Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots

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Overfishing is arguably the greatest ecological threat facing the oceans, yet catches of many highly migratory fishes including oceanic sharks remain largely unregulated with poor monitoring and data reporting. Oceanic shark conservation is hampered by basic knowledge gaps about where sharks aggregate across population ranges and precisely where they overlap with fishers. Using satellite tracking data from six shark species across the North Atlantic, we show that pelagic sharks occupy predictable habitat hotspots of high space use. Movement modeling showed sharks preferred habitats characterized by strong sea surface-temperature gradients (fronts) over other available habitats. However, simultaneous Global Positioning System (GPS) tracking of the entire Spanish and Portuguese longline-vessel fishing fleets show an 80% overlap of fished areas with hotspots, potentially increasing shark susceptibility to fishing exploitation. Regions of high overlap between oceanic tagged sharks and longliners included the North Atlantic Current/Labrador Current convergence zone and the Mid-Atlantic Ridge southwest of the Azores. In these main regions, and subareas within them, shark/vessel co-occurrence was spatially and temporally persistent between years, highlighting how broadly the fishing exploitation efficiently "tracks" oceanic sharks within their space-use hotspots year-round. Given this intense focus of longliners on shark hotspots, our study argues the need for international catch limits for pelagic sharks and identifies a future role of combining fine-scale fish and vessel telemetry to inform the ocean-scale management of fisheries.

animal telemetry | distribution | conservation | fisheries | predator–prey

Oceanic pelagic sharks are iconic top predators with relatively low resilience to exploitation (1–3), yet many tens of millions of individuals are caught each year by high-seas fisheries (2) with significant reductions in catch rates documented for many species (4–6). This level of exploitation is especially problematic because the harvest of oceanic sharks remains largely unregulated (2, 7). For the majority of shark species that make up more than 95% of oceanic shark catches, no international or bilateral harvest limits have been imposed (2, 7). Consequently, analysis indicates that extinction risk in oceanic and coastal sharks and rays is higher than for most other vertebrates (3). Accordingly, there is a critical need and concern for improved management and conservation of oceanic sharks.

Management action for oceanic sharks such as catch quotas, size limits, and/or area closures (i.e., marine protected areas, MPAs) is hampered by a paucity of high-quality data on total catches, landings, species identification, catch locations, and the susceptibility of sharks to fisheries (2, 4, 7). In addition, poor recordkeeping, a lack of reporting or deliberate underreporting of pelagic shark catches by the high seas longlining fleet and/or fishing nations (7), contributes to poor data quality that can lead to increased uncertainty in scientific stock assessments of population trends (8–10). Furthermore, it is particularly difficult to accurately quantify population trends of pelagic sharks and the efficacy of different management tools because these sharks are highly migratory, moving long distances over whole ocean basins (11, 12), which can further complicate conservation strategies (13). Information is urgently needed on the habitat preferences, movements, and migrations of oceanic sharks and the extent of overlap with commercial fisheries (4, 11, 14). For instance, stable or increasing catch per unit effort (CPUE) trends might be linked to changes in areas fished, potentially altering overlap with important habitats of sharks that could mask real population declines already occurring. However, a significant limitation affecting management of oceanic sharks is little knowledge of where, when, and how fish and fishing vessels overlap across their entire ranges (4, 15). There have been recent technological advances in surveillance of the ocean environment (16), fisheries' activities (17), and tracking fish movements and migrations (11, 12). However, high-resolution monitoring (18) of environment–fish–fishery interactions across whole population ranges is lacking, despite the potential of this approach to inform conservation.

In this study, we examine in unprecedented detail, to our knowledge, the spatial dynamics of multiple pelagic shark species and two complete fishing fleets in the North Atlantic Ocean over

Significance

Shark populations are declining worldwide because of overexploitation by fisheries with unknown consequences for ecosystems. Although the harvest of oceanic sharks remains largely unregulated, knowing precisely where they interact with fishing vessels will better aid their conservation. We satellite track six species of shark and two entire longline fishing vessel fleets across the North Atlantic over multiple years. Sharks actively select and aggregate in space-use "hotspots" characterized by thermal fronts and high productivity. However, longline fishing vessels also target these habitats and efficiently track shark movements seasonally, leading to an 80% spatial overlap. Areas of highest overlap between sharks and fishing vessels show persistence between years, suggesting current hotspots are at risk, and arguing for introduction of international catch limits.

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multiple years by using remote telemetry of animals and longline vessels to quantify the overlap between fishing exploitation and shark habitat use. The Atlantic is one of the most heavily fished ocean ecosystems where surface longline deployments can be up to eightfold higher than in the Pacific (14). Pelagic sharks account for approximately 30% of the total elasmobranch catch within the Atlantic Ocean with ~70% of this total comprising a single species, the blue shark *Prionace glauca* (7). The shortfin mako *Isurus oxyrinchus* is the second most frequently caught species on Atlantic longlines, making up approximately 20% of pelagic shark catches (7). The tiger shark *Galeocerdo cuvier* is also known to migrate seasonally into oceanic habitats (19) that are exploited by high seas longliners, whereas coastal/pelagic hammerhead sharks (*Sphyrna mokkaran* and *Sphyrna lewini*) probably overlap with fishers exploiting the continental shelf (20).

To investigate how oceanic and coastal pelagic sharks use distributional ranges with distinct environmental heterogeneity, we satellite-tracked >100 individuals over ~8,000 d by using electronic tags that give a fishery-independent spatial distribution over time (Fig. 1*A*, *Materials and Methods,* and *SI Appendix, SI Materials and Methods* and Tables S1 and S2). Sharks were tagged at seven main locations (coastal and oceanic) spanning the North Atlantic: from southwest England (United Kingdom) to Florida (United States) that included oceanic pelagic species (blue shark, n = 38; shortfin mako, n = 14; longfin mako, n = 1) in addition to coastal/oceanic pelagic species (tiger, n = 32; great hammerhead, n = 12; scalloped hammerhead, n = 2) (*SI Appendix*, Fig. S1 and Table S1). We analyzed these data with simultaneous Vessel Monitoring System (VMS) Global Positioning System (GPS) positions of 186 Spanish and Portuguese longliners (>15 m length) over a 9-y period. These longline fleets are two of the most important in the North Atlantic capturing pelagic sharks (7, 14) (*SI Appendix, SI Materials and Methods*). Our analyses aimed (*i*) to determine the movements and habitat preferences of pelagic sharks and longline vessels, and (*ii*) to identify the areas where sharks and commercial vessels overlapped the most and the temporal persistence of these areas.

