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et al

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1 **Global spatial risk assessment of sharks under the** 2 **footprint of fisheries**

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205 **Industrialised fishing of the high seas (areas beyond national jurisdiction) is a major**
206 **source of mortality to marine megafauna¹⁻³. Effective management and conservation of**
207 **highly migratory species in the high seas depends on resolving overlap between animal**
208 **movements and distributions and fishing effort across far-reaching population ranges^{4,5}.**
209 **Yet, this information at a global scale is lacking^{1,5,6}. Here we show, based on a unique**
210 **big-data approach combining satellite-tracked movements of 1,681 pelagic sharks (23**
211 **species) and global fishing fleets, that 45% of space used by sharks in an average year**
212 **falls under the footprint of pelagic longline fisheries, the gear type catching most pelagic**
213 **sharks^{5,6}. Strikingly, monthly shark-longline overlap remained high at 40%, indicating**
214 **significant overlap in both space and time. Space use hotspots of commercially valuable**
215 **species had the highest overlap with longlines (80–94%) and were also associated with**
216 **significant increases in fishing effort and capture-induced shark mortality compared to**
217 **other species^{7,8}, either because fisheries directly target sharks or sharks occupy habitats**
218 **of targeted fish stocks. Protected species within some national jurisdictions and on the**
219 **high seas overlapped longline fisheries by >80%, emphasising the continued need for**
220 **management measures that minimise bycatch of the most threatened species. Only a few**
221 **large-scale hotspots of shark distribution occurred in areas generally free from**
222 **industrial fishing, with some typically associated with effective local management. We**
223 **conclude that pelagic sharks have limited spatial refuges from current levels of fishing**
224 **effort on the high seas. These results demonstrate an urgent need for conservation**
225 **measures at high-seas shark hotspots and highlight the potential of simultaneous**
226 **satellite surveillance of megafauna and fishers as a tool for near-real time, dynamic**
227 **management of marine megafauna.**

228 Humans have hunted large marine animals (marine megafauna) in open oceans for at least
229 42,000 years⁹, however only since the 1950s have the international fishing fleets that target

230 large, epipelagic fishes spread into the high seas¹⁰. Prior to this, highly mobile fishes
231 occupying this environment inhabited a spatial refuge largely free from exploitation, since
232 fishing mostly concentrated on continental shelves^{3,10}. Of the fishes occupying the high seas,
233 pelagic sharks' movements will likely have a strong impact on their vulnerability to fishing
234 pressure: they are among the widest-ranging of vertebrates, with some species exhibiting
235 annual ocean-basin-scale migrations¹¹, long term trans-ocean movements¹², and/or fine-scale
236 site fidelity to preferred shelf and open ocean areas^{5,11,13}. These species account for ~50% of
237 all identified shark catch worldwide in target fisheries or as bycatch¹⁴. Regional declines in
238 abundance of pelagic sharks have been reported^{15,16}, but it is unclear whether exposure to
239 high fishing effort extends across ocean-wide population ranges and overlaps areas in the
240 high seas where sharks are most abundant^{5,15}. Conservation of pelagic sharks – which
241 currently have limited high seas management^{14,17,18} – would benefit greatly from a clearer
242 understanding of the spatial relationships between sharks' preferred habitats and active
243 fishing zones. However, obtaining unbiased estimates of shark and fisher distributions is
244 complicated by the fact that most data on pelagic sharks comes from catch records and other
245 fisheries-dependent sources^{17,18}.

246 Here, we provide the first global estimate of the extent of space use overlap of marine
247 vertebrates with industrial fisheries. This is based on the analysis of the movements of
248 pelagic sharks tagged with satellite transmitters in the Atlantic, Indian and Pacific oceans,
249 together with fishing vessels monitored globally by the automatic identification system (AIS),
250 developed as a vessel safety and anti-collision system (see Methods). Our study focused on
251 23 species of large pelagic sharks (median maximum total body length = 3.7 m) that occupy
252 oceanic and/or neritic habitats spanning broad distributions from temperate to tropical waters
253 (Supplementary Table 1). All these species face some level of fishing pressure in coastal,
254 shelf and/or high-seas fisheries, with the International Union for the Conservation of Nature

255 (IUCN) Red List assessing 26% of the 23 species globally as having ‘near threatened’ status,
256 48% as ‘vulnerable’ and 17% ‘endangered’ (Supplementary Table 2). Regional fisheries
257 management organizations (RFMOs) are tasked with management of sharks in high seas
258 areas, yet little or no management is in place for the majority of species^{3,5,14-20}
259 (Supplementary Table 2).

260 From 2002–2017 we tagged 1,804 pelagic sharks with satellite transmitters, with 60% of
261 deployments occurring between 2010 and 2017 (Methods; Extended Data Fig. 1,
262 Supplementary Tables 3, 4). Eleven of the largest species/taxa groups accounted for 96% of
263 all tags deployed (blue *Prionace glauca*; shortfin mako *Isurus oxyrinchus*; tiger *Galeocerdo*
264 *cuvier*; salmon *Lamna ditropis*; whale *Rhincodon typus*; white *Carcharodon carcharias*;
265 oceanic whitetip *Carcharhinus longimanus*; porbeagle *Lamna nasus*; silky *Carcharhinus*
266 *falciformis*; bull *Carcharhinus leucas*; and hammerhead *Sphyrna* spp. sharks)
267 (Supplementary Table 3). Tracks with daily locations were reconstructed for 1,681
268 individuals totalling 281,724 tracking days (Methods).

269 Movement patterns indicated that multiple species aggregated within the same large-scale
270 areas within an ocean (Fig. 1). Species co-occurred in major oceanographic features, such as
271 the Gulf Stream (blue, shortfin mako, tiger, white and porbeagle sharks), the California
272 Current (blue, shortfin mako, white and salmon sharks), and in the East Australian Current
273 (blue, shortfin mako, tiger, white and porbeagle sharks) (Fig. 1, Extended Data Fig. 2;
274 Supplementary Results and Discussion 2.1). The global density map reveals distribution
275 patterns of pelagic sharks and locations of space use hotspots (defined here as those areas
276 with $\geq 75^{\text{th}}$ percentile of weighted daily location density). Implementation of a weighted
277 spatial density meant individual location estimates closer to a tagging location received a
278 lower weight than later locations because more sharks had locations earlier in their tracks¹³,
279 thus reducing bias (Fig. 2a) (see Methods). Major hotspots of tracked pelagic sharks in the

280 Atlantic Ocean were in the Gulf Stream and its western approaches, Caribbean Sea, Gulf of
281 Mexico and around oceanic islands such as the Azores (Fig. 2a). In the Indian Ocean,
282 hotspots were evident in the Agulhas Current, Mozambique Channel, the South Australian
283 Basin and northwest Australia, while Pacific hotspots were in the California Current,
284 Galapagos Islands, eastern Equatorial Counter Current, and around New Zealand
285 (Supplementary Table 5). Although tagging sites occurred as expected in some shark space
286 use hotspots – as tagging rates are inherently higher in hotspots – we also identified
287 numerous hotspots where no tagging sites occurred: in the North Atlantic (outer Gulf Stream,
288 Charlie Gibbs Fracture Zone, western European shelf edge and Bay of Biscay); Indian Ocean
289 (Somali Basin, Chagos Archipelago, South Australian Basin); and the Pacific (Alaska
290 Current, outer California Current, white shark ‘Café’ area¹³, North Equatorial Current,
291 northern East Pacific Rise, Isakov/Makarov Seamounts, Chatham Rise) (Extended Data Fig.
292 1).

293 To determine the extent to which shark space use hotspots fall under the footprint of global
294 industrialised fisheries we mapped the movements of fishing vessels carrying AIS
295 transmitters, estimated to be fitted on 50–75% of active vessels >24 m length²¹. In the context
296 of monitoring fishing activity, there are known disadvantages of using AIS data²² compared
297 to vessel monitoring system (VMS) data; for example, longer gaps in data coverage in space
298 and time²³ and the potential for misidentification of fishing activity by different gears²¹.
299 However, given that VMS data is not widely available, the principal advantage of AIS is as a
300 freely available global dataset of fishing activity that provides a useful and valid starting
301 point for investigating the overlap of shark space use by global fisheries. As a first step we
302 mapped the mean annual fishing effort (days) of 83,628 AIS-equipped fishing vessels using
303 various gear types²¹ during 2012–2016 (Extended Data Fig. 3; Methods). In addition to using
304 all fishing vessels within the dataset, the estimated global fishing effort of drifting pelagic

305 longline ($n = 5,565$) and purse seine vessels ($n = 6,941$) were mapped separately as these two
306 gears catch the majority of pelagic sharks^{14,17} (Fig. 2b; Extended Data Fig. 4).

307 The global distribution map of all vessels' fishing effort identifies several large-scale, high
308 use areas such as the western European Shelf in the northeast Atlantic, Mediterranean Sea,
309 Patagonian Shelf off Argentina, Peru Current, the Equatorial Pacific region and off China
310 (Extended Data Fig. 3, Supplementary Table 6). There were also areas where industrial
311 fishing activity appeared sparse, for example the central and southwest North Atlantic,
312 northeast Pacific, and northern Indian oceans. To explore the spatial heterogeneities of sharks
313 and vessels we used generalised additive models to determine how shark relative density and
314 fishing effort were affected by environmental covariates (see Methods; Supplementary Table
315 7). Distributions of pelagic shark density and fishing effort of all vessels, and for pelagic
316 longline vessels separately, were best explained by the same drivers, with all demonstrating
317 strong relationships with habitat types characterised by surface and subsurface temperature
318 gradients (fronts²⁴; thermoclines) and/or high primary productivity (Extended Data Table 1,
319 Extended Data Fig. 5). Relative densities of sharks were higher around ocean areas with
320 specific surface (fronts, $\sim 1.0^{\circ}\text{C}/100\text{ km}$; and mesoscale eddy edges) and subsurface
321 (thermocline, $\sim 40\text{ m}$) boundary conditions and moderate chlorophyll-*a* concentrations (~ 0.3
322 mmol m^{-3}), a proxy for primary productivity. The same set of environmental covariates best
323 explained distributions of shark densities and fishing effort of all vessels and of longlines
324 only (Supplementary Results and Discussion 2.2). This predicts high spatial overlap because
325 sharks are known to aggregate in biologically productive features like fronts to enhance
326 foraging opportunities^{5,6,24}, a behaviour that fishers exploit to increase their chances of
327 making higher catches of commercially valuable sharks and other epipelagic fishes^{5,6}. For
328 pelagic longliners, national fleets that target sharks for fins and meat (or as targeted bycatch)
329 include China, Taiwan, Spain and Portugal^{5,14}, which comprise 67% of all AIS-tracked

330 longlining vessels analysed in this study (Extended Data Table 2). Other large national fleets
331 such as the U.S.A., Canada and Japan potentially take shark as unintentional bycatch¹⁷.
332 Hence, two potential explanations for spatial overlap of sharks and fishing vessels include: (i)
333 fishers track sharks (shark habitats) as target species for valuable fins and, for some species,
334 meat, or (ii) sharks occur in similar habitats as fishers because, for example, they have the
335 same target prey (e.g. tunas, billfishes) or prey on the same species that targeted fish also feed
336 upon (e.g. small-bodied schooling fish).

337 To quantify the actual shark space use occupied by fishing vessels, as indicated by the
338 modelling, we calculated the mean spatial overlap of tracked sharks with fisheries for a mean
339 year within the datasets (Methods). Overlap was defined as shark and vessel spatial co-
340 occurrence within a $1 \times 1^\circ$ grid cell in an average year, where 1° latitude at the equator (110.6
341 km) matches the approximate length of high seas longlines, i.e. 100 km long with an average
342 of 1,200 baited hooks⁵. Globally, the distribution of industrial fishing activity of all vessels in
343 the dataset overlapped 81% of the space use of tracked sharks at the $1 \times 1^\circ$ scale (mean
344 overlap = $80.8\% \pm 29.9$ S.D.; median = 96.2%, $n = 1,681$ tracks). Decreasing grid cell size
345 can reduce percentage spatial overlap estimates²¹, however although we found the mean
346 overlap at $0.5 \times 0.5^\circ$ and $0.25 \times 0.25^\circ$ grid cell sizes decreased as expected, it remained
347 relatively high at 67 and 56%, respectively (Extended Data Table 3). However, there were
348 large regions of oceans where no or very few sharks were satellite tracked despite high
349 fishing activity, for example the Patagonian Shelf and in the northwest and southeast Pacific
350 Ocean (Extended Data Fig. 3). The northwest Pacific Ocean supports major global fishing-
351 effort hotspots off China and Japan, yet there were very limited shark tracking data in this
352 region. This suggests that either sharks are already in low abundance such that tagging
353 studies are less viable, or, more likely, that transmitters are not available or data cannot be

354 accessed. This study highlights an urgent need for fishery-independent shark occurrence data,
355 such as from tracking, to underpin spatial risk assessments in global fishing hotspots.

356 We focused our detailed analysis of shark overlap with that of longline fishing effort, as this
357 gear catches most pelagic sharks globally¹⁷ and since most AIS fishing vessel gear types
358 represented in the dataset do not target or bycatch sharks²¹. Where we were able to determine
359 shark space use directly using tags, coverage by fisheries was dominated by pelagic longline
360 gear (Fig. 2a, b). The mean spatial overlap between sharks and longline fishing effort was
361 45% (mean = 44.8% ± 41.4 S.D.; median = 33.7%) at the 1 × 1° grid size (Extended Data
362 Table 2), with the spatial pattern being very similar to that for sharks and all mapped AIS
363 fishing vessels (compare Fig. 2b with Extended Data Fig. 3a). Across four regions where the
364 majority of sharks were tracked, mean spatial overlap of all 11 most frequently tracked
365 species/taxa groups with longline fishing effort ranged from 24% (east Pacific; *n* = 585
366 tracks) to 55% (north Atlantic; *n* = 656 tracks) and 66% (Oceania: Australia, New Zealand,
367 southeast Asia; *n* = 151 tracks), up to 82% for the southwest Indian ocean (*n* = 114 tracks)
368 (Extended Data Table 4).

369 Hotspots of spatial overlap intensity (see Methods) of sharks and longlines were evident in
370 the Gulf Stream and stretching eastward to the Azores, western European shelf edge, west
371 African upwelling, California Current, east of the Galapagos, Agulhas Current, Seychelles
372 archipelago, the southern Great Barrier Reef, and New Zealand shelf waters (Fig. 2c,
373 Supplementary Table 8). Overlap intensity varied across species and among oceans,
374 reflecting the heterogeneous distributions of space use by sharks and longline fishing activity
375 (Extended Data Fig. 6). For example, spatial overlap of sharks and longline fishing effort,
376 averaged across all oceans, ranged from 92% for the porbeagle, down to 11% for the oceanic
377 whitetip shark. Among oceans, the overlap of space use by blue sharks – the pelagic shark

378 most commonly caught by open-ocean longline fleets¹⁷ – was 94% in the North Atlantic,
379 decreasing to 34% in the east Pacific.

