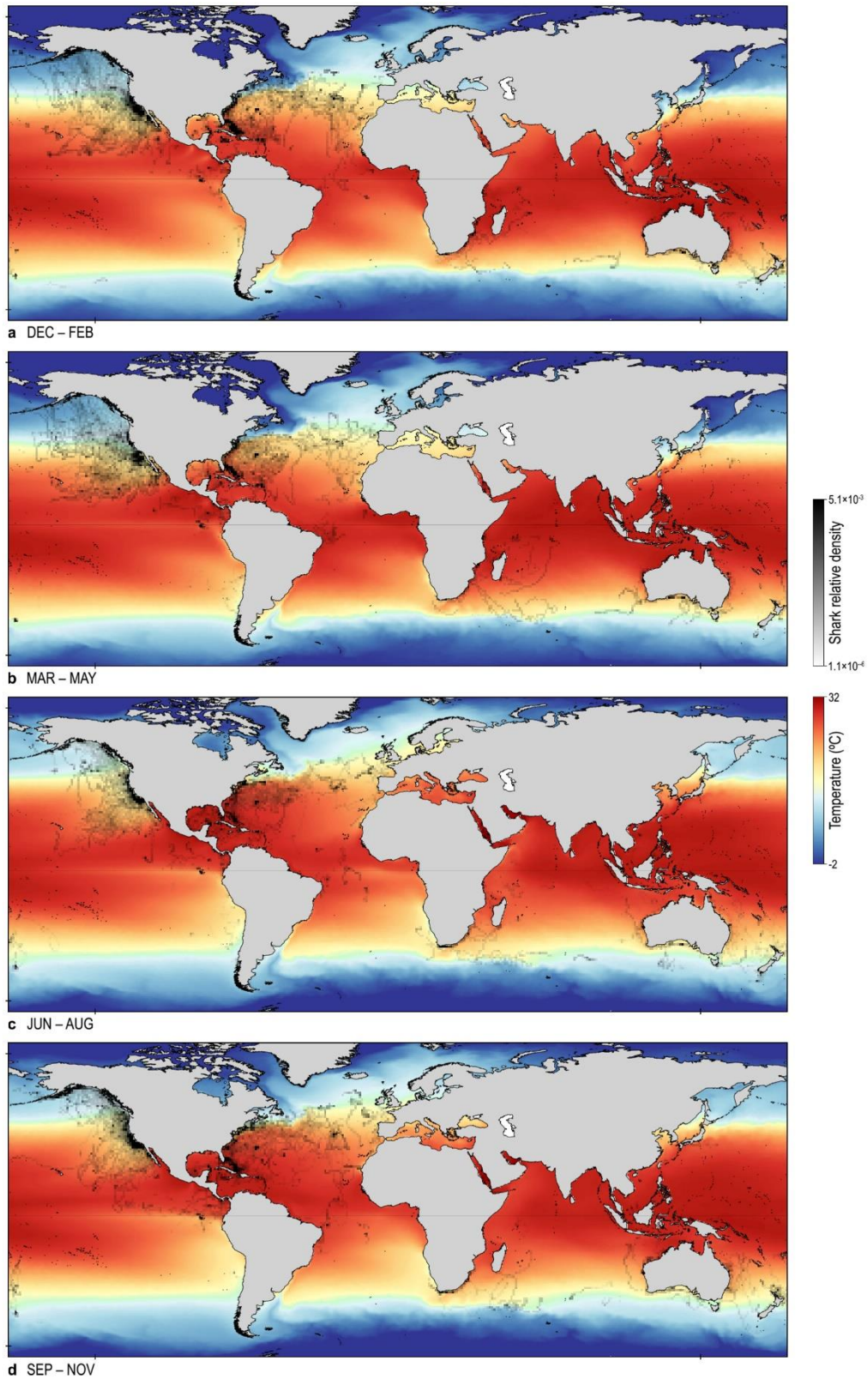


Supplementary Fig. 3. Example maps of environmental data used in shark and vessel habitat modelling. (a) sea water temperature ($^{\circ}\text{C}$) at surface (0 m; left panel) and 100 m depth (right panel) that was also used to calculate maximum gradient maps ($\Delta^{\circ}\text{C}/100 \text{ km}$). (b) mass concentration chlorophyll *a* concentration in sea water (mg m^{-3}) at surface (left) and 100 m (right). (c) mole concentration of dissolved molecular oxygen in sea water (mmol m^{-3}) at

surface (left) and 100 m (right). **(d)** sea surface height above geoid (SSH, in m) and **(e)** ocean mixed layer depth/thickness (MLD, in m).



Supplementary Fig. 4. Effect of grid cell size on risk exposure patterns of sharks to longline fisheries. (a) North Atlantic, (b) east Pacific, (c) southwest Indian oceans and (d) Oceania. Note that regardless of grid cell size at which the mean spatial overlap and mean FEI per species were calculated the species occurring in the highest (red) and the lowest risk zones (green) remain largely conserved, indicating a general pattern not dependent on the scale at which these data were analysed. Shark-species identification codes are given in Fig. 3 and Extended Data Fig. 4. Error bars are ± 1 S.D.



Supplementary Fig. 5. Seasonal distribution of pelagic shark relative density in relation to seasonal sea surface temperature. Seasonal shark relative density (a – d) (grey shading) and global seasonal sea surface temperature (SST, °C).

2. Supplementary Results and Discussion

Monitoring abundance and distributions of pelagic sharks across ocean basin scales is necessary to inform conservation measures in the high seas^{3,5,6,11,13,16}. Poor knowledge of where space use hotspots of wide-ranging sharks are located in relation to where fisheries are active can make fleet catch data (e.g. catch per unit effort, CPUE) collected by fishery management organisations very difficult to interpret accurately, particularly in the absence of significant fisheries observer coverage. Potentially, distributions resolved to fine spatial scales but extending globally will enable both exploitation hotspots and potential ‘refuges’ free from fishing to be identified for spatial management⁵. Presently, the distribution of pelagic shark space use is poorly defined globally and the extent of overlap with areas of fishing vessel activity has not been quantified across oceans. The available global maps of oceanic sharks assembled from historical fisheries capture data (e.g.⁴⁹) are not fine-scale enough spatially or temporally to inform conservation or management. Furthermore, they are unable to locate predator hotspots in areas where fisheries do not operate (since they are not fishery independent), even though such areas may be crucial to ongoing persistence of vulnerable populations. Fishery-independent shark distribution maps determined from satellite tracking individual sharks offer a valuable addition to scientific assessments but are presently under-utilised⁵⁰.

Fishery-independent shark distribution maps have been assembled for some regions of the North Atlantic⁵ and northeast Pacific oceans¹¹, however full analyses at the global scale are lacking. Improvements to shark management will require the spatial extent of overlap of sharks and fisheries to be quantified to identify where sharks are exposed to the greatest risk of capture by fisheries and where management needs to be prioritized. In this study, we provide the first high-resolution spatial mapping of oceanic pelagic sharks from satellite tracking individuals

globally, yielding a distribution map one hundred times more spatially resolved than previous attempts.

2.1 Shark density distribution

The individual movements of pelagic sharks were typically extensive and showed consistent patterns across many species and between oceans. The general pattern for longer tracks (>9 months; $n = 324$) of larger species was of movements from shelf (or island) locations to oceanic habitats before return movements to shallower areas. For example, North Atlantic blue and tiger sharks, North Atlantic and southeast Indian Ocean shortfin mako, and northeast and southwest Pacific white sharks all showed round-trip movement patterns (Fig. 1).