Results

Shark Tracking and Habitat Preferences. We successfully tagged 113 pelagic sharks across the North Atlantic (*SI Appendix*, Fig. S1 and Table S1). Track data were received from 99 tagged sharks totalling 7,990 d of data with an average track time of 80.2 d (range, 4–551 d) (*SI Appendix*, Table S1). However, our results focused on 96 tracked individuals from four species: blue, shortfin mako, tiger, and great hammerhead sharks. Mapping the filtered individual tag geolocations (*Materials and Methods* and *SI Appendix, SI Materials and Methods 1.2*) showed a broad distribution of sharks spanning diverse North Atlantic habitats that are productive and generally bounded at higher latitudes by the 12 °C isotherm (Fig. 1 and *SI Appendix, SI Results* and Fig. S9). Among oceanic sharks, there were some extensive individual movements: A shortfin mako was tracked moving from west to east (50° to 9°W) and individual blue and mako sharks traveled from north to south (35° to 13°N). The distribution of blue and mako sharks shifted seasonally, from more northerly latitudes in spring-summer to lower latitudes and more easterly longitudes in autumn-winter (Fig. 1 *B* and *C*). Tiger sharks tagged in tropical and subtropical coastal locations moved into oceanic habitats of the Gulf Stream during warmer months, whereas tagged hammerhead sharks remained in continental shelf habitats for the study duration (Fig. 1*A* and *SI Appendix*, Fig. S11). Despite these species-specific differences in large-scale space use in the North Atlantic, it was also evident that sharks aggregated in specific regions, with some areas such as the Gulf Stream and North Atlantic Current areas supporting shared space use by four tagged species (i.e., *P. glauca*, *I. oxyrinchus*, *I. paucus*, *G. cuvier*). The majority of filtered track locations were in highly productive areas such as the Gulf Stream and North Atlantic Current/Labrador Current convergence zone (NLCZ), with a general absence of shark locations in oligotrophic regions such as the Sargasso Sea (Fig. 1*A*).

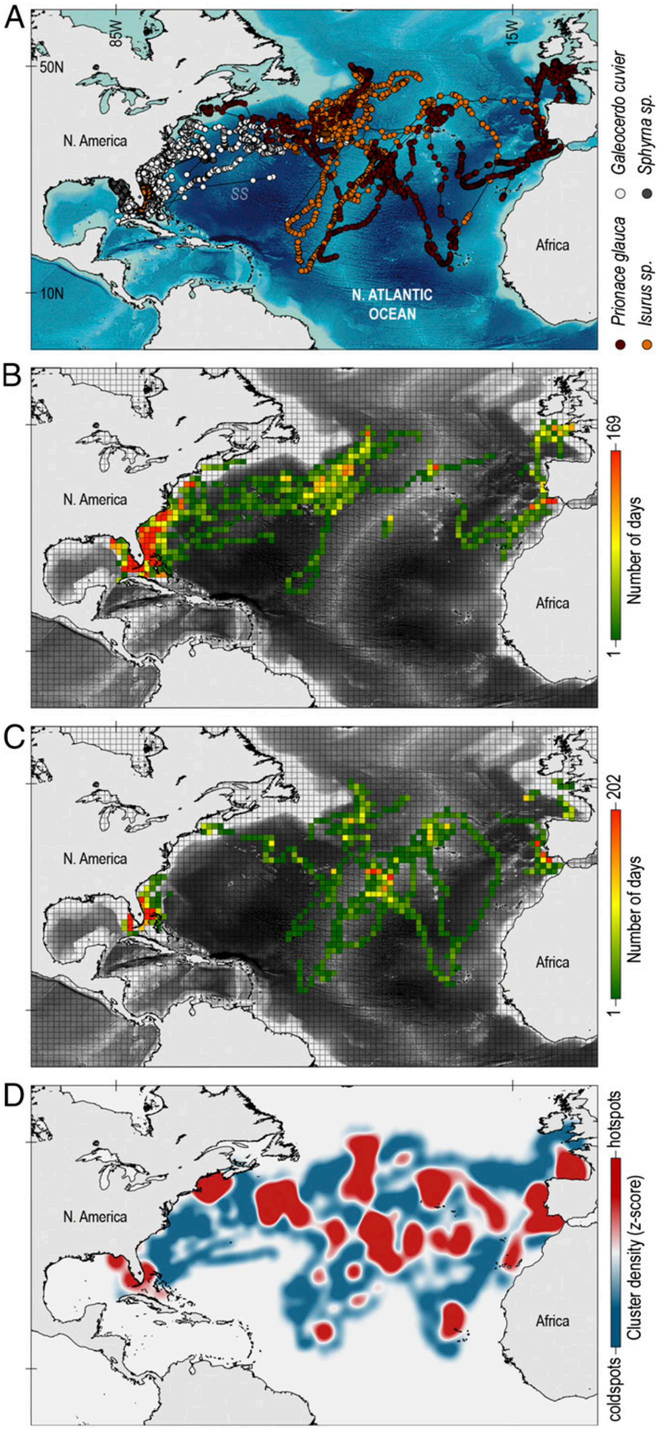

Fig. 1. Spatial distributions of satellite-tracked pelagic sharks. (*A*) Fishery-independent satellite track geolocations of oceanic and coastal/pelagic sharks in the North Atlantic Ocean, 2006–2012. Space use shift between spring-summer (March–August) (*B*) and autumn-winter (September–February) (*C*) determined from tag geolocations. (*D*) Map of the calculated high (hotspot; red) and low (coldspot; blue) use habitats of tracked sharks. SS, Sargasso Sea.

To quantify the focal areas used by tagged sharks, we applied spatial hotspot analysis (21) to identify areas of high use (termed hotspot) versus lower use ("coldspot") among species (Fig. 1*D*). For these analyses, we used an effort-corrected index of occurrence per unit area (number of mean days per grid cell) (22) to reduce biases from tagging location and track length

(*SI Appendix*, Fig. S2 and *SI Materials and Methods 1.3*). The resultant distribution of shark space use hotspots was not sensitive to the total number of shark locations per track (*SI Appendix*, Fig. S3), and the frequency of track gaps between geolocations >10 d was low (<1.4 per track on average; *SI Appendix*, Table S2). Importantly, shared hotspot areas were located in the Gulf Stream, NLCZ, Azores Islands, Mid-Atlantic Ridge (MAR) southwest of the Azores, and the Iberian Peninsula (Fig. 1*D*).