380 An important question is whether significant areas of the high seas used by pelagic sharks
381 exist that are largely free from AIS-monitored fishing activity of longline and purse seine
382 vessels as these could be targeted for shark conservation measures. Identifying such areas can
383 only be addressed with the fishery-independent distributions presented here. We found some
384 large-scale areas with low overlap between shark space use and fishing effort, e.g. the central
385 and south-western North Atlantic (Fig. 2a, b; Extended Data Fig. 4). Similarly, the high seas
386 in the northeast Pacific, the South Australian Basin, and some waters between Australia and
387 New Zealand supported space use by sharks but sparse AIS fishing vessel activity. Although
388 it is possible longliners and purse seiners were present but not using AIS, low fishing activity
389 also occurred in many of the territorial waters around oceanic islands in the Atlantic, Indian
390 Ocean and Pacific (Fig. 2b), indicating these zones, some of which are marine protected areas
391 (MPAs), may offer some refuge to sharks from AIS-monitored fishing vessels. For example,
392 the Chagos Archipelago (Indian Ocean) was identified as a shark hotspot even though no
393 sharks were tagged there, with this archipelago lying within one of the world's largest MPAs
394 that has maintained a ban on commercial fishing since 2010. Furthermore, the shark hotspot
395 in the south-western North Atlantic centred in the Caribbean showed very low overlap with
396 AIS vessels, possibly due to the presence of a large MPA (Bahamas) that prohibits pelagic
397 longline fishing²⁵ or due to few vessels there using AIS. However, a general characteristic of
398 large areas with low longline fishing activity was also one of lower shark densities (<75th
399 percentile of relative density; Fig. 2a), indicating sharks were not remaining in these areas but
400 moving through them, potentially as part of foraging excursions or migrations for
401 reproduction^{11,13}. The lower relative density of sharks suggests lower productivity –
402 confirmed by our modelling results (model 1; Extended Data Fig. 5) – and consequently

403 poorer fishing opportunities, which may explain the low fishing effort. The results also show
404 that very few large hotspots of space use by pelagic sharks occurred in areas free from AIS
405 fishing vessels, particularly longline and purse seine gears (Fig. 2c; Extended Data Fig. 4).

406 To estimate the potential risk of exposure of sharks in different ocean regions to longline
407 fishing effort, we calculated the fishing effort individual sharks were subjected to on each
408 track day, standardised to account for variations in individual track durations (hereafter
409 termed fishing effort per shark space use) (see Methods). As expected across all oceans and
410 species, longline fishing effort per shark space use was highly variable (mean = 34.7 d \pm
411 125.4 S.D.; median = 8.7 d) (Extended Data Table 3). Given this, we tested whether the mean
412 annual longline fishing effort (2012–2016) overlap with mean annual shark space use
413 (2002–2017) was indicative of actual sharks captured and landed by fisheries. We compared
414 the mean annual longline fishing effort for North Atlantic shark species (the ocean for which
415 we had the most species and tracks) with Food and Agriculture Organization of the United
416 Nations (FAO) officially recorded mean annual North Atlantic landings of those species
417 (2012–2016) (Methods). We found a significant positive relationship between landings and
418 AIS longline effort (linear regression, $r^2 = 0.51$, $n = 9$ species or taxa group, $F = 7.14$,
419 $F_{0.05(1),1,7} = 5.59$, $p = 0.032$) (Extended Data Fig. 7), confirming longline fishing effort in
420 shark space use areas reflects major trends in fishing-induced shark mortality.

421 The extent of spatial overlap between shark distribution and longline fishing effort indicates
422 which species are more exposed to fishing and how this exposure is distributed (Fig. 3). Since
423 actual shark mortality (landings) is related to longline fishing effort in shark space use areas,
424 it follows that sharks exposed to high fishing overlap and effort (greater susceptibility) will
425 be at greater risk of capture than those exposed to low overlap and effort (Fig. 3; Extended
426 Data Table 4). We found the main commercially valuable pelagic sharks were grouped within

427 the highest potential risk zone in the North Atlantic and east Pacific (blue and shortfin mako
428 sharks), and in the Oceania region (blue shark) (Fig. 3a,b) (see Supplementary Results and
429 Discussion 2.3, 2.4 for significance tests and results for other species). In the North Atlantic,
430 between 79 and 94% of tracked space used by shortfin mako and blue sharks, respectively,
431 overlapped with longline fisheries, but fishing effort within this overlap was also significantly
432 greater (means: mako = 12.2 d \pm 9.0 S.D.; blue = 14.0 d \pm 9.7 S.D.) compared to other
433 tracked sharks (range, 0.12 – 6.7 d) (Fig. 3a; Extended Data Table 4b; Extended Data Fig. 6).
434 However, exposure risk varied between oceans because although spatial overlap of shortfin
435 mako and blue sharks remained relatively high in the east Pacific (~40%), and at 55.7% for
436 blue shark in Oceania, longline fishing effort was lower there (means: ~1 d in Pacific; 6.6 d
437 in Oceania) (Fig. 3a,b,d; Extended Data Fig. 6).

438 Among sharks generally considered less commercially valuable, including tiger and bull
439 sharks, we found exposure risk to longlines was high in some but not all regions. Bull sharks
440 used spatially limited areas within southwest Indian Ocean shelf and oceanic island habitats,
441 and in those areas they were at increased risk due to high average overlap (100%) and fishing
442 effort (45.6 d) (Extended Data Table 4d; Extended Data Figure 6j). This greater susceptibility
443 could lead to high localised catches, which, if replicated elsewhere, could explain why bull
444 sharks are one of the ten most commonly traded species in the Hong Kong fin market²⁶. In
445 contrast, tiger sharks were exposed to higher than average overlap in the Indian Ocean
446 (87.3%) and Oceania (63%), but fishing effort overlapping this species was lower than
447 average in all oceans (Fig. 3a-d; Extended Data Tables 4d, e).

448 High risk was evident for internationally protected sharks under CITES (Convention on
449 International Trade in Endangered Species) Appendix II and RFMO regulations. The
450 porbeagle shark (IUCN Red List ‘endangered’ globally) and the white shark (‘vulnerable’

451 globally) have low population sizes compared to historic levels (Supplementary Table 2). In
452 the North Atlantic we found an average 97% overlap of porbeagle space use and higher than
453 average fishing effort (6.7 d) (Fig. 3a), indicating high potential for incidental bycatch
454 mortality. We found white sharks in the highest risk zone in all oceans where it was tracked,
455 with mean spatial overlap with longline fisheries ranging from 55% (east Pacific) to 96%
456 (southwest Indian Ocean) and fishing effort in those areas being between 2.7 d (east Pacific)
457 and 17.0 d (southwest Indian Ocean) (Fig. 3a-d; Extended Data Table 4). Our results showing
458 high fishing overlap and effort for porbeagle and white sharks highlight the need for
459 continued protection – including sufficient scientific observer coverage on vessels to
460 underpin accurate data reporting – in the regions we identify where risk is greatest so that
461 stock rebuilding can continue²⁷, which for porbeagle is estimated to take a further 30 years²⁰.

462 The highest levels of exposure risk of sharks to longline fisheries were not constant but
463 varied seasonally as shark and fishing vessel space use shifted in relation to each other (Fig.
464 4; Extended Data Fig. 8). Overall for species with sufficient data (plotted in Fig. 4), the mean
465 monthly overlap of shark space use with longline fishing effort was 40.5% (\pm 26.9 S.D.;
466 median = 24.2%), similar to the mean annual overlap of 45%. This indicates shark-longline
467 overlap remained relatively high in both space and time. Generally, sharks spent 5–6 months
468 per year in the lowest risk zone and 2–6 months in the highest, with differing patterns of
469 changing exposure to fishing evident across species (Fig. 4). For example, overlap and
470 longline fishing effort for North Atlantic blue and southwest Indian Ocean white sharks both
471 remained relatively high (~60% overlap, ~40 d effort), but with highest risk occurring at
472 discrete times in the year (Extended Data Fig. 9). For Indian Ocean white sharks, this pattern
473 arises from long-range seasonal movements (Feb, Jun/Jul, Oct) into annually persistent areas
474 of high longline fishing effort (>60% overlap, >40 d effort) (Extended Data Fig. 9d). For blue
475 sharks, the discrete pattern appears driven by sharks and longline vessels co-occurring

476 maximally in boreal winter and summer, with lower exposure risk occurring in boreal spring
477 and autumn as sharks migrate north before returning south⁵. Longline fisheries also made this
478 seasonal south-north-south movement, but lagging behind movements of blue sharks, thus
479 lower overlap and effort during those times (Extended Data Fig. 9a). Similarly, annual risk
480 patterns of east Pacific white and Australian tiger sharks were driven by migratory behaviour,
481 with highest risk (~20% overlap, ~10 d effort) occurring for three consecutive months in
482 boreal (white) and austral (tiger) spring as sharks arrive in areas with higher longline fishing
483 effort (Extended Data Fig. 9c,e). In contrast, shortfin mako sharks in the North Atlantic were
484 exposed to high overlap (>55%) and effort (>32 d) continually through the boreal summer
485 and autumn (Jun–Nov), principally due to occupation of a space use hotspot located where
486 the Gulf Stream and Labrador Current converge that results in persistent high overlap with
487 high longline fishing effort (Fig. 4b; Extended Data Fig. 9b). Shortfin mako and vessel
488 tracking indicates that fishery-induced mortality within this hotspot is therefore likely to be
489 high. This was confirmed by the high return rate of satellite tags (19.3%) attached to Atlantic
490 shortfin makos ($n = 119$ tags; tracking duration: mean \pm SD = 161.5 d \pm 156.9; median = 109
491 d) that were returned to us after sharks were captured by Atlantic longline fishing vessels. To
492 our knowledge, this is the highest species-specific return rate yet recorded in an ocean scale,
493 as opposed to regional scale, study^{7,8} (Fig. 2c; Extended Data Table 5; Supplementary Results
494 and Discussion 2.4).

495 High fishing effort focused on extensive shark hotspots of commercially valuable species
496 raises particular concern. There is limited high seas management for commercial species,
497 including blue and shortfin mako sharks^{5,20}. The results from AIS indicate a high probability
498 of overexploitation of commercial species as high seas space use hotspots are exposed to high
499 fisheries overlap across their ranges for significant periods of a year (Extended Data Figs. 6,

500 9). Overall, this pattern suggests a future with limited spatial refuge from industrial longline
501 fishing effort that is currently centred on ecologically important shark hotspots.

502 The patterns of high overlap and fishing effort observed for sharks suggest different
503 mechanisms driving shark fishing hotspots. The high overlap and fishing effort observed in
504 commercially important shark hotspots, together with high catches (landings), support the
505 explanation that fishers track sharks. For example, North Atlantic blue and shortfin mako
506 sharks are known target species of Chinese, Spanish and Portuguese longlining fleets^{5,14,17}
507 (Extended Data Table 2). However, this is not necessarily the case for all global hotspots.
508 Internationally protected species such as the white shark was subject to high overlap and
509 effort in the North Atlantic, southwest Indian, and northeast and southwest Pacific oceans
510 despite no target fisheries. This indicates that high overlap is due to white sharks co-
511 occurring in habitats of target fish species (e.g. tunas) that fishers track.

512 Our results show that globally important habitat areas for threatened pelagic sharks overlap
513 significantly with industrial fishing activity in both space and time. Given the high fishing
514 effort in hotspots of many species for significant portions of the year, and the very few
515 tracked hotspots free from exploitation, our study reveals exposure risk of sharks to fisheries
516 in the high seas is spatially extensive – stretching across entire ocean-scale population ranges
517 for some species. The distribution maps reported here are, therefore, a first but essential
518 underpinning for a conservation blueprint for pelagic sharks in this high seas habitat. Our
519 study highlights the scale of fishing overlap with shark hotspots and argues for more effective
520 and timely monitoring, reporting and management of pelagic sharks as a result. To enhance
521 the recovery of vulnerable species, one solution is designation of large-scale MPAs²⁸ around
522 ecologically important space use hotspots of pelagic sharks²⁴, notwithstanding the need for
523 more complete reporting of catch data to support stricter conventional management by catch

524 prohibitions or quotas^{5,18}. This study outlines shark hotspot locations where fishing effort is
525 currently relatively low, which is where shark conservation could be maximized, while
526 minimizing impact on fishing activity not directed at sharks. Although the legal framework
527 remains challenging to develop a legally binding treaty for managing high seas fauna²²,
528 burgeoning technology for global surveillance and enforcement now offers valuable
529 additional options for a step change in ocean management⁶.

530 Satellite monitoring of ocean-scale movements by marine megafauna^{1,5,13,29}, oceanographic
531 features (eddies, fronts)^{6,24} and global fishing vessel distributions²¹ could provide signals of
532 shifting space use by megafauna due to environmental changes that, in turn, could inform
533 designation of new temporary time-area closures to industrial fishing⁶ and tracking of fishers'
534 displacement activities²². The potential of AIS as a global fisheries and conservation
535 management tool suggests that, given the remoteness and vast extent of the high seas, if we
536 are to reverse the observed declines and so rebuild populations of iconic ocean predators³
537 such as pelagic sharks¹⁴, technology-led conservation measures – conservation technology –
538 will be crucial in addition to conventional management methods^{5,18-20}. Conservation
539 technology could evolve in the future toward incorporation of adaptive management
540 strategies that are actionable in real time. The rapid development of autonomous vehicles has
541 created a need to develop machine-learning real-time assessments of risks³⁰, developments
542 that can be readily transposed to assess risks in the overlap between fishing vessels and
543 sharks across the global ocean.

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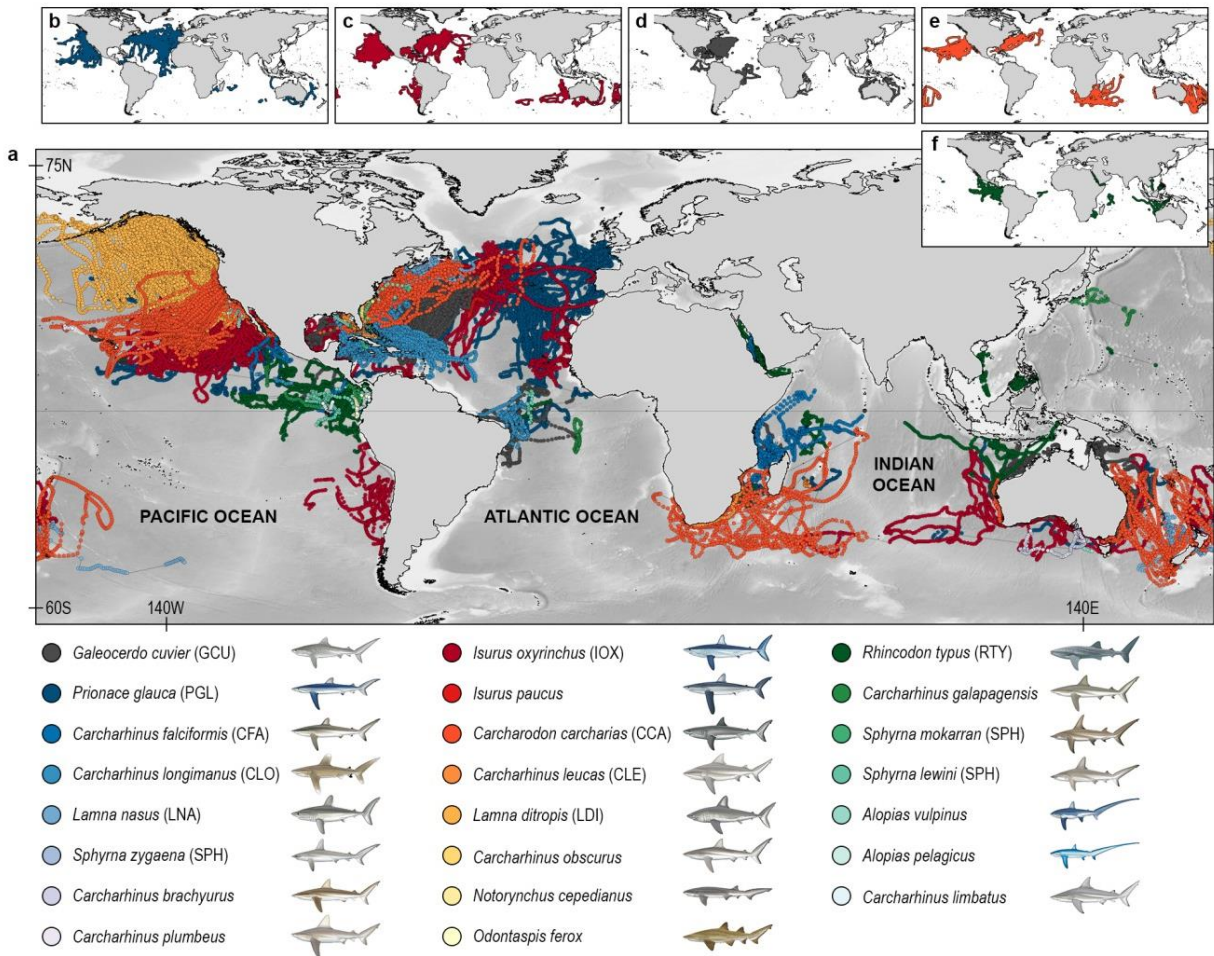
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637 study, N.Q., N.E. Humphries and D.W.S. designed the study, and all authors contributed to
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640 S.J.S. and D.W.S. analysed collated data. D.W.S. drafted the paper with contributions from
641 N.Q., N.E. Humphries and A.M.M.S. All authors contributed to subsequent drafts.