The relative density of pelagic shark locations showed distribution limits in higher latitudes (60° N and 50° S) that were generally constrained for most species by habitats characterised by the seasonal position of the 12°C sea surface temperature (SST) isotherm (Figs. 2a, Supplementary Fig. 5). Thus, poleward seasonal shifts in distribution were observed, particularly in boreal summer (June – August). Exceptions to these latitudinal limits were movements of endothermic sharks into habitats having cooler surface waters ($< 12^{\circ}\text{C}$) during winter and spring for shortfin mako and white sharks in the North Atlantic, southern Indian and southwest Pacific oceans, and year-round for salmon sharks in the northeast Pacific (Figs. 1, 2a, Supplementary Fig. 5).

In the Atlantic the tracked movements of 16 species ($n = 656$ tracks) showed that the Gulf Stream supported multiple species (Fig. 1). Strikingly, the density distribution resembled a ring-like structure broadly mapping onto the north Atlantic gyre bounded by the Gulf Stream and North Atlantic Current to the north, the Canaries Current in the east and by the North Equatorial Current in the south (Fig. 2a; Extended Data Fig. 1). By contrast, few tracked sharks occupied the central and south-western North Atlantic area ($5\text{--}25^{\circ}$ N, $35\text{--}45^{\circ}$ W). The density

of shark locations across 16 species ($n = 585$ tracks) was high in the eastern Pacific in the California Current, North Equatorial and Equatorial Counter currents, while sharks in the southern Indian Ocean associated with the Agulhas Return Current north of the Antarctic Circumpolar Current (Fig. 2a, Extended Data Fig. 1). This indicates shark density distributions are linked with major ocean currents globally.

Interestingly the major global shark location density patterns we found were consistent with those reported⁴⁹ for oceanic shark species richness derived from fishery-dependent catch data available at a coarse scale ($10 \times 10^\circ$ grid cell size). In the coarser resolution study, shark catch data indicate that species richness in the North Atlantic is higher in the Gulf Stream, the Gulf Stream–Labrador Current convergence zone, west of the Azores and off West Africa. Furthermore, catch hotspots were evident in the California Current, the Agulhas Current, and off western and eastern Australia, implying these are areas where pelagic sharks aggregate (see Fig. 1i in ref. 49). This agrees well with the major shark density hotspots found in the current study but, understandably, did not resolve the fine-scale shark hotspots we were able to identify (Supplementary Table 6). This similarity between studies that use very different shark data and spatio-temporal scales suggests that many of the larger space use hotspots we estimated from satellite tracking data are broadly representative of relative habitat use inferred from coarse catch data, and thus probably reflect general patterns of population distributions.

Spatial overlap patterns of sharks and longline fishing effort between ocean regions were not driven by the numbers of tags deployed per region. There was no significant correlation between all species overlap and the numbers of tags deployed per ocean (Supplementary Table 10b-e) (Pearson's $r = -0.27$, $n = 4$, $p = 0.727$), and for individual species within ocean regions (N. Atlantic, $r = 0.31$, $n = 9$, $p = 0.415$; E. Pacific, $r = 0.17$, $n = 9$, $p = 0.656$; S. Indian Ocean, $r = -0.62$, $n = 6$, $p = 0.189$; Oceania, $r = 0.427$, $n = 6$, $p = 0.398$). For example, the North Atlantic and east Pacific had approximately similar numbers of tags deployed, yet the overlap

differed by 30%. This was a pattern repeated between the southwest Indian Ocean and Oceania, with ~150 tags deployed per ocean but a 14% difference in overlap.

2.2 AIS fishing vessel analysis

In the context of monitoring fishing activity, there are known disadvantages of using Automatic Identification System (AIS) data¹⁹⁻²³ compared to Vessel Monitoring System (VMS) data. Longer gaps in data coverage in space and time mean individual tracks are not always recorded entirely²² and many longline vessels do not have AIS at all or may not turn it on so positions are not revealed^{21,23}. There is also potential for misidentification of fishing activity by different gears¹⁹. However, VMS data are not widely available⁵ so the principal advantage of AIS is that it is a freely available global dataset of fishing activity (see www.globalfishingwatch.org) that provides a useful and valid starting point for investigating the overlap of shark space use by global fisheries.

The global distribution map of all vessels' fishing effort identifies several large-scale, high-use areas such as the western European Shelf in the northeast Atlantic, Mediterranean Sea, Patagonian Shelf off Argentina, Peru Current, the Equatorial Pacific region and off China (Extended Data Fig. 2). There were also areas where industrial fishing activity appeared sparse, for example the central and southwest North Atlantic, northeast Pacific, and northern Indian oceans.

For pelagic longlines, national fleets that target sharks for fins and meat (or as targeted bycatch) include China, Taiwan, Spain and Portugal^{5,12}, which comprise 67% of all AIS-tracked longlining vessels analysed in this study (Supplementary Table 17). Other large national fleets such as the U.S.A., Canada and Japan potentially take shark as unintentional bycatch¹⁵. Hence, two potential explanations for spatial overlap of sharks and fishing vessels include: (i) fishers track sharks (shark habitats) as target species for valuable fins and, for some species, meat, or

(ii) sharks occur in similar habitats as fishers because, for example, they have the same target prey (e.g. tunas, billfishes) or prey on the same species that targeted fish also feed upon (e.g. small-bodied schooling fish).

2.3 Shark and vessel habitat modelling

Model 1 received highest relative support ($wAIC = 1$) for all response variables, explaining ~36% of deviance of shark density, and ~30% and 16% of deviance of fishing effort of all vessels (all gear types) and of longlines, respectively (Supplementary Table 8). The estimated relationships between relative density of sharks and vessels' effort and all environmental variables in Model 1 are plotted in Extended Data Fig. 3. Overall, the results indicate that the relative densities of sharks were greater around ocean areas with specific surface (fronts, $\Delta T^{\circ}C$ of $\sim 1.0^{\circ}C/100$ km; and mesoscale eddy edges) and subsurface (thermocline, ~ 40 m) boundary conditions and moderate chlorophyll-*a* concentrations (~ 0.3 mmol m^{-3}), a proxy for primary productivity (Supplementary Table 8; Extended Data Fig. 3). A test using the log link function in the model for transformation of the response variable (as opposed to log transformation of the response variable) also resulted in model 1 being the highest ranked.

The results show significant relationships between the relative density of sharks and mixed layer depth thickness (MLD; indicating thermocline depth), sea surface temperature gradients (TGR) (indicating frontal boundaries), sea surface height (SSH) (indicating mesoscale eddies), surface chlorophyll-*a* concentration (CHL) (a proxy for primary productivity) and salinity at 100 m (SAL_100) depth. Shark relative density showed a strong relationship with MLD showing a slight peak around average values (represented by zero in the standardised estimates; 39.65 m). There was a strong positive relationship between shark relative density and surface TGR, increasing from an average value ($\Delta T^{\circ}C = 0.40^{\circ}C/100$ km \pm 0.96 S.D.) to a peak difference of $1.00^{\circ}C/100$ km, before decreasing with further increasing TGR values. There was

a significant relationship between shark density and SSH with a relative peak at -0.11 m, indicating increasing shark density was associated with areas between warm core (higher relative height, e.g. 0.3 m) and cold core eddies (lower relative height, e.g. -0.3 m). Strong relationships between shark relative density and surface CHL and SAL_100 were also significant, showing a general increase for low and higher CHL values with density peaking between the average (0.01 mg m^{-3}) and at higher values around 0.32 mmol m^{-3} , and a similar convex relationship with SAL (peaking at the average value, 35.2 psu). In addition, we found a significant interaction between the two smooth terms of MLD and TGR (Extended Data Fig. 3), which was expected given that strong temperature gradients (thermal fronts) and sharp vertical gradients at depth (thermocline) are linked features through, for example, surface (horizontal) front formation occurring due to outcropping of the thermocline at the surface^{51,52}. In the thermocline, and where it outcrops at the surface, CHL concentrations can be significantly higher⁵³, which in turn attracts secondary and tertiary consumers to frontal boundaries^{51,54}. For example, other marine megafauna including white sharks and leatherback turtles (*Dermochelys coriacea*) utilise mesoscale eddies during long distance movements presumably for foraging opportunities^{55,56}. The significant relationships we found demonstrate shark density was higher where associated with specific surface (fronts, $\Delta T^{\circ}\text{C}$ of $\sim 1.0^{\circ}\text{C}/100$ km; edges of mesoscale eddies) and subsurface boundary conditions (thermocline, ~ 40 m) that were also characterised by moderately high chlorophyll-*a* concentrations (0.32 mg m^{-3}).