It is poorly understood how the large-scale biophysical structure of the North Atlantic influences individual shark distribution patterns (15, 23) and, consequently, how this could influence catch rates. To investigate shark habitat selection explicitly, we tested associations of individual sharks with oceanographic features by comparing geolocated tracks with simulated random walks of model sharks using resource selection probability functions (RSPFs) (*SI Appendix*, Fig. S6 and *SI Materials and Methods 1.5*). The analysis showed that, overall, tagged sharks selected particular thermal habitat (sea surface temperature, SST; Fig. 2) and within those areas, preferred frontal boundary habitats characterized by steep SST and productivity gradients (Fig. 2). For the oceanic species, mako sharks preferred habitats with high SST gradients and primary productivity, whereas, by contrast, blue sharks only showed habitat preference for productive areas (Fig. 2). Similar to makos, hammerhead sharks favored areas with SST discontinuities and high productivity; however, these habitats were located in shelf rather than oceanic areas, whereas tiger shark habitat preference was for SST gradients in both ecosystems (Fig. 2).

Longliner Tracking and Distributions. For Spanish and Portuguese longliner movements, we removed nonfishing (traveling) GPS locations and identified active fishing locations (*SI Appendix*, Fig. S4 and *SI Materials and Methods 1.4*). Each fishing deployment comprised ∼100 km longline with a mean number of 1,215 baited hooks set at ∼150 m depth. The fishing locations of the combined fleets (n = 1,063,861 data points) spanned most of the North Atlantic, extending from 5° to 62°W and from 57°N to the Equator (Fig. 3*A*). However, fishing locations were highly heterogeneous within the broad distribution (Fig. 3*B*). Overall, longline deployment was concentrated in three main areas of the North Atlantic: (*i*) the large central area bounded by the Gulf Stream, NLCZ, and the Azores Islands in the north and down to 30°N in the south, (*ii*) a smaller area west of the Iberian Peninsula, and (*iii*) several smaller, more dispersed areas off northwest Africa (Fig. 3*B*). There was seasonal variation in fishing locations of the fleets. Generally, more southerly areas of the central North Atlantic were exploited during winter months (December to February) (Fig. 3*C*) with progressive northerly movements through spring into summer, when fishing was concentrated in the NLCZ region (Fig. 3 *D* and *E*), followed by a general southeast shift during autumn (September to November) (Fig. 3*F*). In contrast to the NLCZ region, the west African upwelling area was exploited year-round, whereas the west Iberian area was most heavily fished in autumn and winter (Fig. 3 *C*–*F*).

Not surprisingly perhaps, the habitat modeling (RSPF) analysis showed longliners select productive habitats that, like those of sharks, were also characterized by high thermal front frequency, and thermal and sea surface height (SSH) anomalies (Fig. 2 and *SI Appendix*, Fig. S8). From detailed analysis of the movements of 50 longliners, we found that clusters of fishing locations (n = 874), a pattern associated with higher catch frequency (*SI Appendix*, Fig. S4), represented 73% of all fishing activity and were associated with frontal and productive regions (*SI Appendix*, Fig. S5).

Shark-Longliner Overlap. To evaluate explicitly the spatial overlap between sharks and longlines, we calculated the coincidence of oceanic sharks and longliners within each 1° × 1° grid cell at any time within the datasets (*SI Appendix*, *SI Materials and Methods 1.6*). For this analysis, we principally considered blue (n = 38) and mako sharks (n = 14; for results of tiger and hammerhead sharks, see *SI Appendix*, *SI Results 2.3*). This selection is because, first, blues and makos comprise the majority of pelagic shark landings (>95%), and second, the longlining fleets we analyzed spent the greatest proportion of time in oceanic areas of the central and eastern North Atlantic where blue and mako sharks were the most commonly tagged species in our study. Overall, blue and mako sharks had approximately 80% of their tracked range overlapped by Spanish and Portuguese longliners (80.7% and 79.6% for blue and mako sharks, respectively). Also, the observed spatial and temporal cooccurrence (overlap frequency) corresponded to areas of high seasonal fishing effort and/or shark space-use hotspots (Fig. 4*A*). Although overlap areas were broad, they were predominant in oceanic frontal regions of the Gulf Stream/NLCZ and near the MAR southwest of the Azores. We also found different potential capture risks for oceanic-tagged blue and mako sharks: blue sharks spent on average 2.6 d per month (range, 0.0–20.2) in the same grid cell as a longline, whereas this time was significantly higher overall for makos at 3.0 d per month (range, 0.0 and 12.2) (Mann–Whitney u test = 163.5; $P < 0.05$).

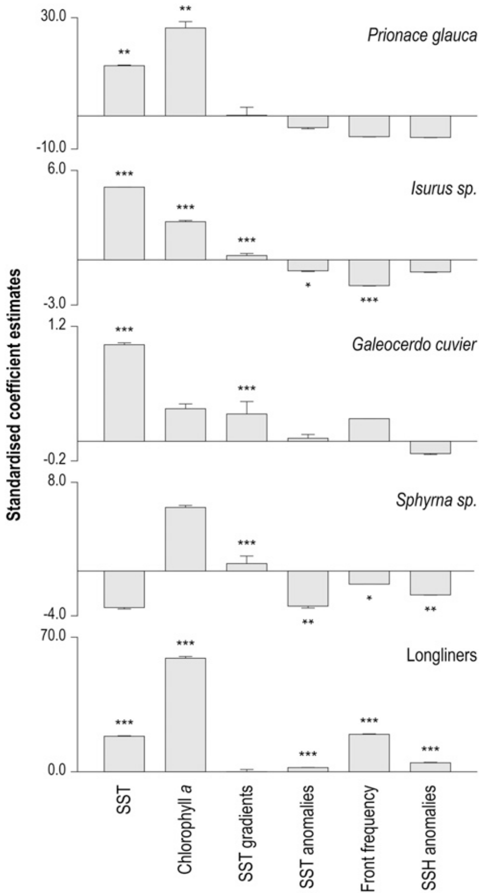

Fig. 2. Habitat selection of pelagic sharks and longliners. Standardized RSPF model coefficient estimates and SEs for the different environmental variables, shark species, and longliners. Note that higher positive values indicates stronger selection for that particular habitat type. Selection indices were post hoc standardized by following ref. 34. Significance levels: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$. SSH, sea surface height; SST, sea surface temperature.

The between-years persistence in areas of high overlap frequency between oceanic sharks and longliners (Fig. 4 *B* and *C*) was tested by comparing two years (2005 and 2009) for which there were sufficient shark track data and geolocation data for both fleets. The principal areas of oceanic shark distribution shifted from the Gulf Stream/NLCZ in spring-summer to the MAR and Azores Islands in autumn-winter (Fig. 1 *B* and *C*). Mapping longliner fishing locations for 2005 and 2009 showed persistence between years for more intense exploitation of the NLCZ area in summer, to the MAR area west and southwest of the Azores in autumn (*SI Appendix*, Fig. S10).