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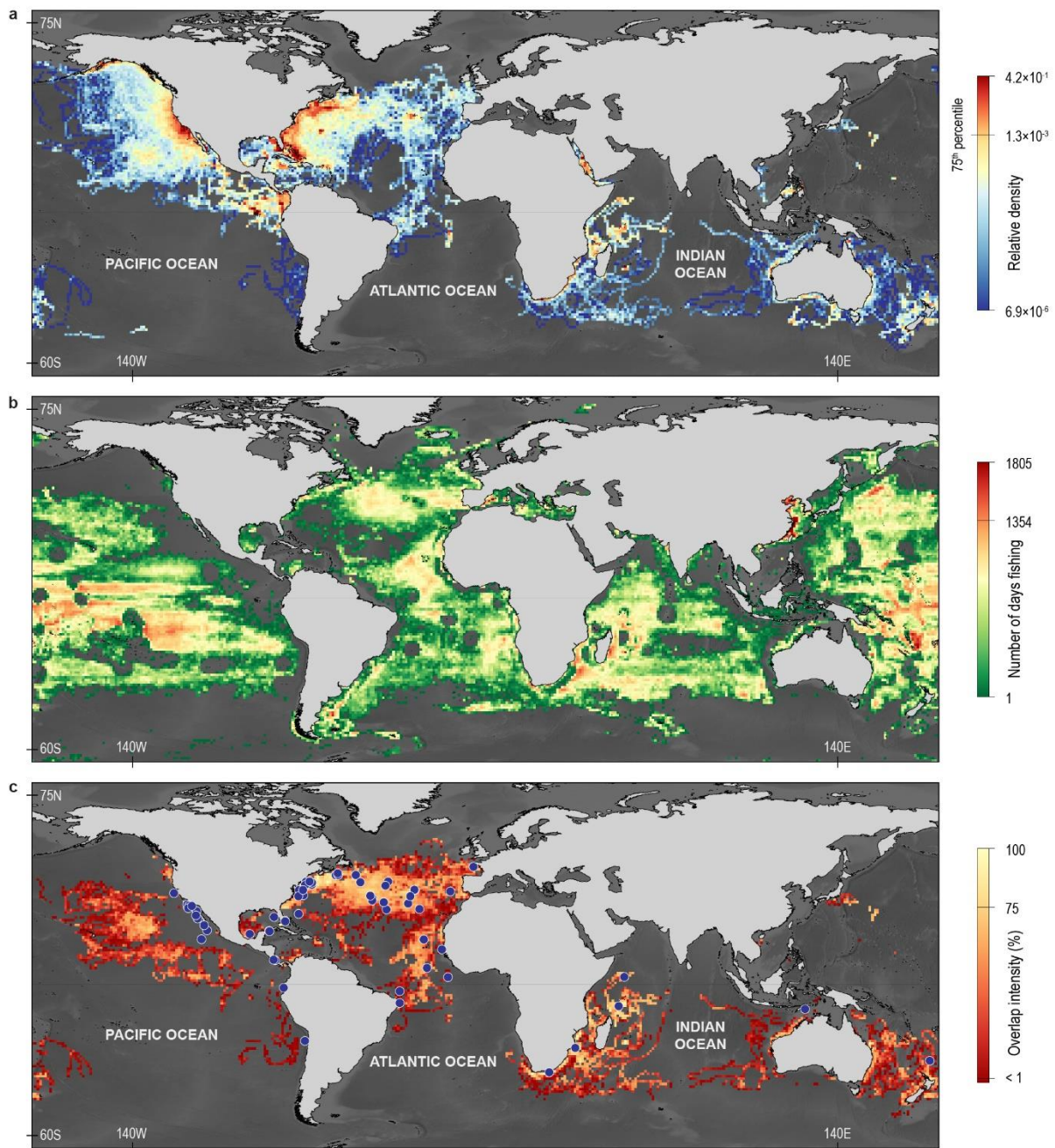


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645 **Fig. 1. Movements of oceanic and neritic pelagic sharks.** (a) Daily state-space model
 646 locations estimates from raw locations relayed by satellites from transmitters deployed on
 647 1,681 sharks from 23 species between 2002–2017. Extent of individual shark species space-
 648 use areas are illustrated for blue *Prionace glauca* (b), shortfin mako *Isurus oxyrinchus* (c),
 649 tiger *Galeocerdo cuvier* (d), white *Carcharodon carcharias* (e) and whale *Rhincodon typus*
 650 sharks (f). Shark images created by M. Dando.

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652

653 **Fig. 2. Spatial distributions and overlap intensity of sharks and longline fishing vessels.**

654 (a) Distribution of the weighted, normalized location density of $\geq 75^{\text{th}}$ percentile (relative

655 density) of tracked sharks in $1 \times 1^\circ$ grid cells. (b) Mean annual distribution of fishing effort

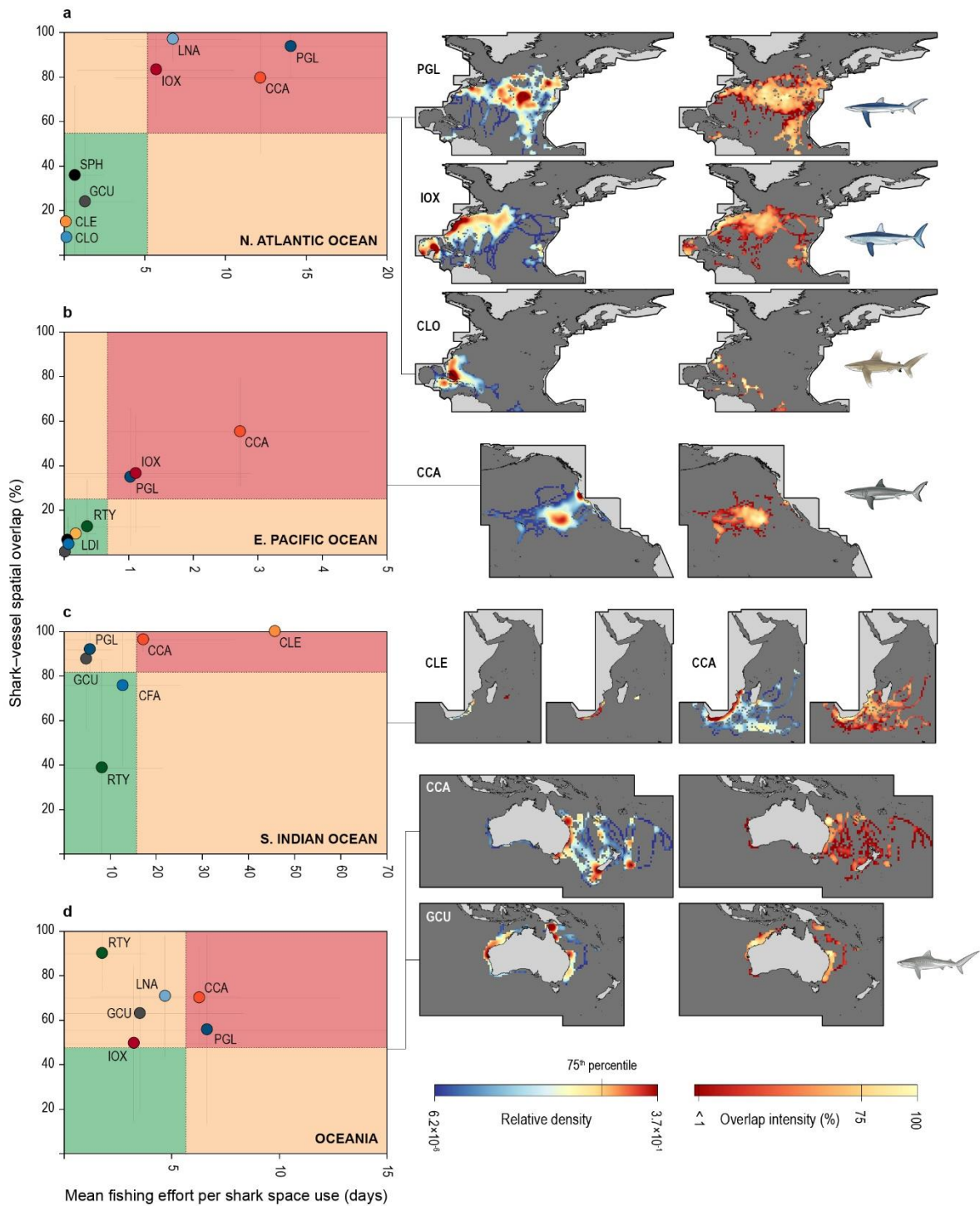
656 (mean days per grid cell) of AIS tracked longlining vessels in 2012–2016 (see Methods). (c)

657 Distribution of the overlap intensity between shark density and longline fishing effort (spatial

658 co-occurrence within $1 \times 1^\circ$ grid cells). Spatial overlap intensity hotspots were defined as $1 \times$

659 1° grid cells with $\geq 75\%$ overlap. Blue circles denote locations where tagged sharks were
660 caught by commercial fishers.

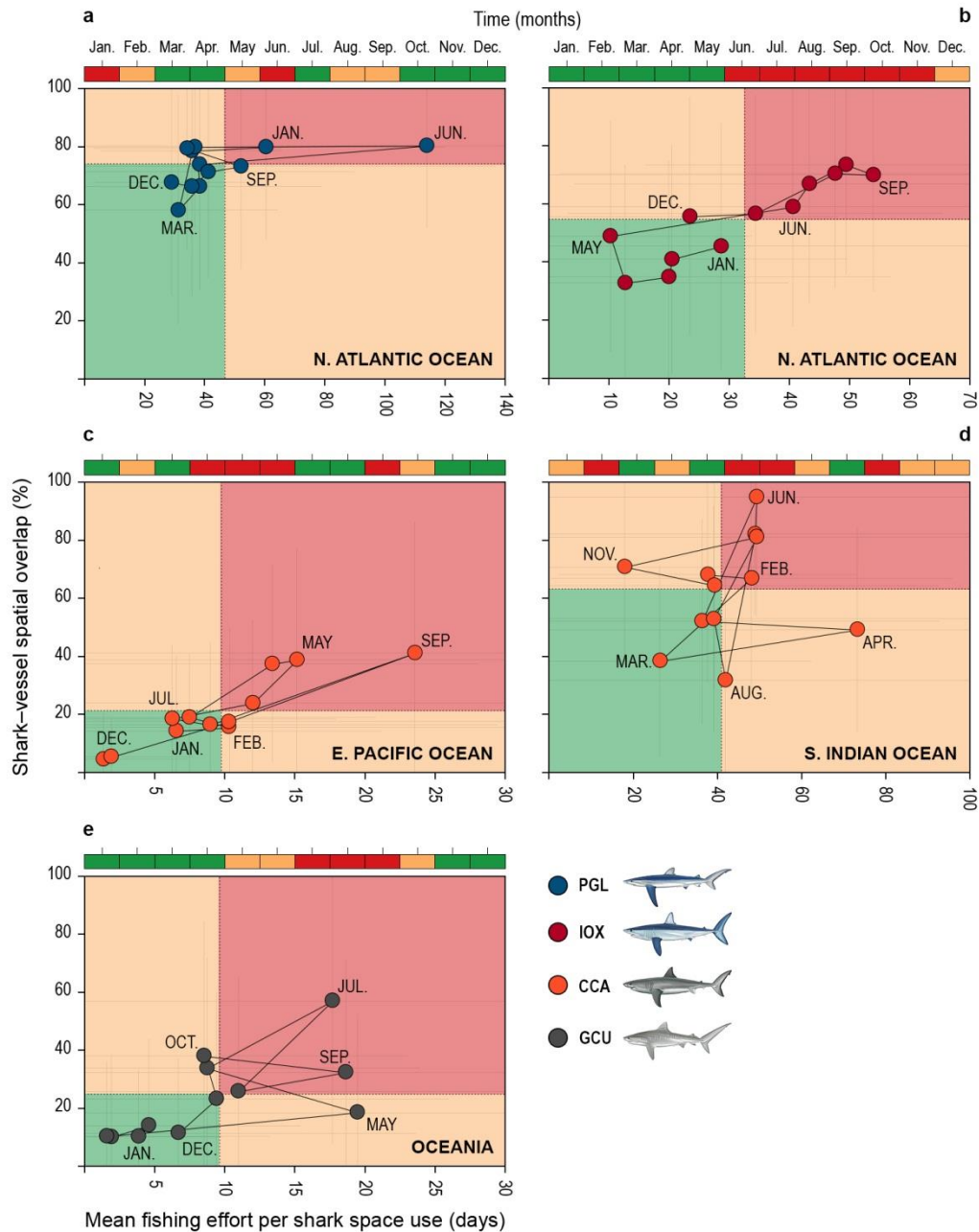
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663 **Fig. 3. Estimated exposure risk of sharks to capture by longline fishing activity.** Plots
 664 (left) showing shark-longline vessel spatial overlap against longline fishing effort per shark
 665 space use indicate species subject to high overlap and fishing effort (higher than average
 666 overlap and effort; higher risk red zone on plot) and those with lower overlap and effort
 667 (lower than average overlap and effort; lower risk green zone) for (a) North Atlantic, (b)

668 eastern Pacific and (c) southern Indian oceans, and (d) for the Oceania region. Lines
669 separating the coloured zones are fixed at the average values of spatial overlap (y axis) and
670 fishing effort per shark space use (x axis) for all species combined. For each ocean, relative
671 density distributions of selected shark species (middle map panels) are shown in comparison
672 to where overlap intensity hotspots of shark-longline vessels occur (map panels on right; see
673 Methods for details). Shark species identification codes (e.g. PGL) used on panels are given
674 in Fig. 1. Error bars denote \pm one standard deviation of the mean. Shark images created by M.
675 Dando.
676



677

678

679 **Fig. 4. Temporal changes in shark exposure risk to longline fishing.** Mean annual shark-

680 longline vessel spatial overlap versus longline fishing effort for the four most data-rich

681 species: (a) blue, (b) shortfin mako, (c, d) white, and (e) tiger sharks. Lines separating the

682 coloured zones are fixed at the respective species average values of spatial overlap (y axis)

683 and fishing effort per shark space use (x axis). Horizontal bars denote months in different

684 fishing exposure risk zones (red, highest risk; green, lowest). Error bars denote \pm one
685 standard deviation of the mean. Shark images created by M. Dando.