For fishing effort, results were similar for both response variables, i.e. the same set of environmental covariates best explained distributions of longline fishing effort in addition to that of all fishing vessels (Supplementary Table 8; Extended Data Fig. 3). Estimated relationships from model 1 showed a peak at average values of MLD (around 44.77 m) for both response variables, but was broader for longline vessels only (between 26.6 – 62.8 m), before decreasing with increasing MLD depth, indicating that higher fishing effort was associated

with a similar MLD to that found for peak shark densities. Fishing effort for all vessels showed peaks at lower ($\Delta T^{\circ}\text{C} = 0.22^{\circ}\text{C}/100 \text{ km}$) and higher ($\Delta T^{\circ}\text{C} = 1.16^{\circ}\text{C}/100 \text{ km}$) TGR values followed by decreasing density with increasing gradient. For longline vessels only, the peak was observed at a $\Delta T^{\circ}\text{C}$ of $-0.01^{\circ}\text{C}/100 \text{ km}$ followed by a dip at mean values of TGR ($\Delta T^{\circ}\text{C} = 0.45^{\circ}\text{C}/100 \text{ km}$). Effort increased with CHL at the surface for both response variables and also with SAL for all fishing vessels, and peaked for SSH of -0.57 and -0.87 m followed by dips at 0.23 and 0.11 m for all fishing vessels and longline vessels only, respectively. The interaction between MLD and TGR was also significant, and mostly reflected the individual relationships with each of these smooth terms for each response variable (Extended Data Fig. 3; Supplementary Table 8). It is worth noting that the Q-Q plots highlighted departure from normality at very high values of the fishing effort response variable (e.g., all vessels' fishing effort ranged from 0 to 30,135 days, with an average of ~ 50 days, and 3rd quantile = 17.49). Tests removing all fishing effort above 100 days (i.e., keeping $\sim 90\%$ of the data) improved the Q-Q plots and still resulted in model 1 being the highest ranked. Other tests using other distributions (e.g., gamma with log link function) or the logged response variable with a Gaussian distribution and identity link also resulted in model 1 being the highest ranked.

Despite all $w\text{AIC}$ being for model 1 for both fishing effort response variables, the percentage of deviance explained by model 6 was also high ($\sim 25\%$ for all fishing vessels and $\sim 15\%$ for longline vessels), highlighting the importance of temperature and salinity at depth as well as of the interaction between these two terms. Collectively, the model results indicate fishing effort was higher where MLD was at $\sim 45 \text{ m}$ depth, with TGR up to a $\Delta T^{\circ}\text{C}$ of $\sim 1.2^{\circ}\text{C}/100 \text{ km}$ and with increasingly high CHL concentrations.

Longline fishing vessels are the principal gear type catching pelagic sharks¹⁵ so strong relationships between shark density and longline fishing effort were expected. Overall, we found the distribution density of 1,681 pelagic sharks (23 species) and fishing effort of pelagic

longline vessels at the global scale were best explained by the same model (of environmental covariates) within our model set. Generally, densities/effort were higher in habitats with specific surface and subsurface thermal structure and moderate to high CHL-a concentrations, suggesting sharks and longliners selected frontal habitats, including mesoscale eddies, with enhanced associated productivity. However, the best ranked model explained less of the variance observed for longline fishing effort (~16% DE) than for sharks (~36% DE) (Supplementary Table 8). We suggest that this was the case because sharks interact with three-dimensional ocean habitats by direct sensing of multiple environmental factors (covariates) to select preferred areas required at certain times (e.g. for feeding, mating). Conversely, the lower deviance explained for fishing vessels may reflect an indirect relationship with following productive habitat occupied by sharks and other target megafauna (tunas, billfishes) through incomplete fisher knowledge and with intermittent sampling of only a few environmental covariates. It seems probable that fishers base decisions about where to go at the large scale on prior knowledge about where to find large fish at particular times (e.g. west of the Azores in summer). When in those general areas, they may then rely more on environmental information at local scales (e.g. sampling SST using thermometers, and/or using remote-sensing satellite images of SST and SSH)^{5,57} that may indicate appropriate habitats likely to be occupied by sharks and other target species. Equally, the lower %DE for longline fishing effort compared to sharks could also be due to several fishing fleets not targeting pelagic sharks directly but directing effort to catching other high value species (tunas, billfishes)⁵⁸ which may only have a partial overlap with the shark species we tracked. Nevertheless, the results indicate that overall AIS longline fishing effort appears to ‘track’ pelagic shark habitats reasonably effectively.

2.4 Spatial overlap of sharks and longline fishing effort

There were large regions of oceans where no or very few sharks were satellite tracked despite high longline fishing activity, for example the Patagonian Shelf and in the northwest and southeast Pacific Ocean, causing a bias in the estimation of shark hotspot areas (Fig. 2c). The northwest Pacific Ocean supports major global fishing-effort hotspots off China and Japan, yet there were very limited shark tracking data in this region. This suggests that either sharks are already in low abundance such that tagging studies are less viable, or, more likely, that tracking data exists but cannot be accessed. This study highlights an urgent need for fishery-independent shark occurrence data, such as from tracking, to underpin spatial risk assessments in global fishing hotspots.

We found some large-scale areas with low overlap between tracked shark space use and fishing effort, e.g. the central and south-western North Atlantic (Fig. 2a, b; Extended Data Fig. 2). Similarly, the high seas in the northeast Pacific, the South Australian Basin, and some waters between Australia and New Zealand supported space use by sharks but sparse AIS fishing vessel activity. Although it is possible longliners and purse seiners were present but not using AIS, low fishing activity also occurred in many of the territorial waters around oceanic islands in the Atlantic, Indian Ocean and Pacific (Fig. 2b), indicating these zones, some of which are marine protected areas (MPAs), may offer some refuge to sharks from AIS-monitored fishing vessels. For example, the shark hotspot in the south-western North Atlantic centred in the Caribbean showed very low overlap with AIS vessels, possibly due to the presence of a large MPA (Bahamas) that prohibits pelagic longline fishing or due to fewer vessels there using AIS. It is noteworthy that some sharks travelled long distances from the tagging sites to move into MPAs. For example, white and silky sharks tagged in the southwestern Indian Ocean off southern Africa travelled several thousand km to move into the Chagos MPA, one of the largest

no fishing zones in the world, highlighting how MPAs can provide a sanctuary for sharks travelling from heavily fished areas (Extended Data Figs. 6, 7).

Decreasing the grid cell size in spatial analyses can lead to concomitant decreases in percentage spatial overlap estimates^{19,20,47}, potentially affecting the species risk exposure patterns we found. To test this possibility, we re-calculated the shark-fishing effort spatial overlap and fishing exposure index (FEI) globally and separately for each ocean area, using a major subset of tracks comprising locations estimated from SSMs fitted to ARGOS observations that, for example, are spatially accurate to 2.2 – 5.5 km (ref. 48) ($n=1,066$ tracks; 63% of total tracks), enabling shark space use to be examined at finer grid cell sizes (Methods). We confirmed that the mean monthly global shark-longline overlap of 29.7% at $2 \times 2^\circ$ grid size for this subset of tracks decreased to 5.0% overlap at $0.10 \times 0.10^\circ$, with similar decreases observed for species mean FEI, as expected, with this trend present for each ocean area (see Methods; Supplementary Table 9). Despite these grid-cell-size induced changes in mean overlap and FEI, the patterns of species occurrence within the high or low risk zones remained largely unchanged regardless of the spatial scale at which they were observed (Extended Data Fig. 4). This indicates that our results quantifying mean monthly risk of capture of shark species by longline fishing are generally applicable at any spatial scale we tested.