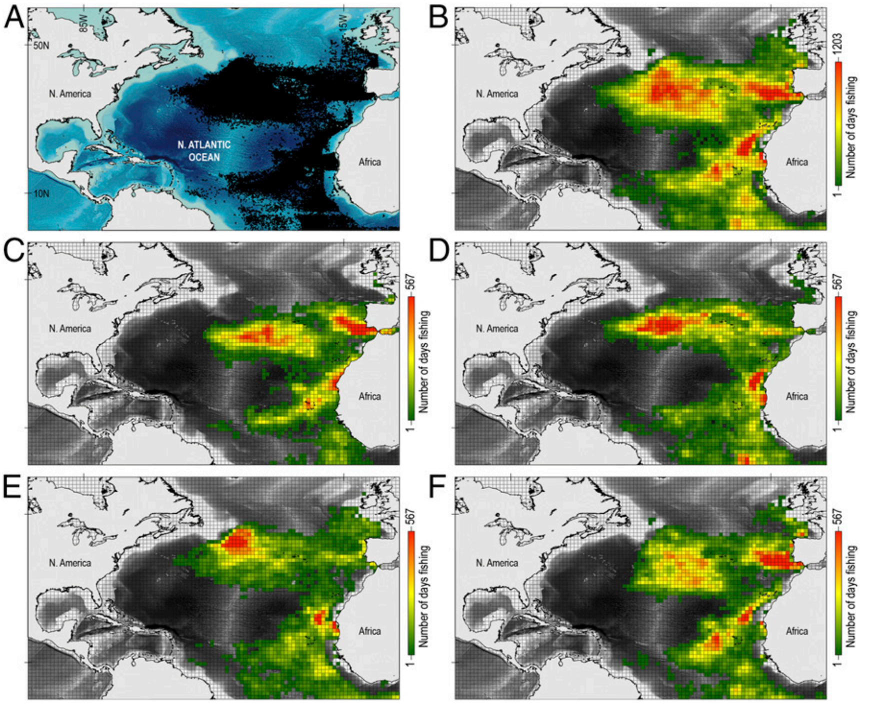

Fig. 3. Annual and seasonal distributions of Spanish and Portuguese longline fishing effort. (*A*) Distribution of longline deployment locations by 186 Spanish and Portuguese vessels, 2003–2011. (*B*) Map showing core fishing areas of the combined fleets. Seasonal shifts and stability in spatial coverage of North Atlantic longliner exploitation intensity; winter (December–February) (*C*), spring (March–May) (*D*), summer (June–August) (*E*), and autumn (September–November) (*F*).

These two oceanic areas showed the highest overlap frequency between tagged sharks and Spanish and Portuguese longliners, with the pattern being very similar between years (Fig. 4 *B* and *C*).

Discussion

The present study is a first step, to our knowledge, in quantifying shark interactions with environment and fine-scale overlap with fishing vessels at the ocean-basin scale. We found that satellite-tracked oceanic and coastal pelagic sharks exhibit movements that extend across vast areas of the North Atlantic during an annual cycle. Analysis of satellite tag geolocations (*SI Appendix, SI Results and Discussion 2.1*) indicated that individual pelagic sharks spent more time in habitats with steep environmental gradients compared with random-walk model sharks with the same movement parameters. Results show that although shark movements and areas occupied appear heterogeneous, the space use of the tagged sharks was well predicted by SST and productivity discontinuities that characterize oceanographic features such as thermal fronts. Analyzing the pelagic longliner movements in the same manner showed a similar preference for habitats with strong thermal and productivity gradients, leading to a high degree of spatial overlap between pelagic sharks and longliners. Areas of high overlap with pelagic longliners included the Gulf Stream/NLCZ in spring-summer, and the MAR southwest of the Azores in autumn-winter. We estimated the shortfin mako shark to have higher potential capture risk than blue sharks, a pattern likely driven by makos showing stronger preference for frontal habitats that are preferentially exploited by longliners.

Previous studies have identified hotspots of oceanic shark biodiversity in the North Atlantic by using fisheries catch data (23), while tag location densities from satellite-tracked blue sharks have also been reported recently for the central and western North Atlantic region (24, 25). Coarse-scale spatial patterns of oceanic shark diversity from catch data indicate that in the North Atlantic, there is higher species richness in the Gulf Stream, the NLCZ, west of the Azores, and off northwest Africa (23), implying these areas are where sharks aggregate. Furthermore, there were some similarities between the pelagic shark space-use hotspots we estimated from tracking 99 sharks and two other recent satellite tracking studies in the North Atlantic. Sexually immature blue sharks ($n = 21$) satellite tagged and released in autumn on the continental shelf and shelf-edge between Nova Scotia and Newfoundland moved south and eastward into the warmer waters of the Gulf Stream, generally remaining there over winter (25). Furthermore, blue sharks ($n = 34$) tagged in the Azores Islands generally displayed wide-ranging movements albeit with a tendency for seasonal returns or annual site fidelity of juveniles to an area bounded by the Azores to the north, down to 30°N south of the Azores, and by the MAR to the southwest (24). The areas used by pelagic sharks in these independent tagging studies confirm several of the main space use hotspots we identified in the Gulf Stream, the NLCZ, and southwest of the Azores (Fig. 1*D*). This similarity suggests the space use hotspots we estimated are broadly representative of relative habitat use across not only spatial and temporal scales of the tracking data, but probably reflect general population patterns.

Oceanographic features such as frontal regions between different water masses with sharp gradients in temperature or salinity, for example, are known to have enhanced primary and secondary productivity and to support high apex predator diversity and abundance (11, 12, 14, 15). Building on this knowledge, our study shows that there was a higher likelihood of finding blue, mako, tiger, and hammerhead sharks on or near specific thermal fronts in oceanic or shelf habitats of the North Atlantic Ocean, with the movement/habitat model showing individual-based active selection for habitats with steep thermal gradients and/or productivity. For example, the stronger habitat preferences we observed in makos compared with blue sharks, especially with regard to thermal anomalies and gradients, may be due to the known wider ranging behavior of blue sharks compared with makos (14). The difference between these species may represent a greater preference of blue sharks for spending significant time in productive habitats adjacent to fronts. Overall, the hotspot analysis and movement/habitat modeling results demonstrate that the space use of pelagic sharks is predictable at the species level for a broad range of habitats, which should inform new models to assess shark availability to different fisheries (4, 15) (*SI Appendix, SI Discussion 2.3* and *2.4*).