686

687 **Methods**

688 **Study animals and tagging.** Satellite transmitter tags were attached to 1,804 large pelagic
689 sharks at multiple tagging sites in the Atlantic, Indian and Pacific oceans (Extended Data Fig.
690 1). The number of tagged individuals varied among species and ranged from one to 280. Two
691 satellite-transmitter tag types (ARGOS, advanced research and global observation satellite
692 transmitter; and PSAT, pop-off satellite-linked archival transmitter) were used. Sharks were
693 either captured with baited hooks (longlines, rod-and-line angling, or with handlines), in
694 purse seine during commercial fishing operations, or tagged free-swimming in the water.
695 Tags were attached to the first dorsal fin or in the dorsal musculature. All animal handling
696 procedures were approved by institutional ethical review committees and completed by
697 trained personnel. Data were provided by the 37 data owners to the senior author and quality
698 checked prior to archiving in a database. Poor quality data were reported for 123 tags (72
699 ARGOS and 51 PSAT) due to, for example, early tag failure, premature tag pop-off, and/or a
700 high percentage of locations estimated with high spatial error, e.g. raw computed
701 geolocations over land, all of which resulted in poor state-space model fits leading to short or
702 unreliable track reconstructions. Hence, analyses were restricted to the remaining 1,681
703 tracks from 1,066 ARGOS and 615 PSAT tags on sharks from 23 species ranging in duration
704 per species from 20 to 57,037 days with a median of 4.1 years total track time per species
705 (Supplementary Table 3). The number of sharks tracked within each region is given in
706 Supplementary Table 9.

707 **Track processing.** Movements of PSAT-tagged sharks were estimated using either satellite
708 relayed data from each tag or from archival data after the tags were physically recovered.
709 Data were provided as: (i) raw shark positions that were previously reconstructed using
710 software provided by the tag manufacturers (e.g. Wildlife Computers, Redmond, USA;
711 Microwave Telemetry, USA), where daily maximal rate-of-change in light intensity was used

712 to estimate local time of midnight or midday for longitude calculations, and day-length
713 estimation for determining latitude^{31,32}; or (ii) filtered positions where a state-space model
714 (SSM) (unscented Kalman filter with sea surface temperature, UKFSST)³³ had been applied
715 to correct the raw geolocation estimates and obtain the most probable track. In the first case,
716 raw positions were corrected using the UKFSST SSM (UKFSST R package) in addition to a
717 bathymetric correction applied to the initial Kalman position estimates (analyzepsat R add-
718 on). A daily time-series of locations was estimated using a continuous-time correlated
719 random walk (CTCRW) Kalman filter³⁴ (crawl R package). UKFSST geolocations were
720 parameterised with standard deviation (SD) constants (K) which produces the smallest mean
721 deviation from concurrent Argos positions³⁵. In the latter case, the CTCRW filter was applied
722 to produce regular time-series.

723 For ARGOS transmitter tags, data were provided as raw ARGOS (Doppler frequency shift)
724 position estimates. Location class (LC) Z data – assigned for a failed attempt at obtaining a
725 position – were discarded from the dataset. The remaining raw position estimates (LC 3, 2, 1,
726 0, A and B) were analysed point-to-point with a 3 m s⁻¹ speed filter to remove outlier
727 locations. Subsequently, the CTCRW SSM was applied to each individual track, producing a
728 single position estimate per day. ARGOS positions were parameterised with the K error
729 model parameters for longitude and latitude implemented in the *crawl* R package³⁴.

730 Shark tracking data from the Tagging of Pacific Predators (TOPP) program were downloaded
731 from the Animal Tracking Network (ATN) hosted by the Integrated Ocean Observing System
732 (<<https://ioos.noaa.gov/project/atn/>>; downloaded September 2017). Both ARGOS and light-
733 based geolocation data in ATN had already been filtered with a Bayesian based SSM³⁶.
734 Briefly, the SSM was fitted to each track individually, using the WinBUGS software that
735 conducts Bayesian statistical analyses using Markov chain Monte Carlo (MCMC) sampling³⁷.
736 For each track, two MCMC chains each of length 10,000 were run and a sample of 2,000

737 from the joint posterior probability distribution was obtained by discarding the first 5,000
738 iterations and retaining every 5th of the remaining iterations. SSM fits were posteriorly
739 inspected for obvious problems (e.g. unrealistic movements¹³). Because two different SSMs
740 were applied to data used in this study, we tested for possible biases in the spatial density
741 analysis (see below) by comparing 1 × 1° density grid maps obtained with both UKFSST and
742 Bayesian-based filtered tracks using a subset of 83 ARGOS-linked tracks in the North
743 Atlantic (blue shark, *n* = 27; mako, *n* = 42; white, *n* = 3; oceanic whitetip, *n* = 11).
744 Differences in spatial grid density between the two methods were negligible (Supplementary
745 Fig. 1).

746 **Spatial density analysis.** To obtain unbiased estimates of shark spatial density, gaps between
747 consecutive dates in the raw tracking data were interpolated to one position per day. The
748 frequency of long temporal gaps in a reconstructed track can result in extensive interpolated
749 movements driven by the underlying random walk model rather than a shark's movement
750 pattern¹³. Although the frequency of long temporal gaps (>20 days) in our dataset was low
751 (Supplementary Table 10), nonetheless, any tracks with gaps exceeding 20 d were split into
752 segments prior to interpolation, thus avoiding the inclusion of unrepresentative interpolated
753 location estimates⁵. Similarly, location estimates derived for periods exceeding 20 d were
754 also discarded from TOPP data¹³.

755 To account for biases in spatial density associated with (i) variable track lengths and (ii)
756 shorter tracks near the tagging location, a weighting procedure was applied¹³ and data were
757 normalised to account for unequal sample sizes across species. Briefly, each daily location
758 estimate was weighted by the inverse number of individuals of a given species with location
759 estimates for the same relative day. Periods with gaps >20 d were not included when
760 weighting the locations. After the 85th percentile of the track length, daily weights were fixed.
761 Under this weighting scheme, individual location estimates closer to the tagging location

762 received a lower weight than later locations because more sharks had locations earlier in their
763 tracks. Also, longer tracks received a higher total weight than shorter tracks because of the
764 higher number of locations received. Therefore, calculated spatial densities were more
765 representative of the actual distributions and less affected by tag loss, failure or a spatial bias
766 towards deployment location. Total weights for each species were normalised to one so that
767 within the study area each species contributed equally to the density patterns. Species with
768 comparatively very low numbers of tracks were grouped and treated as one (these were: *C.*
769 *galapagensis*, *C. limbatus*, *A. vulpinus*, *A. pelagicus*, *O. ferox*, *C. brachyurus*, *C. obscurus*, *N.*
770 *cepedianus* and *C. plumbeus*). Hammerhead (3 species) and mako (2 species) shark species
771 were also clustered and analysed as taxa groups, *Sphyrna* spp. and *Isurus* spp., respectively.
772 Spatial densities (overall averages) were calculated for all species together (Fig. 2a) and per
773 species at a $1 \times 1^\circ$ grid cell resolution (Extended Data Fig. 6).

774 **Fishing vessel geolocation data.** The automatic identification system (AIS) was developed
775 as a vessel safety and anti-collision system with global coverage, rather than to track fishing
776 vessels for fishery management purposes²¹⁻²³. However, its global coverage of locations of
777 many thousands of ships through time enables fishing effort distribution to be analysed^{21,22}.
778 Here, fishing effort (hours of fishing) data gridded at 0.01° by flag state and gear type were
779 obtained from Global Fishing Watch (GFW) (available at
780 <http://globalfishingwatch.org/datasets-and-code/fishing-effort/>). GFW used raw AIS vessel
781 tracking data obtained from ORBCOMM via their AIS-enabled satellite constellation
782 (<https://www.orbcomm.com/eu/networks/satellite-ais>) to calculate fishing effort and derive
783 the gridded data, described in detail in Kroodsma *et al.*²¹. Briefly, GFW uses two neural
784 network algorithms to categorize different types of fishing gear, e.g. drifting longlines, purse
785 seines, in addition to estimating the spatio-temporally resolved locations where fishing gears
786 were most likely deployed by individual vessels^{21,38}. We used the GFW gridded fishing effort

787 data in the years 2012 to 2016 for all gear types, and for drifting pelagic longlines and purse
788 seines. For each type, we summed the number of days fishing in a year within each $1 \times 1^\circ$
789 grid cell and averaged across years. For the seasonal analysis, we summed the number of
790 days fishing in each month within each $1 \times 1^\circ$ grid cell and averaged across years. Global
791 distributions of fishing effort for all gear types, longlines and purse seines were mapped
792 separately and overlaid by shark relative spatial density to determine spatial overlap intensity
793 at the global and ocean scale, and for each species per ocean. AIS data coverage increased
794 from 2012 to 2016 as more satellite AIS receivers were launched and commenced
795 operation²¹. However, the global spatial distribution of longline vessel fishing effort was
796 broadly similar across years (Extended Data Fig. 10) and variation in annual maximum
797 fishing effort displayed no increasing trend over time, indicating our calculated mean annual
798 fishing effort for 2012–2016 did not overestimate spatial overlap or fishing effort but can be
799 considered conservative (Extended Data Fig. 10).

800 **Shark and fishing effort environment modelling.** To model shark and fishing vessel
801 distributions in relation to environmental variables, data were extracted from online databases
802 (Supplementary Fig. 2). The environmental variables were selected based upon their
803 demonstrated importance in affecting shark occurrence and included: (i) sea water
804 temperature ($^\circ\text{C}$) (abbreviation used in models: sea surface temperature, SST; temperature at
805 100 m, TEM_100) known to influence the presence of many pelagic shark species^{5,13}; (ii)
806 maximum thermal gradient ($^\circ\text{C}/100 \text{ km}$) (TGR) influences shark spatial density⁵, and was
807 calculated here based on the SST data and using maximum gradient maps by calculating
808 where for each pixel a geodesic–distance–corrected maximum thermal gradient was
809 calculated; (iii) sea water salinity (psu) (SAL), an important determinant of habitat use in
810 some sharks^{1,38}; (iv) sea surface height above geoid (m) (SSH) that influences shark
811 presence⁵ and catches by fisheries⁶; (v) ocean mixed layer depth thickness or thermocline

812 depth (m) (MLD) that affects pelagic shark foraging behaviour³⁹; (vi) mass concentration
813 chlorophyll *a* in sea water (mmol m^{-3}) (CHL) as a proxy for productivity that often
814 characterises preferred habitats of sharks^{5,39}; (vii) mole concentration of phytoplankton
815 expressed as carbon in sea water concentration (mmol m^{-3}) (PHY) as a direct measure of
816 productivity; (viii) net primary production of biomass expressed as carbon per unit volume in
817 sea water ($\text{g m}^{-3}/\text{day}$) (NPP) quantifying productivity; and (ix) mole concentration of
818 dissolved molecular oxygen in sea water (mmol m^{-3}) (DO) that can strongly influence shark
819 space use¹. Environmental datasets *i* to *v* were downloaded from Copernicus Marine
820 Environment Monitoring Service (CMEMS) Global Ocean Physics Reanalysis product
821 (goo.gl/E4eXDM; downloaded November 2017) and datasets *vi* to *ix* from CMEMS Global
822 Ocean Biochemistry Hindcast product (goo.gl/5hpBs2; downloaded November 2017).
823 CMEMS data were available for 2002 to 2014 from the surface to 5,500 m as monthly
824 datasets. Using custom-written software overall averages (2002-2014) were calculated at a 1
825 $\times 1^\circ$ grid cell resolution for surface and 100 m depth layers (with the exception of SSH and
826 MLD; Supplementary Fig. 2). Most of these variables and interactions are also considered
827 important for explaining fishing patterns^{5,6}.

828 We developed and compared a set of generalised additive models (GAMs) with a gaussian
829 family and an identity link using the log-transformed relative density of sharks (D_{it})¹³ as
830 response variable. Because we were interested in understanding the general environmental
831 preferences of sharks, we considered the relative density for all 23 shark species combined
832 without considering random effects per species. All environmental variables were
833 standardised and collinearity checked prior to inclusion in the models. Highly skewed
834 environmental variables were logged before standardisation, this included most predictors at
835 the surface (except for SAL and SSH) and also NPP (for sharks only) and TGR at 100 m
836 (TGR_100). The selection of variables to include in each model was made to avoid inclusion

837 of colinear variables in the same model and to specifically address key hypotheses. All
838 possible combinations of 16 variables were not undertaken because many of them are
839 colinear and could not be included in the same model. Rather, we focused on testing
840 ecologically relevant hypotheses. A description of the general hypothesis tested with each
841 model included in the model set is given in Supplementary Table 7. Including models with a
842 reduced number of variables was also necessary, as some variables were colinear with
843 variables included in other models. Because sharks respond to surface and subsurface thermal
844 gradients which often support higher biological productivity^{5,6,13,39}, we tested for interactions
845 between MLD and SST, CHL and MLD at 100 m (MLD_100), CHL at 100 m (CHL_100)
846 and TEM at 100 m (TEM_100), MLD and TGR at the surface, MLD and CHL_100,
847 CHL_100 and TEM_100, and between SAL and TEM_100.

848 GAM with a Tweedie distribution and log link function provided the best modelling approach
849 for the fishing effort, as this distribution includes a family of probability distributions
850 including normal, gamma, Poisson and compound Poisson-gamma. We considered two
851 response variables separately: fishing effort of all vessels, and fishing effort of longline
852 vessels only. In our model set we included different combinations of a total of the same 16
853 explanatory environmental variables used for shark density modelling (see previous section;
854 Supplementary Table 7), and also a null (all terms equal to zero), intercept-only model. The
855 dimension basis for all terms was limited to 5 (i.e., $k = 5$) to assist controlling for
856 overfitting⁴⁰. We then used the Akaike's information criterion (AIC)⁴¹ to compare the models
857 in the model set for all sharks and fishing vessels. We assessed the relative strength of
858 evidence for each model using the weights of AIC, and the goodness of fit of each model by
859 calculating the percentage of deviance explained (%DE). All models were implemented in R
860 using the mgcv package⁴².

861 **Shark/vessel spatial overlap and effort.** The spatial overlap (%) between an individual
862 tracked shark and fishing effort was calculated as the number of days that sharks and fishing
863 effort (days) occurred in the same $1 \times 1^\circ$ grid cells in an average year, as a function of all
864 shark grid cells occupied and standardised for shark track length, and summarised as:

$$865 \text{ Spatial overlap (\%)} = (\text{number of days with overlap}) / (\text{total number of track days}) \times 100$$

866 A fixed $1 \times 1^\circ$ geographic grid cell (where 1° latitude at the equator = 110.6 km) was chosen
867 because it encompassed the maximum length of fishing gear deployed by a single vessel, i.e.
868 the length of drifting longlines are typically 100 km in total length⁵. We examined the effect
869 of grid cell size⁴³ on spatial overlap estimates by calculating the overlap of all sharks tracked
870 with ARGOS transmitters ($\sim 0.5 - 11$ km spatial accuracy⁴⁴) with all fishing vessels, then with
871 longliners separately, at $0.5 \times 0.5^\circ$ and $0.25 \times 0.25^\circ$ grid cell sizes. An estimate of fishing
872 effort that an individual shark was exposed to within the space each occupied was termed
873 fishing effort per shark space use and calculated as:

$$874 \text{ Individual shark exposure to fishing effort (d)} = (\text{total number of fishing days}) / (\text{total number} \\ 875 \text{ of track days})$$

876 Spatial overlap and fishing effort were also calculated for each of the most data-rich species
877 per month to assess changes within an average year. To determine the spatial variation in
878 overlap and fishing effort within the space used by sharks for mapping purposes, we
879 calculated the overlap intensity in each $1 \times 1^\circ$ grid cell as the product of shark density
880 (number of daily locations) and the number of fishing days.