Another potential limitation in our analysis was that sharks were tracked in 2002–2017 whereas AIS data were only available for 2012–2016, a mismatch that could lead to unrepresentative patterns of shark risk of exposure to longline fishing. To examine this, we found firstly that broad distributions of shark space use were similar across years (Extended Data Fig. 8), indicating persistence in shark space use patterns over the 16 year period we tracked them. Second, we calculated the mean monthly spatial overlap and FEI for sharks tracked only in 2012–2016, thus matching the years of AIS data used. Results show that the risk patterns of species in 2012–2016 were very similar to those tracked in 2002–2017 (compare Extended

Data Fig. 9 with Fig. 3; Supplementary Fig. 4) with no high-risk species shifting to the lowest risk zone. This indicates that the species patterns of risk of capture from longline fishing effort were not due to temporal differences in the data collection periods compared.

2.5 Exposure risk significance testing

The significance testing was undertaken to determine whether mean spatial overlap plotted against mean FEI differed among species that we calculated to be within different risk exposure zones (coloured quadrants shown in Fig. 3; Methods). We calculated an overall shark risk exposure score as the product of shark-fishing effort spatial overlap (%) and FEI for each individual shark. There were sufficient pelagic shark track data from the North Atlantic and eastern Pacific to undertake significance testing of species differences.

For the North Atlantic we found significant difference between species (>75% of 1000 random tests each attaining significance at the α 5% level; $p < 0.05$) and used post-hoc tests to identify where differences lay (Supplementary Table 18). In terms of overall risk for the most data-rich species of North Atlantic sharks, we found that all three species in the highest risk zone (red zone; Fig. 3a), namely blue, porbeagle and shortfin mako sharks, as well as white shark in the moderate risk zone (higher than average all-species overlap, slightly lower than average all-species FEI), were all significantly different from the species having lower than average overlap-FEI scores (bull, oceanic whitetip, *Sphyrna* spp. and tiger sharks) (Fig. 3a; Supplementary Table 18). In the northeast Pacific, similar results were found for the species risk scores, with white and shortfin mako sharks in the highest risk zone showing higher exposure to fishing than salmon and whale sharks (Supplementary Table 19). Blue shark occurred within the highest risk zone and was different to whale shark but not to salmon shark (blue and salmon sharks were different in only 38% of tests). Collectively, the tests indicated that North Atlantic and east Pacific shark species falling within the higher capture risk zone

(red, Fig. 3a,b), with only one exception (E. Pacific blue shark), had mean overlap-FEI values that were significantly different from species in the lowest risk zone (green, Fig. 3a,b).

Clearly, the risk of exposure of sharks to fishing indicated by our mean overlap-FEI plots only link pelagic shark space use to activity patterns of industrial longline fishing vessels reporting location via AIS, rather than the many smaller vessels not using AIS that operate in coastal and/or shelf habitats where many of the sharks tracked here also occur (Supplementary Table 1). Therefore, the estimates provided in this study are likely to be underestimated in terms of absolute overlap with full fishing effort that is actually occurring across shark population ranges.

2.6 Conservation and management implications

2.6.1 Blue shark

In this study we estimated that the blue shark was potentially exposed to higher than average overlap and fishing effort in North Atlantic space use areas (Fig. 3a), principally from longline fishers but also by purse seiners in the eastern North Atlantic off Africa (Fig. 2; Extended Data Fig. 2c, d). It is noteworthy that of the most frequently tracked species in this study, blue sharks have the highest exposure to longline in all the major space use hotspots we identified with fishery-independent tracking data in the North Atlantic (Figs 1, 3a; Extended Data Fig. 6a).

The blue shark is likely the world's widest ranging chondrichthyan and is the most frequently caught large shark in pelagic fisheries¹⁵. It is commercially valuable for its fins⁵⁹ and also for meat within Europe, with European longlining fleets such as Spain and Portugal having high blue shark retention rates with few discards. Analysis of the Hong Kong fin trade shows blue sharks to be the highest species component²⁵, which reflects the high spatial overlap of fishing effort found for this species in our study. Blue sharks are managed within the Exclusive Economic Zones (EEZ) of Canada, Mexico, New Zealand (a catch quota, albeit higher than

actual catches) and by the USA in the Atlantic and Gulf of Mexico (Supplementary Table 2). However, despite blue shark being classified in the IUCN Red List as Near Threatened both globally and in European waters – and with a decreasing population trend proposed in Europe – there is little or no species-specific management in place in International waters (areas beyond national jurisdictions; the ‘high seas’) (Supplementary Table 2). Whilst the North Atlantic stock was not considered overfished in the last stock assessment, there were sufficient uncertainties in data inputs and model assumptions that it could not be ruled out that the stock was overfished and overfishing was occurring¹⁸. Hence, an International Commission for the Conservation of Atlantic Tunas (ICCAT) recommendation of 2016 coming into effect in 2017 established a catch limit warning (threshold) in the North Atlantic set at 39,102 tonnes (t) (the average of two consecutive years). However, it was noted that the 2016 catch was 42,117 t (ref. 18). The absence of strict catch controls for blue shark may be problematic in the light of our study. Given our results showing major North Atlantic blue shark space use hotspots are nearly entirely overlapped by industrial longline fishing with high attendant fishing effort across their North Atlantic range, and fishing effort remains high in absolute terms throughout the year (Fig. 4a), suggests that overexploitation of key hotspots may already be occurring.

Similarly, overlap of east and southwest Pacific blue sharks was above average but overall fishing effort they were exposed to in overlapped areas was low, with sparse AIS longline and purse seine fisheries in off-shelf waters (Fig. 2, 3b,d; Extended Data Figs. 2, 6; Supplementary Table 10c). In the southwest Indian Ocean the overlap-FEI values for blue sharks were found to be near the lowest risk zone, with moderate overall spatial overlap with longline fisheries (~40%) but at lower than average effort level (Fig. 3c). Results indicate that blue shark space-use areas and hotspots are probably less exploited in these regions than in the North Atlantic.

2.6.2 Shortfin mako shark

Shortfin mako are IUCN Red Listed as Endangered globally (as of 2019) with a decreasing population trend and a high commercial value for its meat and fins. This species is managed within the EEZs of Australia, Canada, Chile, New Zealand and the U.S.A., and from 2018 within the EEZs of European Union nations and Atlantic International waters through ICCAT (Supplementary Table 2). In this study North Atlantic shortfin mako space use hotspots in the Gulf Stream (including its western approaches) and where it converges with the Labrador Current, as well as the upwelling zone off west Africa showed higher than average overlap with industrial fishing vessels together with high fishing effort (Fig. 3a). Our results suggest current fishing exploitation covers key large-scale habitats of shortfin mako across its North Atlantic range that complements other recent analyses indicating overfishing.

North Atlantic shortfin mako were stock assessed in 2017 as overfished and experiencing overfishing¹⁷ with an ICCAT recommendation coming into effect in 2018 for mandatory release if caught (brought alongside a vessel) alive⁶⁰. Potentially, this recommendation, if adhered to, could result in about 1,800 t of mako being released alive and likely to survive⁶¹. However, this measure alone will not allow stock rebuilding since it will still result in catches about three times greater than proposed as a maximum annual quota⁶¹. Indeed, models suggest that if the catch is reduced to zero (prohibition) the probability of stock rebuilding by 2040 was still only 54% (refs. 17, 18). Our results add spatial context to this level of exploitation by showing that major space use hotspots across its North Atlantic range may be fully exploited in those habitats where it remains, increasing the potential for overexploitation and population collapse. The findings here argue that there is an urgent need for spatial conservation measures in the high seas in addition to catch controls to conserve this population.