It is possible that active behavioral preference for fronts by pelagic sharks may lead to significantly higher encounter rates with longliners that target frontal regions because of the high density of pelagic fishes that occur there. Pelagic longliners in the North Atlantic target high value tunas and swordfishes, but given general reductions in abundance of these species, and in view of management measures to limit catches, pelagic sharks are now

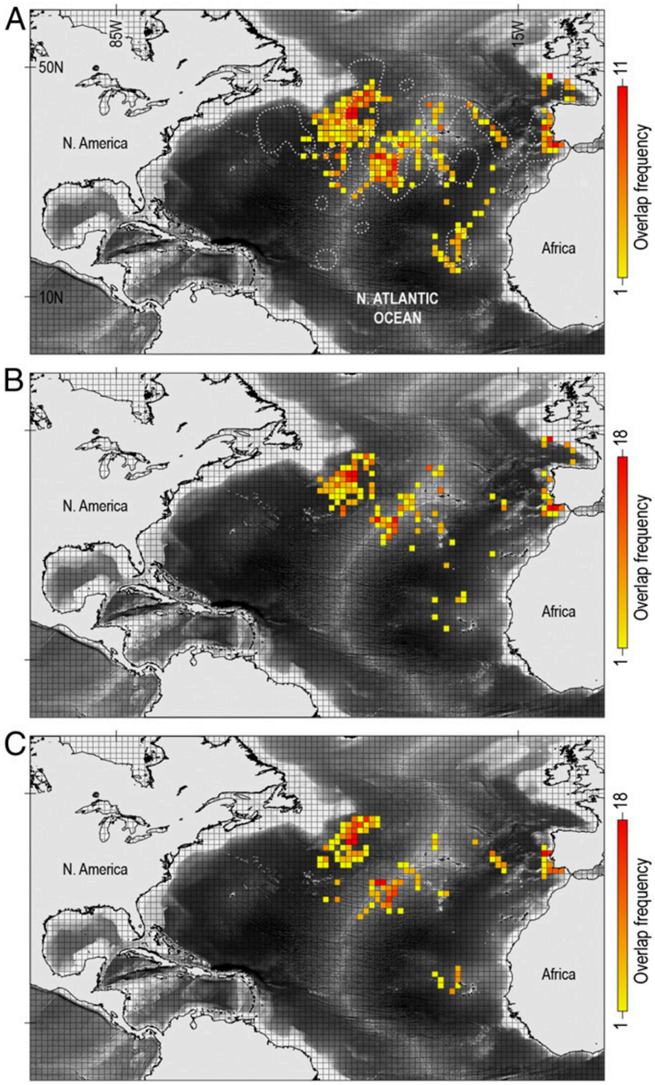

Fig. 4. Oceanic shark spatial and temporal overlap with longline vessels. (*A*) Distribution of the temporal cooccurrence (shared grid cell) between satellite-tracked oceanic sharks and Spanish and Portuguese pelagic longliners. Dotted white lines denote edges of space-use hotspots in Fig. 1*D*. Temporal persistence across years of the cooccurrence of tracked oceanic sharks and longliners: 2005 (*B*) and 2009 (*C*).

generally targeted by the longlining fleet (14). The longliners we studied are also known to routinely use SST remote-sensing images to locate fronts and spatially cluster their longline deployment locations when catches near them are higher (*SI Appendix*, Figs. S4 and S5), as documented for other longliner fleets (26). This behavior was confirmed in our study by movement/habitat modeling showing active selection for deploying longlines in regions with thermal and productivity fronts. When considering overall ranges, longliners overlapped areas occupied by tagged sharks by ~80% largely because fleets shifted seasonally, essentially "tracking" shark seasonal movements highly effectively. The results reveal that the highest longline deployment intensity is focused in areas of high shark space use, and particularly where oceanic blue and shortfin makos aggregate in the NLCZ and southwest of the Azores. Hence, although the mean overlap frequency (spatial and temporal cooccurrence) between longliners and sharks was ~3 d of risk per month (10% of the time), in high space-use areas, blue sharks were at potential risk of capture up to a maximum of 67.3% of the time (20.2 d at risk per month), with makos at potential risk up to 40.7% of the time (12.2 d at risk). Therefore, some characteristics of the longlining fleet, namely the vast geographic extent occupied, appear influenced by the wide distribution of target species, whereas by contrast, the spatially heterogeneous space use and targeting of productive frontal regions are influenced by both species-specific preferences (e.g., makos selecting fronts) and general higher abundance of sharks in more productive regions.

Satellite-tracking provides a means of determining the movements, space use, and broader-scale distributions of pelagic sharks that are independent of fisheries. For pelagic sharks such as blue and mako sharks that are targeted because of the high price of shark fins, a significant overlap between shark habitats and longliners is expected because fishers have good information about where to locate large marine fish. However, to our knowledge, there have been no previous studies that have attempted to quantify this overlap at the ocean-basin scale at such fine-spatial and temporal resolution. The longliner GPS (VMS) movement data we have analyzed is from two of the most important fleets operating in the North Atlantic, historically responsible for, as an example, 84% of the total number of blue sharks landed in 1997–2005 (27). Access to VMS data with this level of detail is unusual; for example, the longline fishing effort data generally available (10) is only coarsely resolved spatially to 5° × 5° grid cells and aggregated by quarter or year. Hence, there has not been the opportunity in recent studies (e.g., ref. 28) to determine marine predator/longliner spatial overlap or spatiotemporal cooccurrence at the fine scale but extending to the ocean-basin scale. The longliner fishing distribution and shark/longliner overlap maps in this study have 25 times the resolution of previous broad-scale studies that have examined marine predator/longliner cooccurrence (e.g., refs. 28 and 29). However, the picture we are able to present is still incomplete because although we analyzed two whole fleets, there are at least five other North Atlantic longline fleets. The apparent absence of pelagic longlining in the western North Atlantic illustrated by our distribution maps (e.g., Fig. 3) is most likely because we did not have access to VMS data from the United States, Canadian, and Japanese longliner fleets that target the western and northwestern areas extensively. Indeed, longliner GPS data from national fleets are not freely available internationally, which reduces the possibility for multifleet analyses to gain a fuller picture of the spatial dynamics of exploitation (*SI Appendix, SI Discussion 2.4*). The shark/longliner percentage overlap and spatiotemporal cooccurrence (overlap frequency) we report must be an underestimate therefore, highlighting the urgent need for better quantity and quality of fisheries and biological data to be reported.

Even with this understandable data limitation, our results demonstrate that the areas of highest coincident overlap (spatiotemporal cooccurrence) between sharks and both Spanish and Portuguese longliners persisted between years. Persistent hotspots are most likely to arise because longliners exploit repeatedly those habitats that are most predictably selected by sharks, i.e., those with strong SST and/or productivity gradients. Philopatric behavior by the sharks will also play a role (30). We found evidence for blue, mako, tiger, and hammerhead sharks remaining within relatively localized areas for extended periods of time, in addition to long-distance movements away from and return to preferred habitats. This behavioral trait can contribute to how frequently aggregations are exploited because area-focused longlining in preferred habitats of sharks will have higher catch rates than elsewhere. For the species in our study, the persistent use of localized areas that overlap fishing effort indicates potential for overexploitation at the ocean-basin scale.