881 To test for differences in exposure risk of sharks to fishing activity between different species
882 within the general fishing areas designated by the Food and Agriculture Organization of the
883 United Nations (FAO) (Supplementary Fig. 3), we undertook statistical analysis of exposure
884 risk calculated for each shark as the product of the mean spatial overlap and mean fishing

885 effort. Since data were not normal (Shapiro-Wilk normality test, $p < 0.05$), a Kruskal–Wallis
886 (KW) test was performed (with pairwise Wilcoxon rank sum tests as a post-hoc test).
887 Because of differences in the number of tagged individuals per species, groups of >25 sharks
888 per species were randomly selected and the KW test performed. This procedure was repeated
889 1,000 times and the percentage of times that significant differences were observed were
890 recorded. Species with fewer than 25 individuals tracked were removed from the analysis.
891 Given the relatively low number of sharks tracked in the southwest Indian Ocean and
892 Oceania regions (Supplementary Table 10), statistical tests were restricted to the North
893 Atlantic and eastern Pacific regions. In the Atlantic selected species were: *P. glauca* ($n =$
894 152), *Isurus* spp. ($n = 120$), *G. cuvier* ($n = 131$), *C. carcharias* ($n = 26$), *C. longimanus* ($n =$
895 99), *L. nasus* ($n = 46$), *C. leucas* ($n = 38$) and *Sphyrna* spp. ($n = 40$); Pacific, species were: *P.*
896 *glauca* ($n = 112$), *I. oxyrinchus* ($n = 113$), *L. ditropis* ($n = 172$), *R. typus* ($n = 77$) and *C.*
897 *carcharias* ($n = 59$).

898 **Shark landings.** Annual pelagic shark landings by species/taxa groups were obtained from
899 the FAO database (<FAO.org/fishery/statistics/global-capture-production/query/en>;
900 downloaded September 2018) and related to fishing effort per shark space use of each
901 species/taxa group. Landings reported for the North Atlantic (northwest, northeast, western
902 central and eastern central Atlantic) between 2012 and 2016 were used in the analysis since it
903 spanned the period that longline fishing effort was monitored (2012–2016). Data were
904 extracted for nine species or taxa groups that are regularly caught by shelf and/or high-seas
905 fisheries in the North Atlantic, the region in which most tags were deployed. The species/taxa
906 groups were: *P. glauca*, *I. oxyrinchus*, *C. longimanus*, *C. leucas*, *C. falciformis*, *L. nasus*, *G.*
907 *cuvier*, *C. carcharias*, and hammerheads (*Sphyrna* spp.) comprising *S. lewini*, *S. mokarran*
908 and *S. zygaena*. Mean annual landings (t) per species/taxa group were calculated and related
909 to AIS longline fishing effort per shark space use.

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947 **Extended Data Table 1.** Summary of fitted generalised additive models (GAM) relating the
 948 log-transformed weighted relative density of all sharks (D_{it}) and the fishing effort of all
 949 vessels and of longlines only to environmental variables. Environmental variables included in
 950 each model are detailed in Supplementary Table 7. $wAIC$ indicates the weight of the Akaike's
 951 information criteria for each model in the model set with bold highlighting the highest ranked
 952 model. The percentage of deviance explained (%DE) by each model is given and the highest
 953 and second highest values for each response variable are highlighted in bold.

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Model	D_{it}		Fishing effort (all vessels)		Longline fishing effort	
	$wAIC$	%DE	$wAIC$	%DE	$wAIC$	%DE
1	1.000	26.25	1.000	29.88	1.000	16.12
2	0.000	20.23	0.000	16.12	0.000	12.90
3	0.000	9.42	0.000	14.52	0.000	14.62
4	0.000	8.21	0.000	9.49	0.000	5.73
5	0.000	5.83	0.000	7.20	0.000	11.14
6	0.000	21.13	0.000	24.89	0.000	14.99
7	0.000	12.01	0.000	17.72	0.000	6.21
8	0.000	0.00	0.000	0.00	0.000	0.00

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959 **Extended Data Table 2.** The number (a) and total hours fished (b) by flag state of the 5,565
 960 AIS longline fishing vessels analysed in this study arranged by the largest twenty values
 961 (totals for 2012 – 2016). In (a) the number of vessels per flag state is the total number of
 962 unique Maritime Mobile Safety Identity (MMSI) codes present in the dataset in 2012 – 2016.
 963 In (b), the total longline hours fished is the total during 2012 – 2016.
 964 (a)

Flag state	No. AIS longline vessels	% 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

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973 (b)

Flag state	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

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976 **Extended Data Table 3.** Effect of different grid cell size on the global mean spatial overlap
 977 of sharks and fishing vessels calculated for all ARGOS transmitter tracked sharks ($n = 1066$)
 978 and all fishing vessels (including longline), and sharks and all longline vessels separately.
 979 ARGOS tracked sharks were used in the analysis because the spatial accuracy of locations
 980 was <11 km (see Methods for explanation).

	Grid cell size	Mean spatial overlap (%)	One standard deviation
Sharks and all fishing vessels (incl. longline)	$1 \times 1^\circ$	81.77	28.48
	$0.5 \times 0.5^\circ$	67.17	35.39
	$0.25 \times 0.25^\circ$	56.47	36.31
Sharks and all longline vessels	$1 \times 1^\circ$	39.21	40.91
	$0.5 \times 0.5^\circ$	30.26	37.63
	$0.25 \times 0.25^\circ$	24.00	33.62

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Extended Data Table 4. Calculated mean spatial overlap and fishing effort for ocean regions and species. 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 Supplementary Figure 3). There were 70 individual sharks that did not fall into FAO regions and these were not included in this analysis.

(a) All ocean regions. Calculated spatial overlap and longline fishing effort for the 11 most data-rich species/taxa groups.

Species	N tags	Mean spatial overlap (%)	Median	S.D.	S.E.	Mean fishing effort (days)	Median	S.D.	S.E.
<i>Prionace glauca</i>	280	68.5	90.5	37.3	2.2	8.4	5.4	9.7	0.6
<i>Carcharhinus leucas</i>	41	21.2	0.0	36.5	5.7	3.4	0.0	13.1	2.0
<i>Isurus oxyrinchus</i>	262	57.9	61.3	36.9	2.3	6.4	1.9	8.2	0.5
<i>Carcharhinus longimanus</i>	105	10.9	1.3	20.8	2.0	0.2	0.0	0.4	0.0
<i>Lamna nasus</i>	56	92.1	100.0	17.2	2.3	6.4	5.7	4.1	0.5
<i>Lamna ditropis</i>	172	8.8	2.8	13.1	1.0	0.2	0.0	0.3	0.0
<i>Carcharhinus falciformis</i>	51	52.2	69.5	45.2	6.3	8.0	1.0	11.6	1.6
Sphyrna spp.	66	29.3	10.5	37.7	4.6	0.7	0.0	1.9	0.2
<i>Galeocerdo cuvier</i>	254	40.8	27.3	41.0	2.6	2.0	0.4	3.7	0.2
<i>Rhincodon typus</i>	164	27.7	0.0	39.6	3.1	2.8	0.0	8.0	0.6
<i>Carcharodon carcharias</i>	160	72.2	78.2	26.0	2.1	7.1	3.8	11.2	0.9
Total tags or Mean	1611	43.8				4.2			

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

Species	N tags	Mean spatial overlap (%)	Median	S.D.	S.E.	Mean fishing effort (days)	Median	S.D.	S.E.
<i>Prionace glauca</i>	152	93.7	100.0	14.2	1.2	14.0	11.5	9.7	0.8
<i>Carcharhinus leucas</i>	38	15.0	0.0	29.9	4.9	0.1	0.0	0.2	0.0
<i>Isurus oxyrinchus</i>	120	79.4	99.6	33.8	3.1	12.2	11.3	9.0	0.8
<i>Carcharhinus longimanus</i>	99	8.0	0.5	17.4	1.7	0.1	0.0	0.4	0.0
<i>Lamna nasus</i>	46	96.8	100.0	9.3	1.4	6.7	6.0	4.2	0.6
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>	1*	100.0	100.0			1.0	1.0		
Sphyrna spp.	40	35.8	15.0	40.1	6.3	0.7	0.1	1.7	0.3
<i>Galeocerdo cuvier</i>	131	23.9	12.7	29.6	2.6	1.3	0.1	2.9	0.3
<i>Rhincodon typus</i>	3	60.2	56.3	25.6	14.8	6.2	0.9	9.7	5.6
<i>Carcharodon carcharias</i>	26	83.3	90.9	21.3	4.2	5.7	4.5	4.8	0.9
Total tags or Mean	656	55.1				4.8			

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

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

Species	N tags	Mean spatial overlap (%)	Median	S.D.	S.E.	Mean fishing effort (days)	Median	S.D.	S.E.
<i>Prionace glauca</i>	112	34.5	24.7	31.3	3.0	1.0	0.3	1.8	0.2
<i>Carcharhinus leucas</i>									
<i>Isurus oxyrinchus</i>	113	36.1	34.3	26.4	2.5	1.1	0.8	1.8	0.2
<i>Carcharhinus longimanus</i>	2	62.1	62.1	3.0	2.1	0.4	0.4	0.2	0.1
<i>Lamna nasus</i>									
<i>Lamna ditropis</i>	172	8.8	2.8	13.1	1.0	0.2	0.0	0.3	0.0
<i>Carcharhinus falciformis</i>	17	4.2	0.0	11.9	2.9	0.1	0.0	0.2	0.1
<i>Sphyrna</i> spp.	21	6.0	0.0	10.7	2.3	0.0	0.0	0.1	0.0
<i>Galeocerdo cuvier</i>	12	0.6	0.0	1.6	0.5	0.0	0.0	0.0	0.0
<i>Rhincodon typus</i>	77	12.2	0.0	20.9	2.4	0.4	0.0	1.1	0.1
<i>Carcharodon carcharias</i>	59	55.0	58.2	24.4	3.2	2.7	2.8	2.0	0.3
Total tags or <i>Mean</i>	585	24.4				0.7			

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

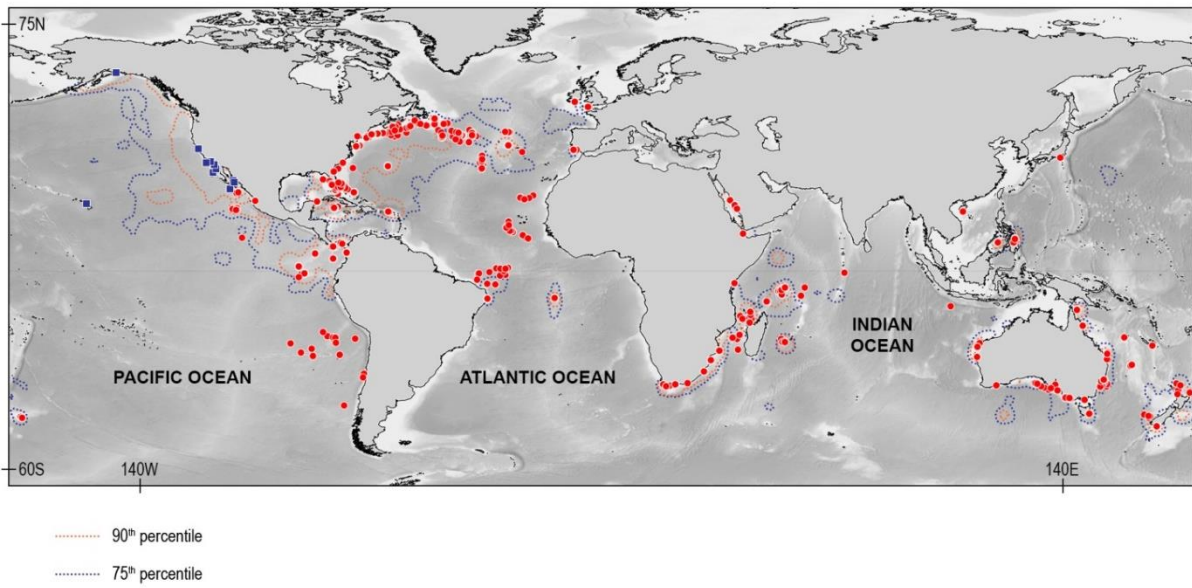
Species	N tags	Mean spatial overlap (%)	Median	S.D.	S.E.	Mean fishing effort (days)	Median	S.D.	S.E.
<i>Prionace glauca</i>	5	91.9	100.0	11.4	5.1	5.4	4.4	4.9	2.2
<i>Carcharhinus leucas</i>	3	100.0	100.0	0.0	0.0	45.6	47.2	23.6	13.6
<i>Isurus oxyrinchus</i>									
<i>Carcharhinus longimanus</i>									
<i>Lamna nasus</i>									
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>	33	75.5	93.6	35.7	6.2	12.4	8.4	12.5	2.2
Sphyrna spp.									
<i>Galeocerdo cuvier</i>	26	87.3	100.0	31.0	6.1	4.7	4.0	4.8	0.9
<i>Rhincodon typus</i>	48	38.7	0.0	48.2	7.0	8.0	0.0	13.1	1.9
<i>Carcharodon carcharias</i>	34	96.3	98.6	5.2	0.9	17.0	8.3	19.8	3.4
Total tags or <i>Mean</i>	149	81.6				15.5			

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

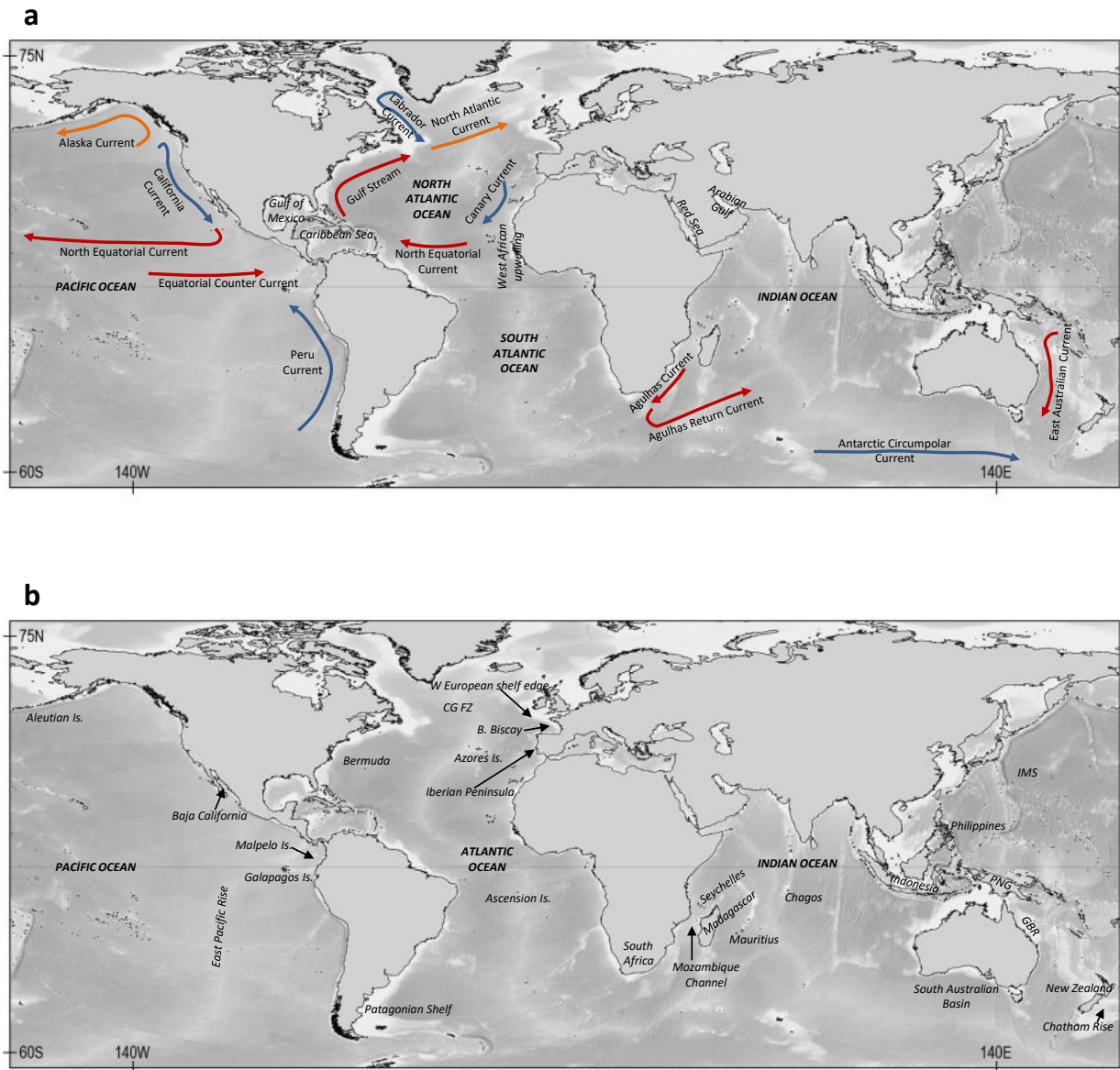
Species	N tags	Mean spatial overlap (%)	Median	S.D.	S.E.	Mean fishing effort (days)	Median	S.D.	S.E.
<i>Prionace glauca</i>	11	55.7	71.4	42.3	12.8	6.6	1.6	9.3	2.8
<i>Carcharhinus leucas</i>									
<i>Isurus oxyrinchus</i>	15	49.5	40.3	34.8	9.0	3.2	1.0	3.6	0.9
<i>Carcharhinus longimanus</i>									
<i>Lamna nasus</i>	10	70.5	78.0	27.2	8.6	4.7	4.0	3.4	1.1
<i>Lamna ditropis</i>									
<i>Carcharhinus falciformis</i>									
Sphyrna spp.									
<i>Galeocerdo cuvier</i>	58	62.8	89.4	44.2	5.8	3.5	1.3	4.8	0.6
<i>Rhincodon typus</i>	16	89.8	100.0	16.6	4.1	1.7	0.6	2.0	0.5
<i>Carcharodon carcharias</i>	41	70.0	76.1	22.3	3.5	6.3	3.9	6.5	1.0
Total tags or Mean	151	66.4				4.3			

Extended Data Table 5. Tag recapture data for the most data-rich species studied.