The fishing overlap and effort on shortfin mako space use appears less extensive in the eastern Pacific, southern Indian Ocean and for the Oceania region compared to the North Atlantic (Fig.

3b-d). The management in place for this species in the EEZs of Australia, Chile, New Zealand and the U.S.A., for example, may be sufficient to reduce landings in those areas. However, in this study there were fewer tracks of shortfin mako in the southeast and southwest Pacific and southern Indian oceans (Fig. 1; Extended Data Fig. 6b), which will contribute to reducing the potential for fully assessing spatial overlap with fishing vessels (hence the effort sharks are exposed to) in those regions. More detailed identifications of shortfin mako space use in key areas where data were entirely missing in this study, such as the South Atlantic, western and central Pacific and Indian oceans, will help to improve the coverage and accuracy of global estimates of shark overlap with fishing effort.

High fishing effort focused on extensive shark hotspots of commercially valuable species causes particular concern. Blue shark and shortfin mako have high commercial value for fins (and meat from mako) and make up 90% of all large pelagic sharks caught in pelagic fisheries⁶². Despite this, there is limited high seas management for both species^{5,16,18,62}. The results indicate a high probability of overexploitation of blue and shortfin mako sharks, particularly in the North Atlantic, because high-seas space use hotspots are almost entirely overlapped across their ranges (Extended Data Fig. 6), a pattern recently supported by the 2017 shortfin mako stock assessment demonstrating they are overfished and experiencing overfishing in the North Atlantic¹⁷.

2.6.3 Atlantic oceanic whitetip sharks

Oceanic whitetip sharks are IUCN Red Listed as Critically Endangered in the northwest and western central Atlantic and catch retention of this species is prohibited in the Atlantic due to dramatic declines having occurred over the last few decades¹³ (Supplementary Table 2). As such, oceanic whitetip sharks might be expected to be subject to high overlap and effort. However, our analysis indicates tracked space use was not subject to high overlap and effort (Fig. 3a) despite movements being spatially extensive⁶³ (Extended Data Fig. 7). The Caribbean

area of the south-western North Atlantic where we tracked them may be one of the few ocean refuges left for this species in the North Atlantic. In this region they may remain relatively abundant locally because shark protection measures in the spatially extensive Bahamas EEZ, where tracked sharks spent most time, have been in place since 1990 (ref. 63) and industrial fishing activity in that area is comparatively low, which accounts for the low overlap and effort we observed. The low effort in the region could also be explained by the areas being exploited by small vessel fleets operating from islands not being equipped with AIS. Furthermore, the heterogeneous habitats present in the Caribbean may make them problematic to fish by large industrial longline and purse seine vessels.

2.6.4 Western North Atlantic porbeagle and white sharks

Space use of porbeagle and white sharks determined by satellite tracking that is fishery-independent showed both species to have hotspots in the Gulf Stream ecosystem (Extended Data Figs. 6, 7). There was high overlap and effort co-occurring with porbeagle and white shark space use, with porbeagle within the high risk zone of the overlap-FEI plot (Fig. 3a) and white shark with slightly below average FEI. This predicts catches should also be high or moderate in this ocean region. However, porbeagle and white sharks are IUCN Red Listed as globally Endangered and Vulnerable respectively, and are both CITES Appendix II listed (Supplementary Table 2). Furthermore, the white shark is protected within the EEZs of the U.S.A. and Canada, while management plans for porbeagle are in place in Canada and U.S. waters (Supplementary Table 2), which encompass a significant portion of the Gulf Stream ecosystem where they occur. If the high levels of fishing activity and area coverage we observed were similarly distributed in the past then such persistent patterns of shark and fishing effort co-occurrence could explain the historical overfishing for these species, where sharp declines in catches have been observed^{16,18,26}. Our results demonstrate that the potential for incidental capture by pelagic longlines remains high where there is high overlap with high

fishing effort in the Gulf Stream and adjacent shelf habitats (western approaches). This may be one reason why white shark abundance appears to have been slow to rebuild in U.S. waters despite catch prohibition (no commercial or recreational harvest) since 1997 (ref. 26). Our results showing high fishing overlap and high or moderate FEI for these species highlight the need for continued catch controls in this region to continue rebuilding stocks, which for porbeagle is estimated to take several more decades even if fishing mortality is zero¹⁸.

2.6.5 Southwest Pacific porbeagle sharks

Porbeagle sharks in the southwest Pacific off New Zealand were also identified in our analysis as having relatively high spatial overlap with longline vessels and exposed to higher than average fishing effort in those space use areas (Fig. 3d; Extended Data Fig. 7). This result seems at odds with recent fisheries studies in the region. These studies all support a lower exposure risk than estimated here on the basis of recent catch per unit effort (CPUE) and other indicator analyses studies in New Zealand waters⁶⁴, a large decline in fishing effort over the last 30 years⁶⁵, and a quantitative risk assessment of the Southern Hemisphere porbeagle population⁶⁶. These other studies present a more optimistic population status than several years ago with the potential for a stable or increasing population size.

Whereas the biologically distinct porbeagle of the North Atlantic has been the subject of a directed pelagic longline fishery as well as bycatch from bottom trawls and gillnets, in the south Pacific catches are made primarily as bycatch from tuna longline vessels⁶⁷. Porbeagle off New Zealand are taken as bycatch by drifting pelagic longlines but also by trawlers (bottom and midwater) and bottom longliners⁶⁸. They have been managed in New Zealand waters with catch quotas since 2004 given the uncertainty in stock status at that time and the observed rapid declines in CPUE in the early 2000s (ref. 68). Furthermore, shark finning was banned in New Zealand in 2014 resulting in porbeagle catch by longliners being discarded⁶⁵. Although there is high mortality of porbeagle from longliners due to the discarding, with nearly 40% of

individuals hauled in dead⁶⁹, the proportion being released alive and potentially surviving has increased⁶⁵. Importantly, the study by Hoyle *et al.*⁶⁵ demonstrated that porbeagle biomass was high south of New Zealand and south of where most pelagic fishing occurs throughout the Southern Hemisphere, indicating the likelihood of a spatial refuge for porbeagles there. Mature females are rarely caught in their fished range⁷⁰ which suggests the spatial refuge may be important for pregnant sharks in particular. Given these data, an explanation for the relatively high exposure risk we found was likely due to the space use estimated from tracked sharks' movements being less extensive than the species geographic range. Nevertheless, methods of bycatch mitigation for porbeagle should be put in place to protect the population given the high mortality from discarding.

2.6.6 Pacific and Indian Ocean white sharks

There was higher than average fishing overlap and exposure to longline fishing effort (FEI) across white shark distribution in the northeast Pacific and southwest Pacific (Oceania region). This was principally from longline vessels and to a lesser extent purse seiners (Fig. 2; Extended Data Figs. 2, 6e), that indicated higher risk of capture than most other tracked sharks in the region (red zone, Fig. 3b inset CCA and d). Similarly, white shark space use in the southwest Indian Ocean was subject to higher than average overlap (>60%) in addition to higher than average fishing effort they were exposed to in those areas (Fig. 3c, inset CCA). Space use hotspots occurring in shelf and open ocean areas for white sharks in all three regions overlap significantly with longline fishing vessels (Fig. 3b-d).