Our results indicate that fishers are present in key oceanic shark habitats for much of the year, and therefore raise questions about the future sustainability of the fisheries. The areas we identify as supporting persistently high overlap frequencies may require special conservation measures to adequately protect sharks selecting those habitats. Given the large, persistent, overlap regions we identified, implementing management solutions based on spatial closures such as marine protected areas (MPAs), seasonal or otherwise, would likely entail prohibitive economic costs to the target fishery for swordfish and tunas and lead to the development of expensive incentive schemes (31) to overcome low compliance. Therefore, high seas MPAs may not be a viable solution at present for reducing pelagic shark catches at the ocean-basin scale. Attention could instead be focused on lower cost solutions that would affect shark–fishing vessel interactions directly through greater catch selectivity. Examples include the use of monofilament leaders (which sharks can sever by biting for escape), changes in hook depth (outside of sharks' preferred depths), hook type (precluding shark capture) and, more recently, development of gear that sharks avoid (e.g., use of electropositive metals and permanent magnets) (32). Nonetheless, consideration needs to be given to the inconsistent results so far obtained by using these approaches, not least the variable results on the same species between geographic regions. Hence, the application of selective gears to ocean-wide commercial operations appears to have some limitations in effectiveness at present and may also be difficult to regulate.

In light of the mixed results found for catch reduction of sharks using new gears, attention should instead focus on other available regulatory management procedures, such as the introduction of catch quotas and/or size limits. Although the implementation of these measures can often result in higher discards, postrelease survival rates of pelagic sharks are relatively high (65%; ref. 33), emphasizing that catch quotas/size limits may well be the simplest option to regulate/limit pelagic shark catches in international waters. Therefore, greater international efforts are needed to approach implementation of regulations aimed at limiting the catches of pelagic sharks by longlining fishing vessels that we have found to overlap their preferred habitats almost entirely.

Materials and Methods

Tagging and Tracking. Pelagic sharks (n = 113) were tagged with pop-off satellite archival transmitters or Argos satellite transmitters at seven North Atlantic locations. Ethical approval for shark tagging was given by the Marine Biological Association Animal Welfare and Ethical Review Body (AWERB) and licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986, and by the University of Miami Institutional Animal Care and Use Committee (IACUC). Spanish and Portuguese surface longline fishing vessels (n = 186) were GPS tracked. For data processing details see *SI Appendix, SI Materials and Methods*.

Spatial Density Analysis. Spatial hotspot analysis (21) was used to identify areas of high/low shark space use. Details given in *SI Appendix, SI Materials and Methods*.

Habitat Selection Modeling. Shark and longliner habitat selection in relation to oceanographic features was tested by comparing geolocated tracks with simulated random walks of model sharks/longliners by using RSPFs. Details given in *SI Appendix, SI Materials and Methods*.

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Supporting Information

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1. Supporting Methods

1.1. Study animals and tagging methods

Overall, 113 sharks were tagged between 2006 and 2012; however, since 14 tags reported poor data, we restricted our analysis to 99 tracks collected over 7,990 cumulative days and representing six species: blue (*Prionace glauca*) *n* = 38 individuals; shortfin mako (*Isurus oxyrinchus*) *n* = 14; longfin mako (*Isurus paucus*) *n* = 1; tiger (*Galeocerdo cuvier*) *n* = 32; great hammerhead (*Sphyrna mokarran*) *n* = 12, and scalloped hammerhead (*Sphyrna lewini*) *n* = 2. Figure S1 shows the tagging locations and numbers of sharks tagged at each location. Table S1 provides summary information of individuals tagged including size, sex, and tag type.

At coastal locations in the north-eastern Atlantic (southern England and mainland Portugal) capture and tagging methods of blue sharks followed Queiroz *et al*. (1, 2). Briefly, sharks were captured using rod and line and brought on-board for body-length measurement and tagging. Pop-off satellite-linked archival transmitter tags (PSATs; models PAT4 and PAT-Mk10, Wildlife Computers, Redmond, WA, USA) were attached via a monofilament tether (250 lb test) connected to a 5-cm long stainless steel T-bar arrowhead or an ‘umbrella’ type nylon dart. Tags were inserted into the dorsal musculature at a 45º angle to a maximum depth of 10 cm. Argos satellite platform transmitter terminals (PTTs) (Smart position-only tags, SPOT; model SPOT5, Wildlife Computers, Redmond, WA, USA) were attached to the first dorsal fin with stainless steel bolts, neoprene and steel washers, and steel screw-lock nuts. In the north-western Atlantic, tiger and hammerhead capture and tagging methods followed Hammerschlag *et al*. (3, 4). Sampling was conducted within the U.S. east coast (southern Florida) and off the Bahamas (Grand Bahamas). Sharks were captured using standardised circle hook drumlins, each consisting of a submerged weight base tied to a line running to the surface by means of an attached, visible float. Captured sharks were secured alongside the boat or on a partially submerged platform. A seawater hose was placed in the sharks’ mouth, permitting oxygenation of the gills while the shark was temporarily immobilised. SPOT tags were affixed to the first dorsal fin using titanium bolts, neoprene and steel washers, and high-carbon steel nuts. A subset of tiger shark data published previously (3) was analysed differently in this study.

At oceanic locations blue and mako sharks were captured on baited longlines deployed from a commercial fishing vessel. Sharks were brought alongside the vessel in the beginning of the gear-hauling phase, lifted and tagged while suspended against the vessel's side in the vertical position. PSAT tags were rigged with a monofilament tether covered with silicone tubing and looped through a small hole made in the base of first dorsal fin; SPOT tagging at oceanic locations followed a similar procedure to coastal deployments.

All shark tagging procedures undertaken in this study were approved by institutional ethical review committees and completed by licensed, trained and experienced personnel. The procedures used by the UK personnel were licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986.