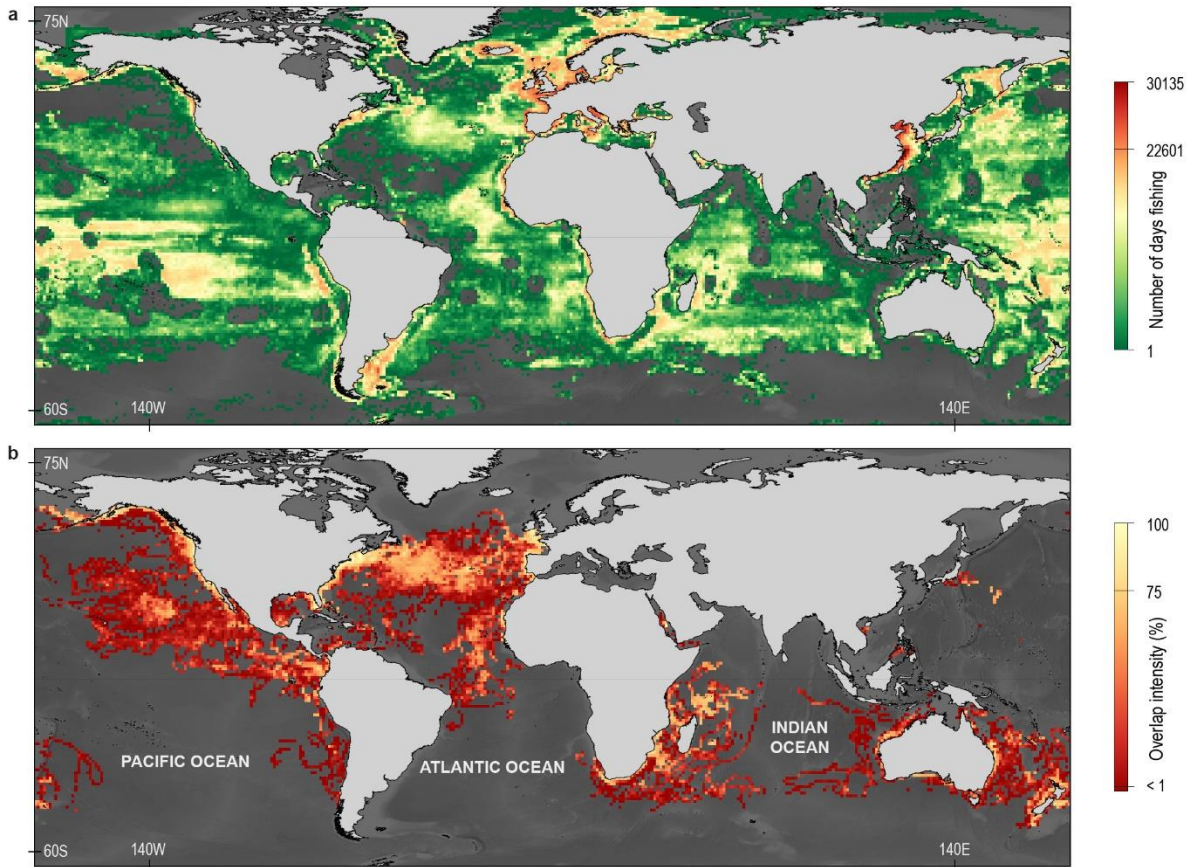
Shark species	Global			North Atlantic			Eastern Pacific			Indian Ocean			Oceania		
	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%	Total tagged	No. recaptured	%
Silky	51	4	7.84	1	0	0	17	2	11.76	28	2	7.14			
Tiger	254	7	2.76	131	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>



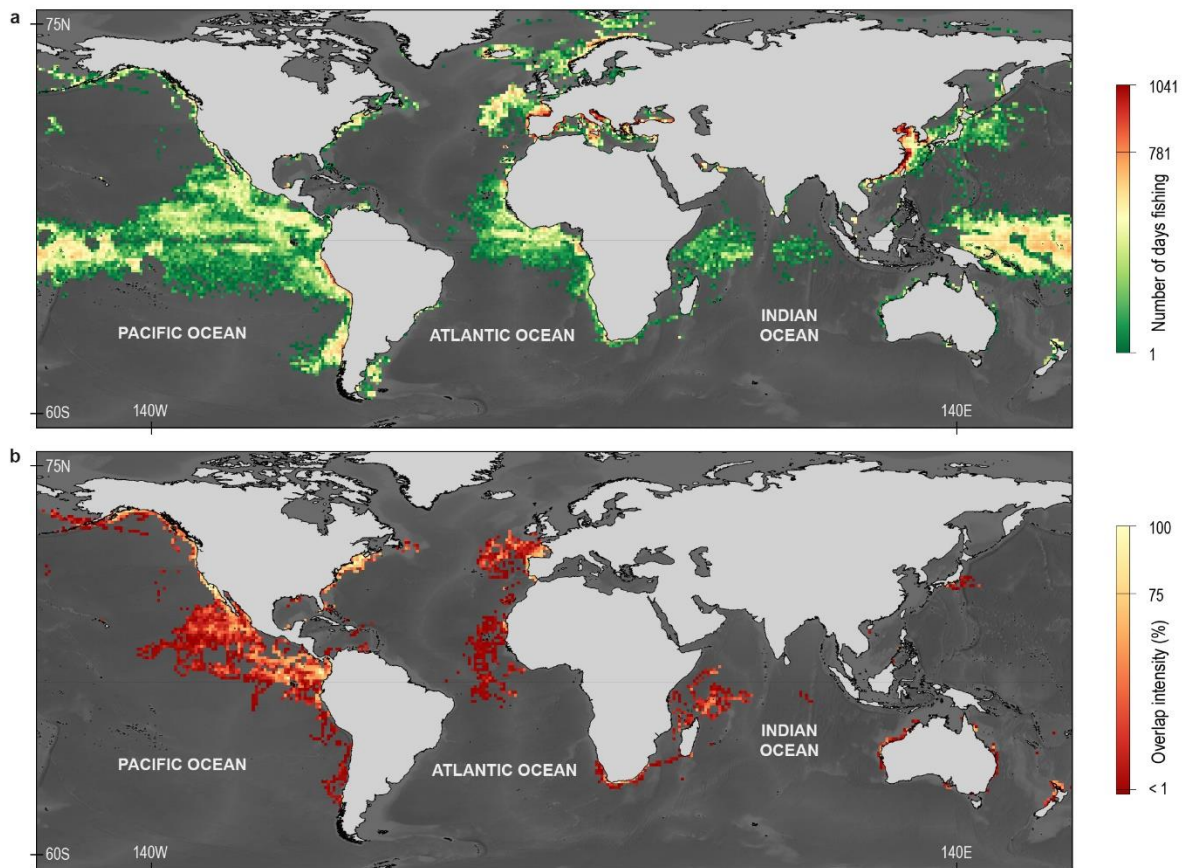
Extended Data Fig. 1. The location of shark tag deployment sites in relation to shark space use hotspots. Red circles denote the locations where satellite transmitters were attached and sharks released, and blue squares in the eastern Pacific denote annual median deployment locations of tags by the Tagging of Pacific Predators (TOPP) program (ref. 13). Shark space use hotspots are shown as the 75th (blue dotted lines) and 90th percentiles (red dotted lines) of the relative density of estimated shark positions within $1 \times 1^\circ$ grid cells given in Fig. 2a.



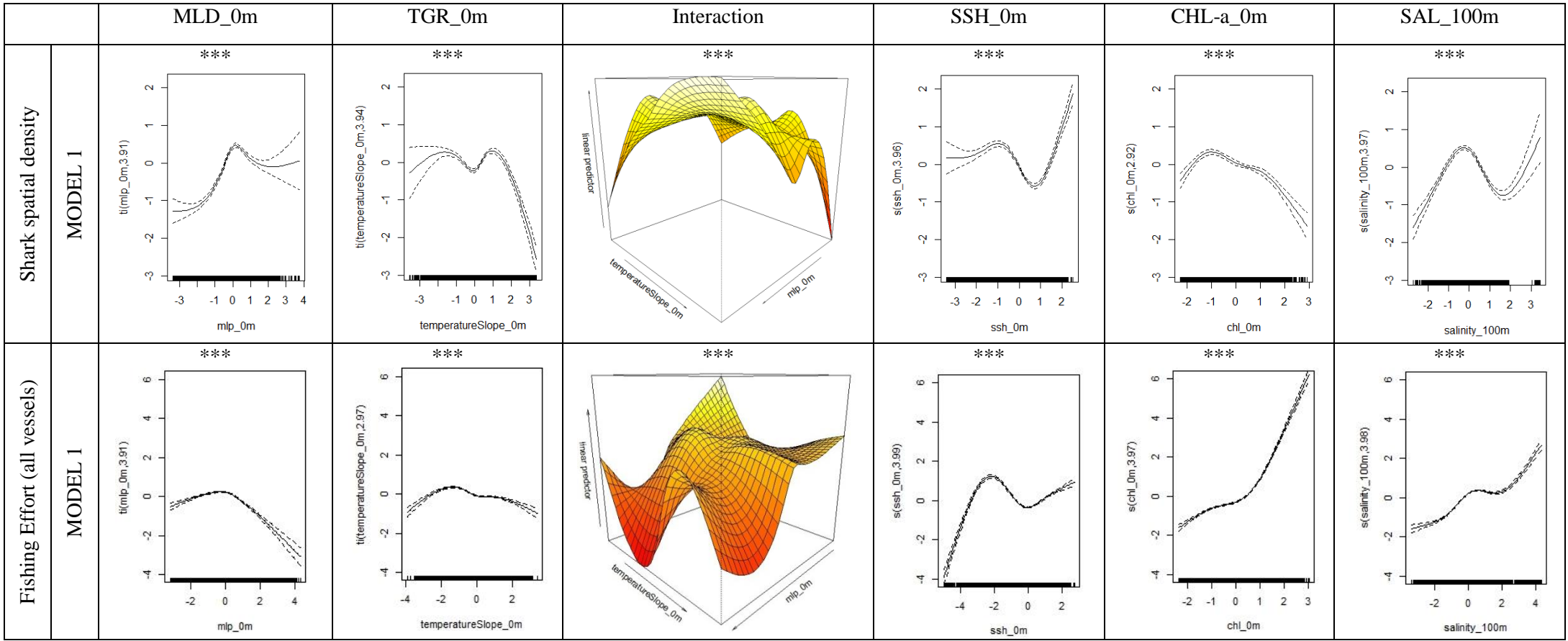
Extended Data Fig. 2. Schematic maps of oceanographic and physical features. Major ocean currents (a) and physical features (b) referred to in this paper. Coloured arrows in a denote thermal regime of currents, with warmer colours indicating greater water temperature. Abbreviations in b denote: CGFZ, Charlie Gibbs Fracture Zone; GBR, Great Barrier Reef; PNG, Papua New Guinea; IMS, Isakov and Makarov Seamounts.

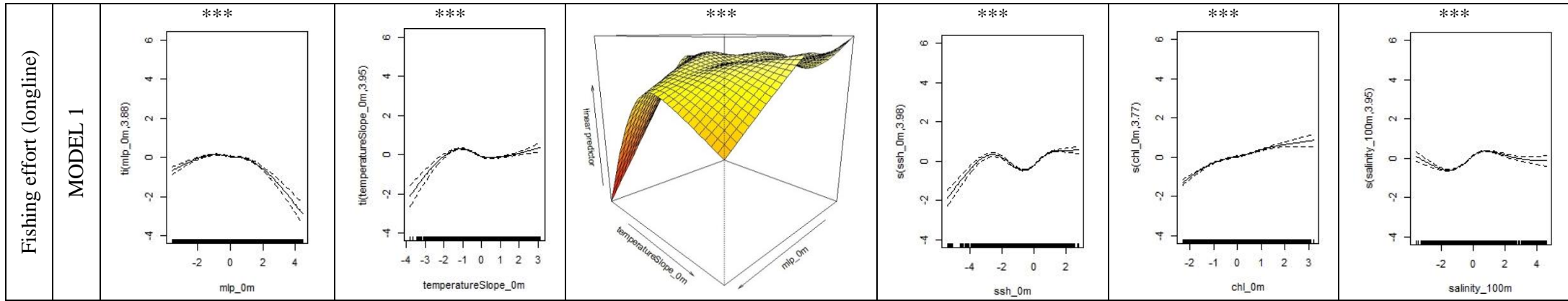


Extended Data Fig. 3. Spatial distribution of fishing vessels and overlap intensity with sharks. (a) Distribution of 83,628 AIS tracked fishing vessels' effort (mean annual days spent per grid cell) between 2012 and 2016 (see Methods). (b) Distribution of the overlap intensity between shark density and fishing effort (spatial co-occurrence within $1 \times 1^\circ$ grid cells). Spatial overlap intensity hotspots were defined as $1 \times 1^\circ$ grid cells with $\geq 75\%$ overlap. Note the similar overlap intensity pattern of sharks and all mapped AIS fishing vessels as that determined for sharks and longline vessels in Fig. 2c.