Protection measures for white sharks are in place within Australia, Europe, New Zealand, South Africa and U.S.A. EEZs (Supplementary Table 2). For high seas areas where white sharks occur, the high overlap and exposure to longline fishing effort that we observed raises concern about the potential for high incidental bycatch of white sharks from longliners. However, in the southwest and northeast Pacific and perhaps elsewhere, captures by the

oceanic fleets of tuna longliners, purse seiners and trawlers are relatively low. For example, records from observers on New Zealand surface longline vessels show only three white sharks reported in the last 30 years⁷¹. Although observer coverage of the fleets was variable (low in the early years, higher for the foreign/chartered vessels in recent years, but low for domestic vessels recently), the relative capture rate of white sharks compared to other species was extremely low, suggesting high-seas longline bycatch of white sharks in this region, and perhaps others, was rare. In contrast, white sharks are taken in set net, line and trawl net fisheries throughout much of the New Zealand's Territorial Sea and EEZ^{72,73}. Reported and observed captures in trawl fisheries are comparable to those in set net fisheries⁷⁴, and while some of the small inshore vessels do not use AIS, all of the deep water fleet does. Reported captures of white sharks in trawls are more common in the deep water fleet, and mainly occur south of the Chatham Rise (on the Campbell Plateau, sub-Antarctic waters of the EEZ), but also in the other deep water fisheries (e.g. west coast of South Island and the Chatham Rise). These studies confirm that although we found high spatial overlap of higher than average effort with white shark space use in the southwest and northeast Pacific, it seems that actual fishing mortality due to high seas longline effort may be low. However, this may not be the case in other regions such as the southwest Indian Ocean where overlap is high in absolute terms (>60 %) and covers much of the white shark distribution in this region. The actual fishing mortality due to other gear types (e.g. set nets, bottom longlines) in shelf habitats of all three regions suggests the continued need for high observer coverage on vessels to enable reporting of white shark incidental bycatch, which could potentially increase if stocks rebuild from currently low population levels^{26,75} and sharks become more abundant. Our maps showing where the highest overlap and effort with fisheries occurs (Fig. 3; Extended Data Fig. 6e) could be useful to determine where bycatch may most likely occur and where limited observers could be deployed.

2.6.7 Salmon shark

The salmon shark is an endothermic species with a North Pacific distribution, which migrates annually between cold temperate and subtropical waters⁷⁶ (Supplementary Table 1). We found that salmon sharks have space use patterns with lower than average overlap with industrial longline fisheries (~1.5%) and low fishing effort in overlap areas (Fig. 3b) suggesting very low susceptibility to capture by this gear. It was evident that the highest overlap with fisheries was in shelf waters of Alaska and Canada where other gears are primarily used, including purse seines and bottom trawls (Extended Data Fig. 2). This species is IUCN Red Listed as Least Concern with a stable population level (Supplementary Table 2). Targeted shark fishing prohibitions have been in place in Alaska state waters since 1997 indicating that fishing-induced mortality of this epi- and mesopelagic predator is probably low there, which presumably contributes to conserving this population in key space use areas of the northeast Pacific⁷⁷.

2.6.8 Whale shark

We found spatial overlap and exposure to fishing effort from industrial fisheries in whale shark space use hotspots to be in the lowest risk zones in the Atlantic, Indian and east Pacific oceans when averaged across all species (Figs. 1, 3; Extended Data Fig. 2) suggesting that unintentional capture by industrial pelagic fisheries, e.g. purse seiners⁷⁸ may be concomitantly low. Only in the east Pacific region was spatial overlap with purse seines higher than average (>50th percentile of fishing exposure index). Generally, pelagic baited longlines present little risk to whale sharks from direct capture due to them being planktivorous, however there is potential for entanglement with gear. Nonetheless, we found the overlap of whale sharks with pelagic longlines was low relative to other species, and with exposure to lower than average fishing effort in whale shark space use areas. Among whale shark hotspots the region with highest exposure risk to longlines was the southwest Indian Ocean (Extended Data Fig. 6d),

whereas in Oceania the overlap and exposure to fishing were both low (Fig. 3d) despite there being whale shark space use hotspots off northwest Australia and in the Philippines (Extended Data Fig. 6d).

AIS is not used by small coastal vessels which are known to make illegal catches of whale shark⁷⁸ even though it is an internationally protected species (Supplementary Table 2). The whale shark is a species capable of connecting intra- and inter-ocean centres of abundance on roughly 5-year timescales^{10,78}. Therefore, to assess more accurately the global capture rate of whale shark in fisheries will require broad-scale data on coastal vessel movements in the waters of nations where whale sharks are found (e.g. Indonesia, Ecuador).

2.6.9 Tiger shark

In this study, tiger sharks were satellite tracked in the North and South Atlantic, Indian and Pacific Oceans (Fig. 1d). Coastal and shelf movements were more common in the southwest Indian Ocean and Oceania region whereas Atlantic and eastern Pacific tiger sharks undertook movements into the open-ocean in addition to shelf or island orientated behaviour⁹. We found that in the North Atlantic and east Pacific Ocean, spatial overlap and effort from longline fisheries were both low (8 and 13% respectively) (Supplementary Table 10b,c), whereas in the southwest Indian Ocean and in Oceania spatial overlap was higher (32 and 28% respectively). Although the fishing effort tiger sharks were exposed to was below average in the southwest Indian Ocean (Fig. 3c), this species was in the highest risk zone Oceania, principally due to overlap with longline fishing vessels in shelf habitats off northwest and northeast Australia (Fig. 3d; Extended Data Fig. 6c).

The tiger shark is a large neritic/oceanic pelagic shark that has low commercial importance in pelagic fisheries. The FAO global landings database records just 78 t in 2014, however this species, like most large pelagic sharks, is also subject to illegal, unreported and unregulated

(IUU) fisheries⁷⁹. In 2009, tiger shark was assessed as Near Threatened in the IUCN Red List, albeit with an unknown population trend (Supplementary Table 2). In the Oceania region, the higher than average spatial overlap with higher longline fishing effort (FEI) we found indicates the potential for incidental capture by vessels that operate in shelf habitats there (Extended Data Figs. 2, 6c). There are no species-specific management measures in place for this species in this region (Supplementary Table 2) but tiger sharks are protected in Australian Commonwealth Marine Reserves and coastal barrier reef marine protected areas (MPAs) in adjacent areas such as the Coral Sea^{79,80}. Clearly though, the large scale movements they make away from relatively small protected areas expose them to the fisheries that we have shown overlap their monthly space use in Oceania by 28% (Fig. 3d). Therefore, it is possible that incidental bycatch and IUU catches, the latter potentially north of Australia⁷⁹ where we identify a tiger shark space-use hotspot (Fig. 3d, inset GCU), could be higher than recorded at present. Equally, the high overlap of tiger sharks with longlining vessels in the southwest Indian Ocean and with purse seine vessels in the eastern tropical Pacific may have similar potential impacts (Extended Data Figs. 2, 6c).

In the North Atlantic, by contrast, tiger shark space use was estimated to have low spatial overlap (~8%) and relatively low exposure to fishing effort from longline fisheries (Fig. 3a). This pattern was due to tracked tiger sharks spending much of the spring, summer and autumn months in oceanic regions of the western North Atlantic where AIS fishing vessels were sparse, except at the northerly limit of their boreal summer migration into the Gulf Stream^{9,81} (Fig. 3a; Extended Data Figs. 3, 4 and 6). At this northerly extent (~40°N), tiger sharks co-occur with space use hotspots of both blue and shortfin mako sharks that are heavily exploited there (Fig. 3a; Extended Data Figs. 6a-c). This indicates the potential for incidental bycatch of tiger sharks in major high seas fishing areas of the North Atlantic where this species is not subject to management.

In contrast, tiger sharks in the U.S. Atlantic and Gulf of Mexico EEZ this species in managed under the U.S. Fisheries Management Program (Supplementary Table 2). The marine reserves of The Bahamas, British Virgin Islands and Saba probably also protect tiger sharks during winter months, where tracked individuals are known to spend the winter⁸¹. Our results suggest exposure risk of tiger sharks to fisheries may be generally lower than other large sharks in the western North Atlantic.