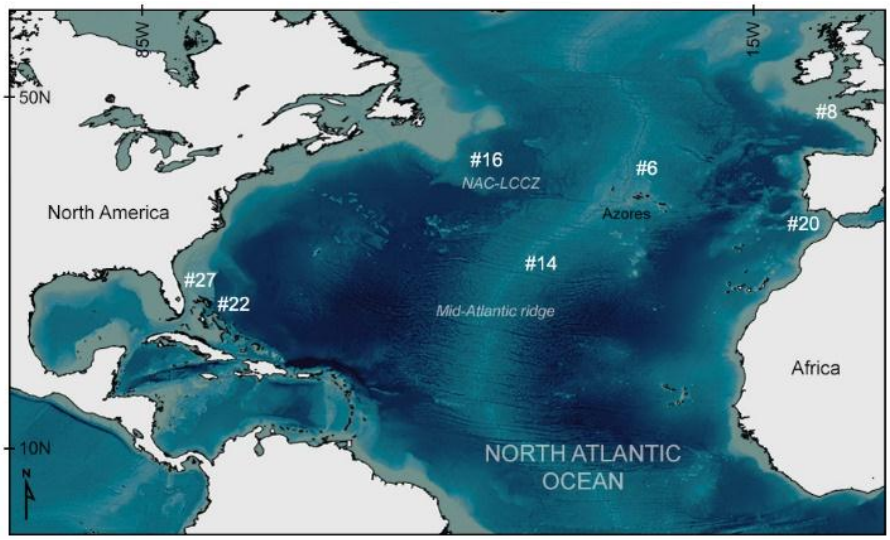

Fig. S1. Shark tagging locations showing the number of tags (#) deployed at each location. NAC-LCCZ denotes the North Atlantic Current – Labrador Current convergence zone.

Table S1. Summary data for satellite tagged sharks; F – female; M – male; * poor transmission.

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 1	40390	*Prionace glauca*	210	F	SPOT5	Oceanic	29 Aug. 2011	46
Shark 2	40406	*Prionace glauca*	150	F	PAT-Mk10	England	21 Aug. 2007	69
Shark 3	40421	*Prionace glauca*	180	F	PAT-Mk10	Portugal	04 Jun. 2008	11
Shark 4	40461	*Prionace glauca*	180	F	PAT-Mk10	Portugal	04 Jun. 2008	50
Shark 5	49022	*Prionace glauca*	199	F	PAT4	England	06 Jul. 2006	29
Shark 6	66935	*Prionace glauca*	200	F	PAT-Mk10	Portugal	03 Jun. 2008	28
Shark 7	66936	*Prionace glauca*	95	F	PAT-Mk10	Portugal	10 Oct. 2006	19
Shark 8	66938	*Prionace glauca*	199	M	PAT-Mk10	Oceanic	17 Jun. 2007	23
Shark 9	66940	*Prionace glauca*	130	F	PAT-Mk10	England	01 Aug. 2007	12
Shark 10	66942	*Prionace glauca*	115	F	PAT-Mk10	Portugal	04 Oct. 2007	41
Shark 11	66945	*Prionace glauca*	153	F	PAT-Mk10	England	21 Jul. 2006	19
Shark 12	66946	*Prionace glauca*	130	F	PAT-Mk10	England	08 Aug. 2006	20
Shark 13	66951	*Prionace glauca*	186	F	SPOT5	England	15 Aug. 2006	8
Shark 14	66952	*Prionace glauca*	170	F	SPOT5	England	18 Aug. 2006	14
Shark 15	66954	*Prionace glauca*	160	F	SPOT5	England	31 Aug. 2007	21
Shark 16	66955	*Prionace glauca*	145	F	SPOT5	Portugal	01 Jun. 2009	23
Shark 17	66957	*Prionace glauca*	220	M	SPOT5	Portugal	01 Jun. 2009	102
Shark 18	66963	*Prionace glauca*	90	M	SPOT5	Portugal	10 Oct. 2006	23
Shark 19	66967	*Prionace glauca*	130	F	SPOT5	Portugal	06 Jun. 2008	101

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 20	66969	*Prionace glauca*	130	M	SPOT5	Portugal	17 Jun. 2008	112
Shark 21	84174	*Prionace glauca*	190	F	SPOT5	Oceanic	30 Aug. 2011	18
Shark 22	84175	*Prionace glauca*	220	F	SPOT5	Oceanic	02 Sep. 2011	33
Shark 23	85136	*Prionace glauca*	260	M	PAT-Mk10	Oceanic	21 Aug. 2011	91
Shark 24	85140	*Prionace glauca*	250	M	PAT-Mk10	Oceanic	22 Aug. 2011	119
Shark 25	85693	*Prionace glauca*	240	M	PAT-Mk10	Oceanic	26 Aug. 2011	81
Shark 26	85697	*Prionace glauca*	200	M	PAT-Mk10	Oceanic	26 Aug. 2011	119
Shark 27	86395	*Prionace glauca*	185	M	PAT-Mk10	Oceanic	26 Jun. 2010	88
Shark 28	86396	*Prionace glauca*	192	F	PAT-Mk10	Oceanic	27 Jun. 2010	56
Shark 29	86403	*Prionace glauca*	125	F	PAT-Mk10	Portugal	26 May 2009	120
Shark 30	91026	*Prionace glauca*	240	F	PAT-Mk10	Oceanic	21 Aug. 2011	89
Shark 31	91658	*Prionace glauca*	260	F	PAT-Mk10	Oceanic	26 Aug. 2011	121
Shark 32	96034	*Prionace glauca*	260	F	PAT-Mk10	Oceanic	29 Jun. 2010	119
Shark 33	96035	*Prionace glauca*	240	F	PAT-Mk10	Oceanic	30 Jun. 2010	26
Shark 34	96036	*Prionace glauca*	200	M	PAT-Mk10	Oceanic	25 Jun. 2010	13
Shark 35	96037	*Prionace glauca*	210	M	PAT-Mk10	Oceanic	25 Jun. 2010	7
Shark 36	96039	*Prionace glauca*	235	M	PAT-Mk10	Oceanic	25 Jun. 2010	179
Shark 37	107084	*Prionace glauca*	220	F	PAT-Mk10	Oceanic	27 Aug. 2011	119
Shark 38	107085	*Prionace glauca*	220	F	PAT-Mk10	Oceanic	28 Aug. 2011	93
Shark 39	40392	*Isurus oxyrinchus*	210	F	SPOT5	Oceanic	05 Sep. 2011	58