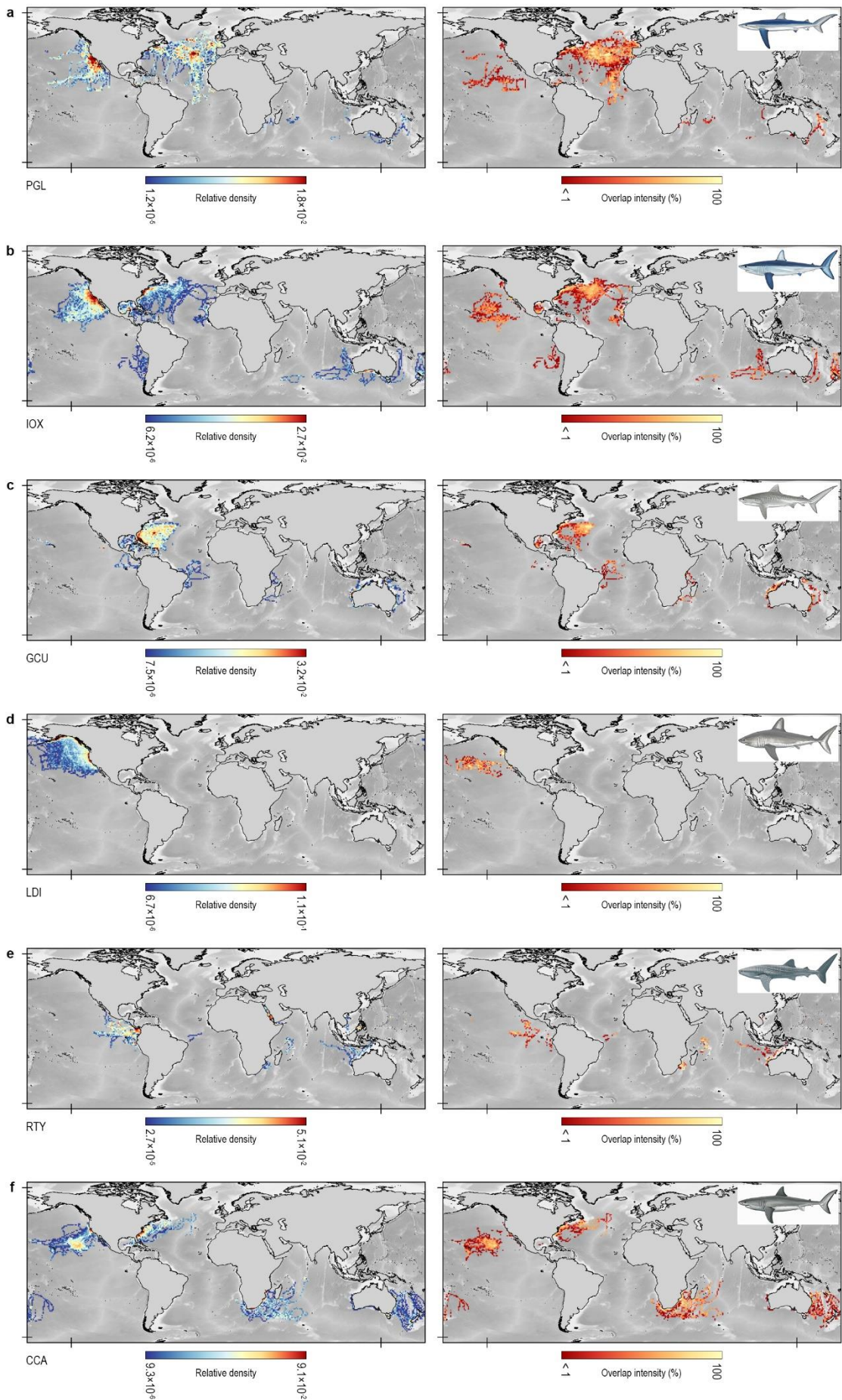


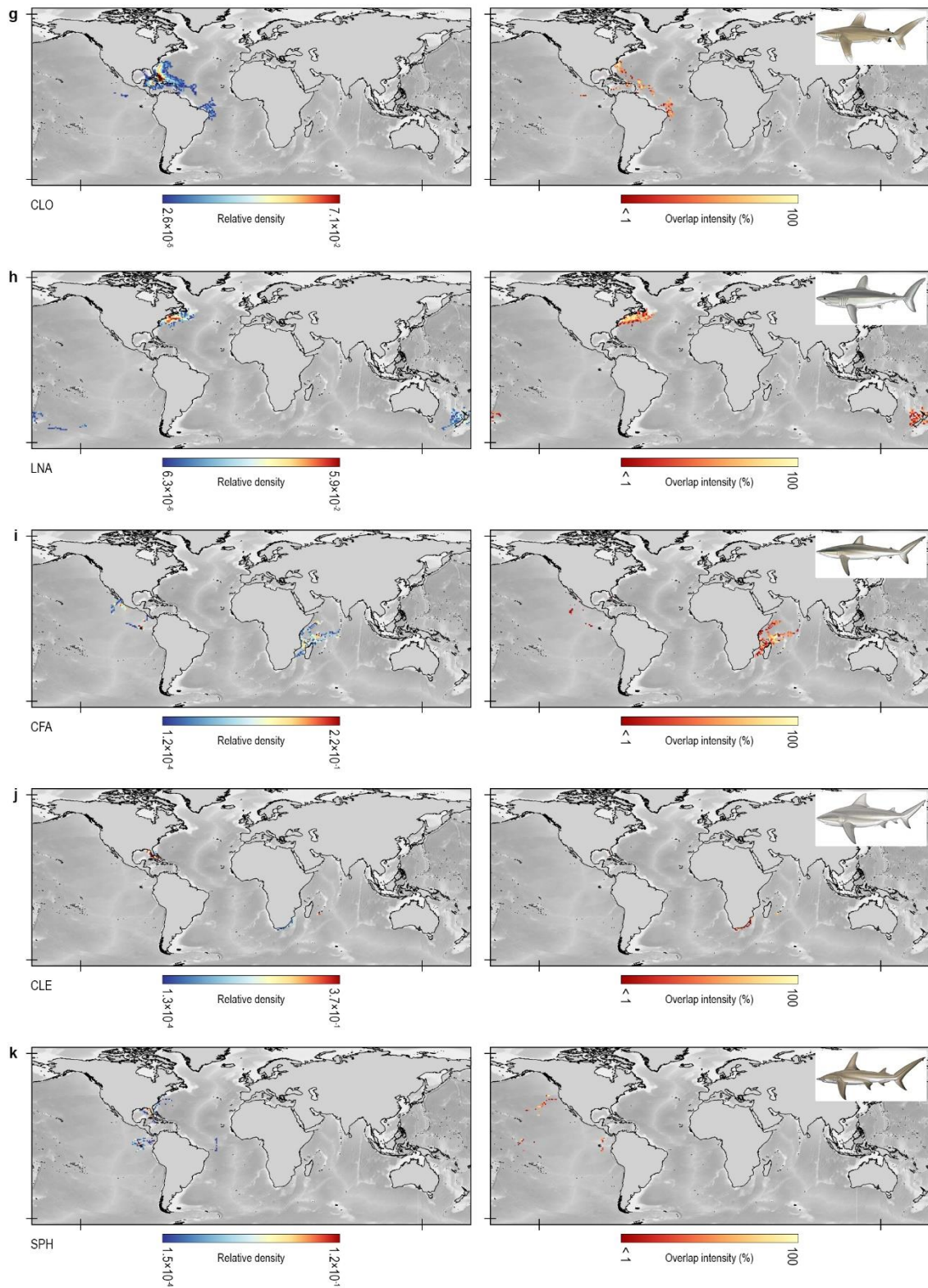
Extended Data Fig. 4. Spatial distribution of purse seine fishing vessels and overlap intensity with sharks. (a) Distribution of 6,941 AIS purse seine vessels' fishing effort (mean annual days spent per grid cell) between 2012 and 2016 (see Methods). (b) Distribution of the overlap intensity between shark density and fishing effort (spatial co-occurrence within $1 \times 1^\circ$ grid cells). Spatial overlap intensity hotspots were defined as $1 \times 1^\circ$ grid cells with $\geq 75\%$ overlap.





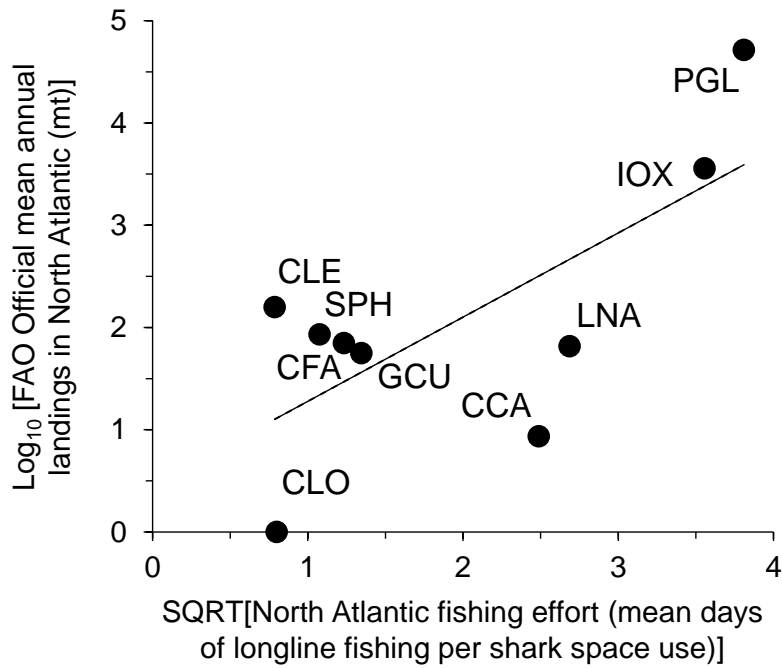
Extended Data Fig. 5. Estimated relationships between relative density of all sharks (top panel) and AIS fishing effort of all vessels (middle panels) and longlines only (bottom panels) with all environmental variables in the highest ranked (Model 1) of the generalised additive models (GAM) tested. Third column shows the interaction results between the two variables described in the first and second columns. Asterisks indicate significance level for each smooth term included in the GAM, representing $p < 0.001$ (***), < 0.01 (**).



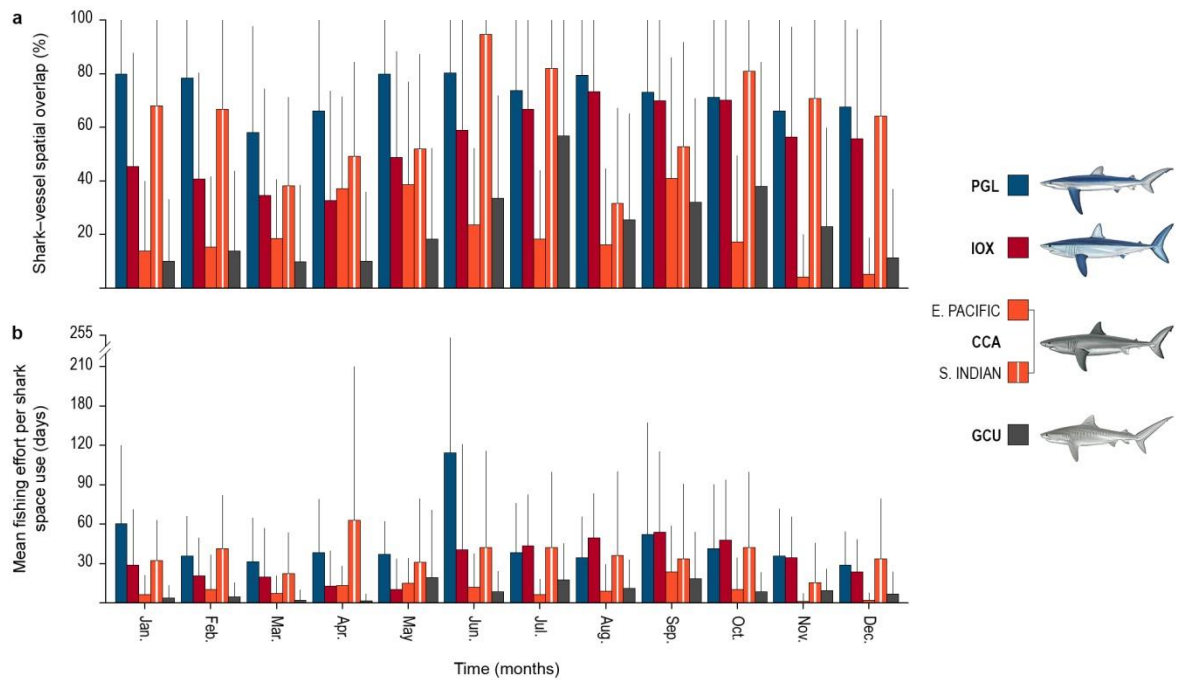


Extended Data Fig. 6. Relative density and spatial overlap intensity distributions for individual shark species. Relative density of sharks (left panels) tracked in 2002–2017 in comparison with shark-vessel spatial overlap intensity with AIS longline fishing vessels

(2012–2016) (right panels) for the 11 most data-rich species/taxa groups: (a) blue, *Prionace glauca*; (b) shortfin mako, *Isurus oxyrinchus*; (c) tiger, *Galeocerdo cuvier*; (d) salmon shark, *Lamna ditropis*; (e) whale shark, *Rhincodon typus*; (f) white, *Carcharodon carcharias*; (g) oceanic whitetip, *Carcharhinus longimanus*; (h) porbeagle, *Lamna nasus*; (i) silky, *Carcharhinus falciformis*; (j) bull, *Carcharhinus leucas*; and (k) hammerhead sharks, *Sphyrna* spp. (comprising: scalloped, *S. lewini*; great, *S. mokarran*; and smooth, *S. zygaena*). Shark images created by M. Dando.

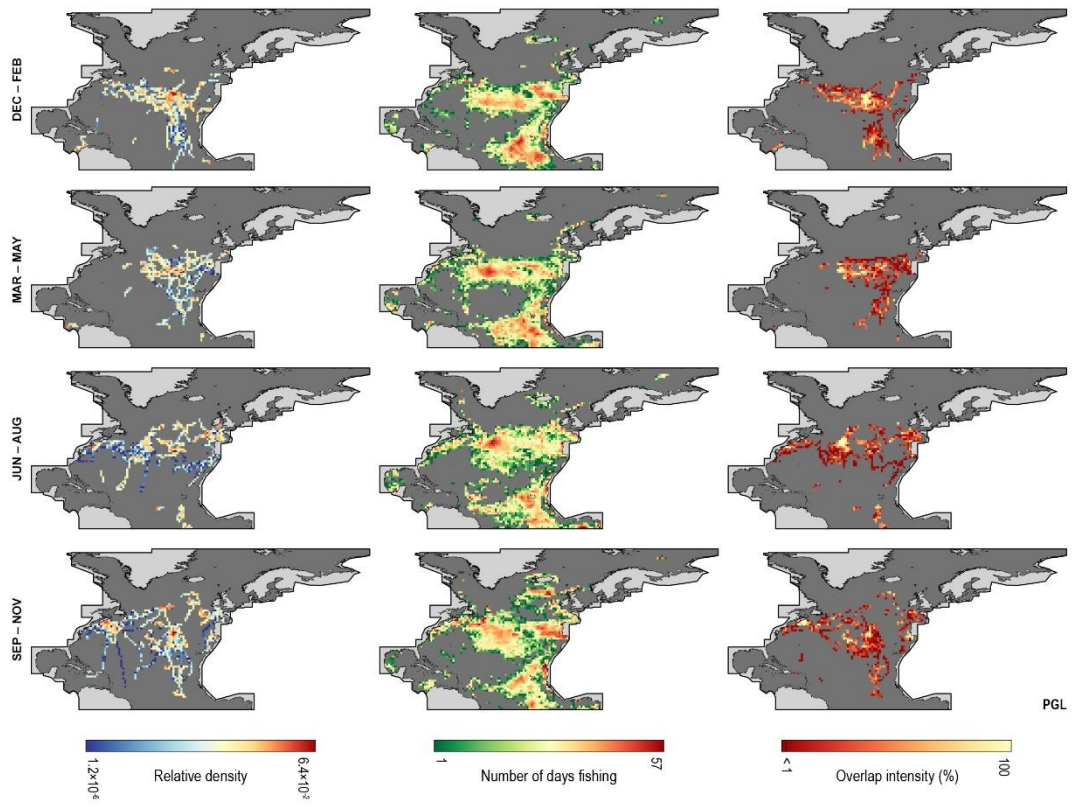


Extended Data Fig. 7. Relationship between North Atlantic fisheries’ shark landings and AIS longline fishing effort in shark-vessel overlap areas. Plot showing shark landings from the North Atlantic (mean, 2012–2016) extracted from the Food and Agriculture Organization of the United Nations (FAO) total capture production database (see Methods) is dependent upon fishing effort of AIS longline vessels (2012–2016) in shark species space use areas in the North Atlantic (2002-2017). For linear regression analysis, we tested the null hypothesis (H_0) that $\beta = 0$ after normalising landings by log transformation and fishing effort by square-root transformation. We computed $r^2 = 0.51$, $F = 7.14$ and $F_{0.05(1),1,7} = 5.59$, therefore rejecting H_0 at the 5% level of significance with $p = 0.032$. Species identification codes are given in Fig. 1.