2.6.10 Tag Recaptures

Overall, 65 of 1,681 tracked sharks were known to have been caught by fisheries in our study (3.9%). This fishery-induced mortality was highly variable by ocean and species (Fig. 2c; Extended Data Table 5). Shark mortality was highest in the North Atlantic (6.5%) and southwest Indian (3.5%) oceans and lowest in the eastern Pacific (2.1%) and Oceania (1.3%).

The shortfin mako – IUCN Red Listed as Endangered globally – was the most frequently caught species over the study’s duration (16.7% across all oceans) and reaching a fishery return rate of 19.3% (23 of 119 tracked) in the North Atlantic based upon movements that spanned the entire North Atlantic range of *I. oxyrinchus* (Figs. 1c, 3a). To our knowledge, this is the highest recapture rate observed for shortfin mako, or of any oceanic shark species, in an ocean-basin scale study^{27,28}. A recent study in the Western North Atlantic, that forms a subset of the data here, recorded a recapture rate of 30% (12 of 40 shortfin makos tracked), indicating that the tag return rate was higher in the western North Atlantic than across the rest of the North Atlantic range of *I. oxyrinchus* studied. Nevertheless, previous studies using conventional (number) tags to mark >100 shortfin makos, as in the present study, have reported tag return rates of between 1.9 and 10.9% (ref. 27). Our results suggest tag return rates that can be used to calculate annual fishing mortality (F) for assessments of the entire North Atlantic shortfin mako stock are likely to be underestimated^{18,28}. Given this, the level of exploitation shortfin

makos are exposed to is likely to be greater than currently recorded, necessitating urgent management action to set specific catch limits¹⁸ that will act to rebuild the population⁶¹.

2.7 Future perspectives

The patterns of high overlap and exposure to fishing effort observed for some sharks but not others suggest different mechanisms driving shark fishing hotspots. The high overlap and fishing effort observed in commercially important shark hotspots, together with high catches (landings), support the explanation that fishers may track sharks. For example, North Atlantic blue and shortfin mako sharks are known target species of Chinese, Spanish and Portuguese longlining fleets^{5,12,15} (Extended Data Table 2). However, this is not necessarily the case for all global hotspots. Internationally protected species such as the white shark were subject to high mean overlap and FEI in the North Atlantic, southwest Indian, and northeast and southwest Pacific oceans despite no target fisheries. This indicates that high overlap is due to sharks co-occurring in habitats of target fish species (e.g. tunas) that fishers track^{5,6,82}.

High fishing effort that is focused on extensive shark hotspots of commercially valuable species raises particular concern. There is limited high seas management for commercial species, including blue and shortfin mako sharks^{5,16}. The results from shark and AIS vessel tracking indicate the distinct possibility that commercial species are exposed to unsustainable levels of exploitation across vast areas. For these species, hotspots of space use in the high seas are exposed to high fisheries overlap across their ranges for significant periods of a year. Internationally protected species within some national jurisdictions and on the high seas overlapped longline fisheries by up to 64%, emphasising the continued need for management measures that minimise bycatch of the most threatened species.

Strict controls on catches of commercially important pelagic sharks through limits such as quotas can contribute to protecting populations^{16,61}. However, scientific stock assessments have

not been undertaken for the majority of pelagic sharks because of a paucity of good quality, long-term data resolved to the species level. The combination of poor record-keeping, lack of species-specific data reporting or deliberate underreporting of catches by open-ocean fishing fleets and/or nations contributes to the difficulties of assessing the population status of many commercially important species^{12,15,16,23,62}. Therefore, despite being exploited as targeted or incidental bycatch due to high prices for meat and fins, the measures in place to control fisheries for most pelagic shark species are relatively weak compared to teleost fishes¹⁶. It is possible that populations of some species will decline further before sufficient data can be collected to support scientific assessments on which to base catch limits. Examples include the oceanic whitetip shark that was CITES Appendix II listed in 2013 leading to catch prohibitions in some oceans (e.g. Atlantic Ocean) after observations of dramatic declines documented in key regions of their range, e.g. western North Atlantic¹³, some 10 years earlier. We show here that vast ocean areas used regularly by wide-ranging sharks are significantly overlapped by industrial fisheries, and that fishery-induced mortality indicated from tag recaptures appears high for key commercial species (e.g. ~20% for North Atlantic shortfin mako). This suggests large-scale, no-take marine reserves may have an important role to play in controlling high seas exploitation of pelagic sharks in the absence of catch controls for the majority of species.

The space use hotspots of pelagic sharks identified here could provide a foundation from which to consider high-seas marine reserves for sharks. Conservation efforts could be directed to prioritize areas where pelagic sharks are potentially subject to both high overlap and effort from longline and purse seine fisheries. However, this would likely result in low compliance as it would act to exclude some fishers that primarily target other species (tunas and billfishes)^{5,6,82}. Time-area closures of shark space use hotspots in the months of highest estimated susceptibility may be feasible if there is low overlap of shark hotspots with those of other target species. Recent studies have demonstrated from satellite-monitoring of vessels that well enforced,

large-scale Marine Protected Areas (MPA) set up around oceanic islands can very effectively lead to a cessation of fishing activity in those areas²¹. This technology could also play a crucial role in helping to enforce no-take zones, at least for those vessels carrying AIS transmitters. Moreover, new advances in satellite telemetry⁸³, including further miniaturisation of transmitters and new satellite-borne receivers⁸⁴⁻⁸⁷, may lead to cheaper tags and greater location frequency of individual tag positions (more locations per day) enabling monitoring of many thousands of individual marine animals and fishing vessels simultaneously in near-real time. This prospect would transform how high commercial/conservation value animals are spatially managed in our oceans, unlocking the potential for dynamic ocean spatial management that is proposed to increase the efficacy of fisheries management^{88,89}.

Although the spatial resolution of our pelagic shark density distribution is a hundred times greater than for previous global maps for oceanic sharks⁴⁹, there remain substantial gaps in ocean regions where no or very few sharks have apparently been satellite tracked, despite high fishing activity, e.g. the Patagonian Shelf and northwest and southeast Pacific. Therefore, a more accurate estimate of spatial overlap will be determined when fishery-independent assessment of pelagic shark space use in these vast ecoregions is undertaken or when existing data are made available.

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5. Supplementary Author Contributions

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Designed study: N.Q., N.E. Humphries, D.W.S.

Drafted paper: D.W.S.

Contributed to draft paper: N.Q., N.E. Humphries, A.M.M.S.

Contributed to subsequent drafts: All authors

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Compiled raw data: N.Q., N.E. Humphries, A.C., M.V., I.C., M.T., D.W.S., F.J.A., K.A., A.S.A., D.A., A.B., N.P.A.B., A.V.B., B.A.B., R.B., R.W.B., C.D.B., M.E.B., A.B.C., R.D., J.E.M.C., M.D., F.Ferretti, J.D.F., M.P.F., M. Heard, A.R.H., B.J.H., L.A.H., C.H., D.T.I., R.J., L.K.B.J., S.J.J., W.J., A.A.K., F.O.L., J.S.E.L., B.C.L.M., M.A.M., E.R.N., J.G.P., A.J.R., P.J.R., C.A.R., D.R.L.R., G. Shillinger, S.S., G.B.S., M. Soria, K.M.S., M.T.T., A.T., J.P.T., F.V., J.J.V., B.M.W., T.D.W. and P.M.Z.

Analyzed data: N.Q., N.E. Humphries, A.C., M.V., I.C., A.M.M.S., L.L.S., S.J.S., D.W.S., F.B.J., D.A.-M., P.B., D.B., S.B.L., A.V.B., B.A.B., C.D.B., B.D.B., S.E.C., A.B.C., L.D., R.D., D.D.C., F. Ferretti, J.D.F., M.F., A.R.H., B.J.H., L.A.H., L.K.B.J., S.J.J., F.L., J.S.E.L., H.M., T.A.P., C.P.-P., J.G.P., L.M.Q., A.J.R., P.J.R., D.R.L.R., G.B.S., M. Soria, K.M.S., M.T.T., J.P.T., F.V., S.B.W., B.M.W., T.D.W. and P.M.Z.