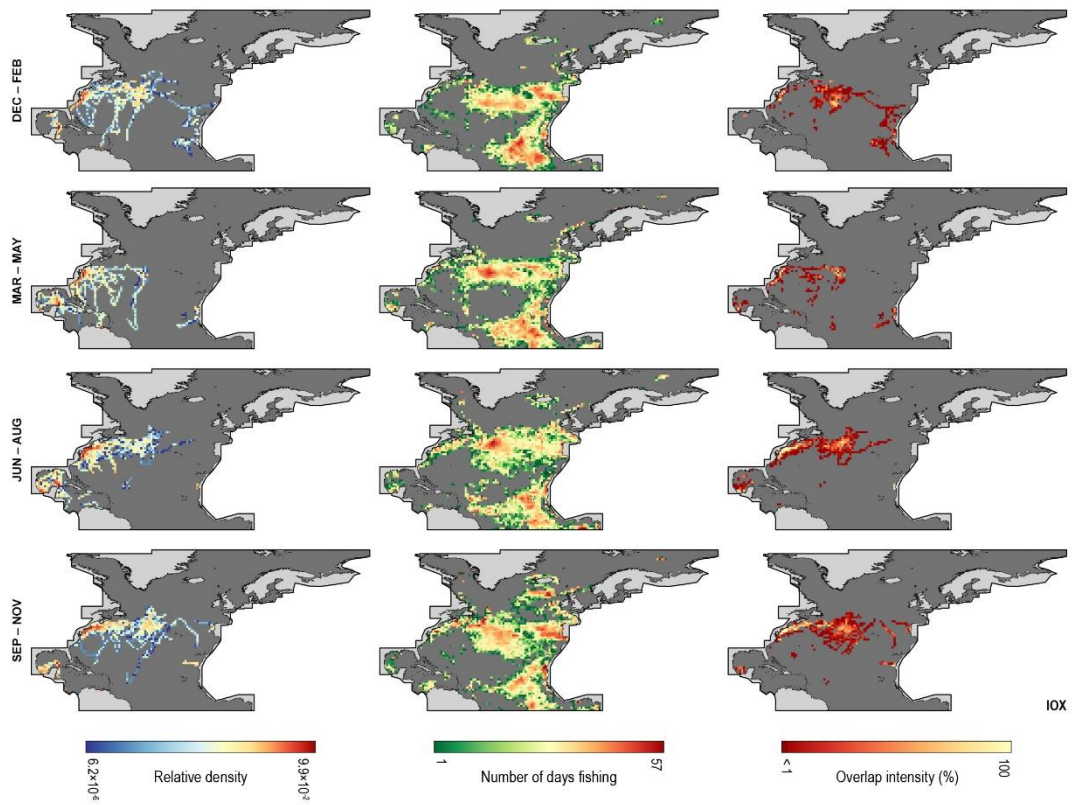


Extended Data Fig. 8. Example of temporal changes in spatial overlap and fishing effort. (a) Annual variation in shark-longline vessel spatial overlap and (b) longline fishing effort per shark space use. Shark species identification codes are given in Fig. 1. Error bars are ± 1 S.D. Shark images created by M. Dando.

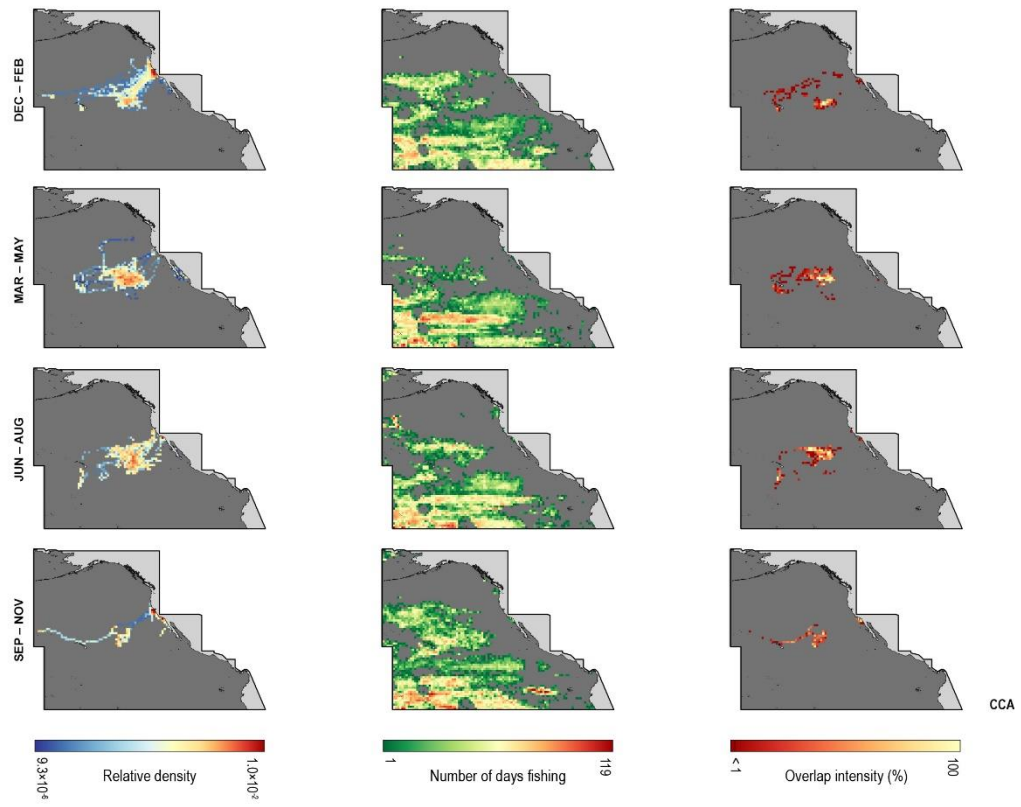
a



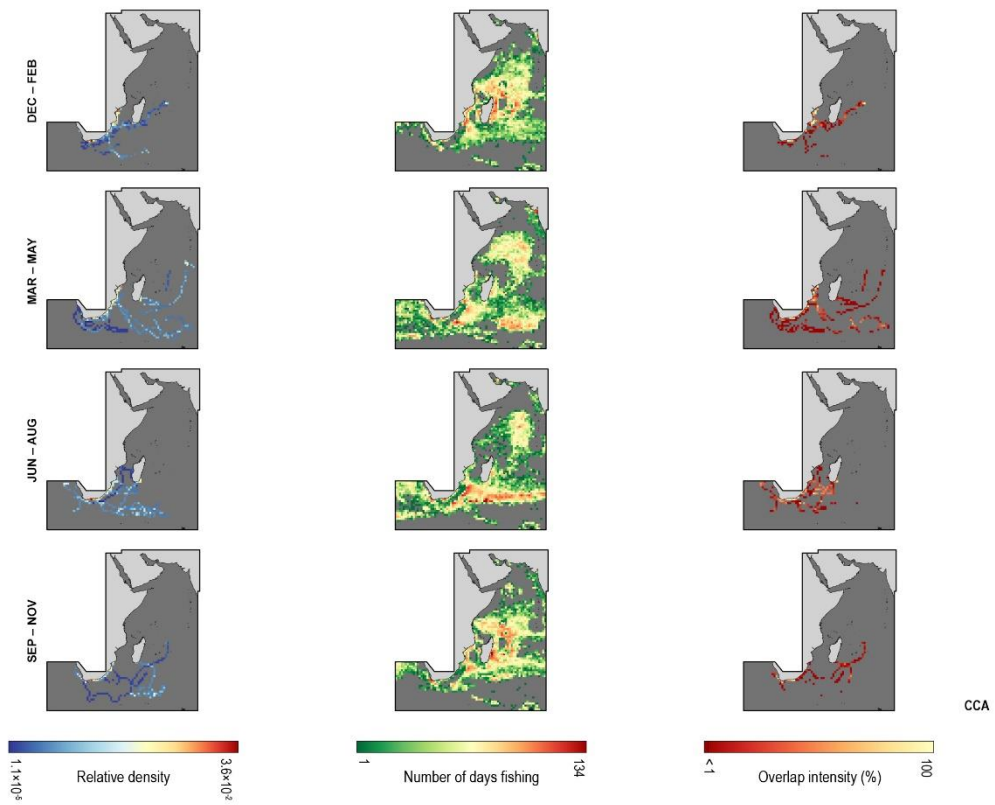
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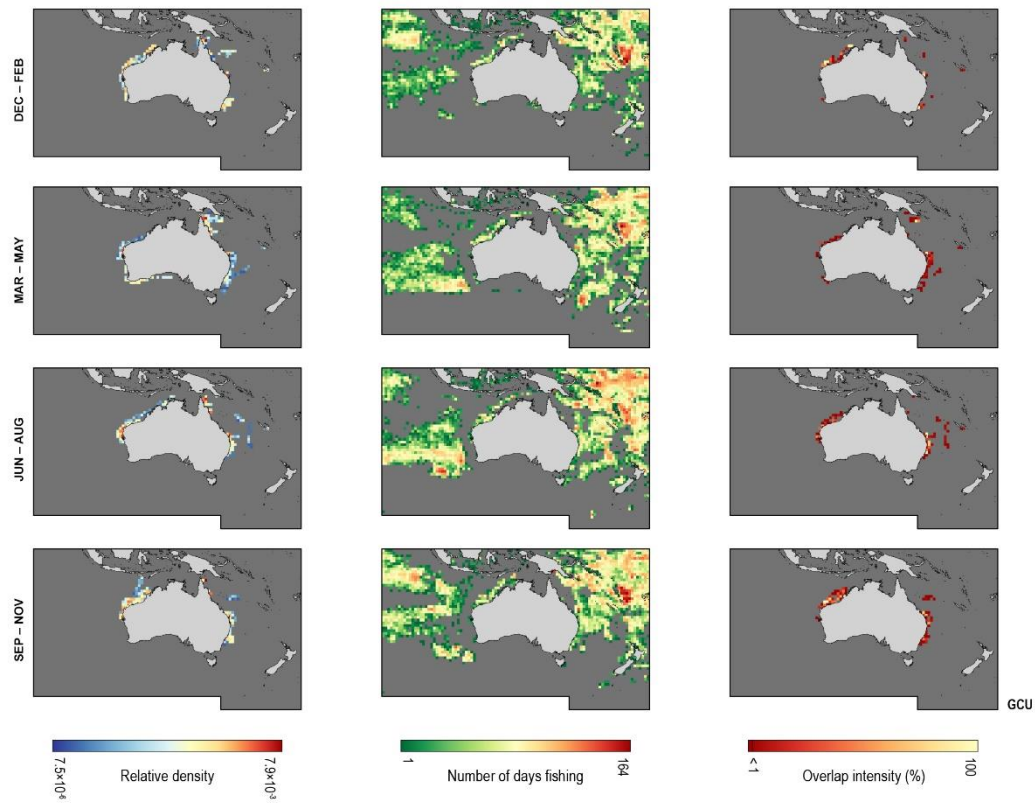
c



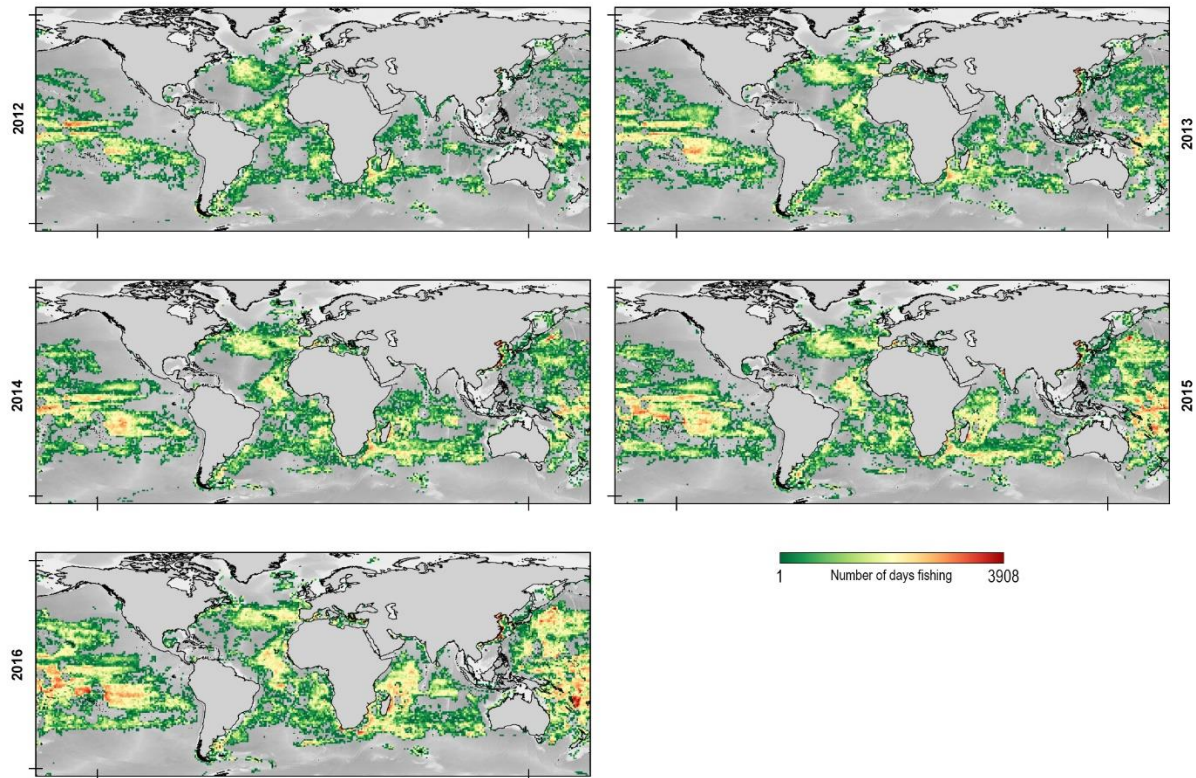
d



e



Extended Data Fig. 9. Seasonal shifts in sharks, longline vessels and shark-vessel overlap intensity. Relative spatial density of sharks (left panels), longline fishing effort (middle), and percentage spatial overlap intensity (right panels) in each seasonal quarter for (a) North Atlantic blue and (b) shortfin mako sharks, (c) east Pacific and (d) southwest Indian Ocean white sharks, and for (e) tiger sharks in the Oceania region. Shark species identification codes at bottom right of each panel are given in Fig. 1.



Extended Data Fig. 10. Annual spatial distribution of AIS longline fishing effort, 2012–2016. The global distribution of AIS monitored fishing effort varied across years as new AIS satellite receivers became operational which increases global coverage (for details see ref. 21). 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 per shark space use (see Methods).