Contributed tools: N.Q., N.E. Humphries, A.M.M.S., A.M.S., M.G.M., M.T., X.I., V.M.E., C.M.D., D.W.S., D.B., C.D.B., B.A.B., L.D., M.J.G., N.H., L.A.H., L.K.B.J., S.J.J., M. Sheaves, M. Shivji, J.D.S., P.T., S.B.W and B.M.W.

6. Details of ethical compliance and approvals

All animal handling and tagging procedures were completed by trained personnel under permissions granted by ethical review bodies and complied with all relevant ethical regulations in the jurisdictions in which they were performed.

Specifically, tagging procedures were approved by the Marine Biological Association of the UK (MBA) Animal Welfare Ethical Review Body (AWERB) and licensed by the UK Home Office through Personal and Project Licences under the Animals (Scientific Procedures) Act 1986 (**D.W.S., N.Q.**).

Tagging was performed according to national Portuguese laws for the use of vertebrates in research, and the work and tagging protocol approved by the Azorean Directorate of Sea Affairs of the Azores Autonomous region (SRAM 20.23.02/Of.5322/2009), which oversees and issues permits for scientific activities (**P.A.**).

Tagging procedures for all sharks in TOPP were approved by Stanford University Institutional Animal Care and Use Committee (IACUC), NOAA, and California Department of Fish and Wildlife in accordance with permissions granted to B.A. Block (**B.A.B.**).

In New South Wales (NSW) samples were collected under NSW DPI Animal Care and Ethics Committee permit number 12/07-CSIRO and NSW DPI Scientific Collection Permit P07/0099- 6.0 (and their precursors). In South Australia (SA) samples were collected under SA Department of Environment, Water and Natural Resources Scientific collection permit U26255-4, Marine Parks. Permit to Undertake Scientific Research MR00025-1, and Ministerial Exemption ME9902940 (including all precursors). An overarching Animal Ethics Permit was granted by the Tasmanian Department of Primary Industries, Parks, Water and Environment (AEC 22/2015-16), along with an authority to possess biological material from a listed species under the Living Marine Resources Management Act 1995 (permit 17109, and

all precursors) and a Permit to Take Threatened Fauna for Scientific Purposes (permit TFA 17150, and all precursors) (**R.W.B.**).

Tagging procedures were approved by Fisheries and Oceans Canada following the guidelines of the Canadian Council on Animal Care (**S.E.C.**).

Tagging procedures were approved by the Environment departments of Southern and Northern provinces of New Caledonia (**E.G.C.**).

Tiger shark tagging in 2015 at Ningaloo Reef was carried out under permit numbers: 2563 (WA Department of Fisheries), SF010311 (Department of Biodiversity, Conservation and Attractions), and in accordance with approved guidelines by Animal Ethics Committees from the University of Western Australia (RA/3/100/1209). Tiger shark tagging in 2007-2010 at Ningaloo Reef was conducted under permit number DPIW 7/2007-0 and 8SF6104 (Department of Biodiversity, Conservation and Attractions), 2007-30-32 (WA Department of Fisheries), and animal ethics approvals A07035 (Charles Darwin University Ethics Committee). (**L.C.F., M.G.M., M.T.**)

Tagging procedures were conducted by researchers with accredited training for animal experimentation from the Ecole Nationale Vétérinaire de Nantes, France (**J.D.F.**).

Tagging procedures were in accordance with the ethical standards and fish tagging protocols of the New Zealand National Institute of Water and Atmospheric Research (**M.P.F.**).

Permit (no: MAF/LIA/22) to conduct scientific marine animal research was supplied by the Department of Marine Resources, Bahamas. Research was conducted in Florida State waters under FWC Special Activity License 16-0397SRP and in United States Federal waters under NMFS Highly Migratory Species Exempted Fishing Permit SHK- EFP-16-05 and FSU IACUC Protocol 1411 (**T.L.G.**).

Whale shark tagging procedures were approved by the Smithsonian Tropical Research Institute Animal Care and Use Committee (IACUC) and the government of Panama provided the research permits (**H.M.G.**).

This work was conducted under permits from the National Marine Fisheries Service Highly Migratory Species Division, Florida Keys National Marine Sanctuary, Florida Fish and Wildlife, Bahamas Department of Marine Resources, Biscayne and Everglades National Parks, and the University of Miami Institutional Animal Care and Use Committee (IACUC) (**N.H.**).

Tagging procedures were approved by Universidade Federal Rural de Pernambuco, Institutional Ethics and Animal Care and Use Committee (**F.H.V.H.**).

Tagging procedures were approved by the University of California, Davis Institutional Animal Care and Use Committee (IACUC) (#16022) and by the Galapagos National Park Directorate (**A.R.H.**).

All procedures were approved by the University of Queensland Animal Ethics Committee (CMS/300/08/DPI/SEAWORLD and CMS/326/11/DPI), the Department of Primary Industries and Fisheries (permit numbers 100541, 165491 and 56095) and the Department of Environment and Resource Management (permit numbers QS2009/GS001, QS2010/MAN26 and QS2010/GS059) (**B.J.H.**).

Tagging procedures were approved by Mote Marine Laboratory's Institutional Animal Care and Use Committee (IACUC) (**R.E.H.**).

Tagging procedures were approved by the University of Windsor Animal Care Committee (ACC) in accordance with the Canadian Council on Animal Care (**N.E. Hussey**).

Tagging was conducted under the Flinders University Animal Welfare Ethics Permit E349 and E360 and authorised by the Victorian Department of Primary Industries under the General Research Permit RP 1048 (**C.H.**).

Tagging methods were fully reviewed and approved by the ZSL ethical review committee **(D.M.P.J.)**.

The animal handling and tagging methods were performed in accordance with the approved guidelines of London University and the University of Plymouth, UK **(J.S.E.L.)**.

Animal tagging and handling procedures were approved by the Ascension Island Government under consideration of the Wildlife Protection Ordinance, 2013 **(A.J.R.)**.

Tagging procedures were undertaken under SARDI/PIRSA Ministerial exemptions (Section 115; 9902094, and S59; 9902064), DEWNR Permit U25570 and Flinders University Animal Welfare Committee approval (Project 309) **(P.J.R.)**.

All methods used were approved by the University of Tasmania Animal Ethics Committee (Approval No. A0011590) **(J.M.S.)**.

The research was performed in accordance with the Stanford University Protocol for the Care and Use of Laboratory Animals **(G. Shillinger)**.

Tagging procedures were approved by the Nova Southeastern University Institutional Animal Care and Use Committee (IACUC) (# 064-398-15-0203) **(M. Shivji, B.M.W.)**.

Tagging procedures were approved by the Woods Hole Oceanographic Institution and University of Massachusetts Institutional Animal Care and Use Committees (IACUC) **(G.K.S.)**.

Tagging procedures were approved by the University of Cape Town, Rhodes University, Port Elizabeth Museum and the Department of Environmental Affairs Animal Care and Ethics committees **(M.J.S.)**.

Tagging procedures were approved by the Institutional Animal Care and Use Committee of the CYROI (Cyclotron Réunion Océan Indien, n° 114) reliant on the University and the University health center of Reunion Island (**M. Soria**).

All work was carried out under permits number SF006870, CE002833 and CE003171 from the Western Australia Department of Parks and Wildlife and ethics approval from the Animal Ethics Committee of the University of Adelaide, South Australia (Animal ethics committee project no: S-2009–109) (**M.T., M.G.M.**).

Tagging procedures were approved under a Research Fishing Permit provided by the Undersecretary of Fishing and Aquaculture in Chile. (**P.M.Z.**).