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 40	40393	*Isurus oxyrinchus*	200	M	SPOT5	Oceanic	08 Sep. 2011	50
Shark 41	86399	*Isurus oxyrinchus*	140	M	PAT-Mk10	Oceanic	25 Jun. 2010	59
Shark 42	86400	*Isurus oxyrinchus*	125	M	PAT-Mk10	Oceanic	23 Apr. 2009	29
Shark 43	86401	*Isurus oxyrinchus*	220	M	PAT-Mk10	Oceanic	30 Jun. 2010	86
Shark 44	86402	*Isurus oxyrinchus*	170	F	PAT-Mk10	Oceanic	24 Apr. 2009	59
Shark 45	86407	*Isurus oxyrinchus*	130	M	PAT-Mk10	Oceanic	03 Jul. 2010	89
Shark 46	86408	*Isurus oxyrinchus*	180	M	PAT-Mk10	Oceanic	27 Jun. 2010	113
Shark 47	96030	*Isurus oxyrinchus*	130	F	PAT-Mk10	Oceanic	04 Jul. 2010	117
Shark 48	96031	*Isurus oxyrinchus*	165	F	PAT-Mk10	Oceanic	05 Jul. 2010	117
Shark 49	98334	*Isurus oxyrinchus*	270	F	SPOT5	USA	13 Nov. 2010	150
Shark 50	107089	*Isurus oxyrinchus*	220	F	PAT-Mk10	Oceanic	21 Aug. 2011	119
Shark 51	107090	*Isurus oxyrinchus*	255	F	PAT-Mk10	Oceanic	22 Aug. 2011	119
Shark 52	107091	*Isurus paucus*	245	F	PAT-Mk10	Oceanic	30 Aug. 2011	49
Shark 53	107092	*Isurus oxyrinchus*	170	M	PAT-Mk10	Oceanic	03 Sep. 2011	119
Shark 54	33992	*Galeocerdo cuvier*	203	F	SPOT5	USA	26 May 2010	34
Shark 55	34020	*Galeocerdo cuvier*	164	M	SPOT5	USA	26 May 2010	41
Shark 56	34021	*Galeocerdo cuvier*	217	F	SPOT5	USA	26 May 2010	25
Shark 57	34029	*Galeocerdo cuvier*	205	F	SPOT5	USA	26 May 2010	191
Shark 58	34203	*Galeocerdo cuvier*	210	F	SPOT5	USA	13 Nov. 2010	47
Shark 59	55494	*Galeocerdo cuvier*	210	F	SPOT5	USA	10 Jun. 2010	96

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 60	55495	*Galeocerdo cuvier*	206	F	SPOT5	USA	09 Jun. 2010	129
Shark 61	68471	*Galeocerdo cuvier*	245	F	SPOT5	USA	29 Jan. 2011	28
Shark 62	68477	*Galeocerdo cuvier*	201	M	SPOT5	USA	29 Oct. 2010	128
Shark 63	68485	*Galeocerdo cuvier*	162	F	SPOT5	Bahamas	19 Feb. 2011	95
Shark 64	68486	*Galeocerdo cuvier*	280	F	SPOT5	Bahamas	20 Feb. 2011	99
Shark 65	68488	*Galeocerdo cuvier*	267	F	SPOT5	Bahamas	20 Feb. 2011	252
Shark 66	68494	*Galeocerdo cuvier*	245	F	SPOT5	Bahamas	19 Feb. 2011	191
Shark 67	68495	*Galeocerdo cuvier*	306	F	SPOT5	Bahamas	20 Feb. 2011	232
Shark 68	68496	*Galeocerdo cuvier*	271	F	SPOT5	Bahamas	20 Feb. 2011	217
Shark 69	68529	*Galeocerdo cuvier*	232	F	SPOT5	Bahamas	19 Feb. 2011	551
Shark 70	68554	*Galeocerdo cuvier*	271	F	SPOT5	Bahamas	19 Feb. 2011	185
Shark 71	68555	*Galeocerdo cuvier*	340	F	SPOT5	Bahamas	20 Feb. 2011	253
Shark 72	68556	*Galeocerdo cuvier*	237	F	SPOT5	Bahamas	20 Feb. 2011	240
Shark 73	98332	*Galeocerdo cuvier*	269	F	SPOT5	USA	12 Nov. 2010	85
Shark 74	105594	*Galeocerdo cuvier*	148	F	SPOT5	Bahamas	19 Feb. 2011	10
Shark 75	105595	*Galeocerdo cuvier*	315	F	SPOT5	Bahamas	22 Feb. 2011	35
Shark 76	105599	*Galeocerdo cuvier*	271	F	SPOT5	Bahamas	19 Feb. 2011	9
Shark 77	106660	*Galeocerdo cuvier*	285	M	SPOT5	Bahamas	10 Apr. 2011	53
Shark 78	106661	*Galeocerdo cuvier*	167	F	SPOT5	Bahamas	10 Apr. 2011	49
Shark 79	112986	*Galeocerdo cuvier*	267	F	SPOT5	Bahamas	23 Jul. 2012	25

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 80	112987	*Galeocerdo cuvier*	204	F	SPOT5	Bahamas	22 Jul. 2012	26
Shark 81	113534	*Galeocerdo cuvier*	246	F	SPOT5	Bahamas	15 Dec. 2011	33
Shark 82	113536	*Galeocerdo cuvier*	268	F	SPOT5	Bahamas	15 Dec. 2011	86
Shark 83	113537	*Galeocerdo cuvier*	254	F	SPOT5	Bahamas	05 Feb. 2012	72
Shark 84	115906	*Galeocerdo cuvier*	290	M	SPOT5	USA	27 May 2012	40
Shark 85	115907	*Galeocerdo cuvier*	162	M	SPOT5	Bahamas	10 Feb. 2012	24
Shark 86	33933	*Sphyrna mokarran*	204	M	SPOT5	USA	04 Jun. 2010	20
Shark 87	33938	*Sphyrna mokarran*	193	M	SPOT5	USA	12 Mar. 2010	42
Shark 88	33994	*Sphyrna lewini*	155	F	SPOT5	USA	17 Mar. 2010	23
Shark 89	68472	*Sphyrna mokarran*	212	F	SPOT5	USA	29 Jan. 2011	26
Shark 90	68480	*Sphyrna mokarran*	196	F	SPOT5	USA	29 Jan. 2011	116
Shark 91	68481	*Sphyrna mokarran*	218	F	SPOT5	USA	29 Jan. 2011	101
Shark 92	98328	*Sphyrna mokarran*	173	M	SPOT5	USA	20 Feb. 2010	10
Shark 93	98329	*Sphyrna mokarran*	184	M	SPOT5	USA	20 Feb. 2010	62
Shark 94	105597	*Sphyrna mokarran*	255	M	SPOT5	Bahamas	19 Feb. 2011	49
Shark 95	106662	*Sphyrna lewini*	197	M	SPOT5	USA	30 Apr. 2011	65
Shark 96	106663	*Sphyrna mokarran*	199	F	SPOT5	USA	13 Jul. 2011	156
Shark 97	106895	*Sphyrna mokarran*	204	F	SPOT5	USA	05 Aug. 2011	32
Shark 98	106896	*Sphyrna mokarran*	222	M	SPOT5	USA	18 Jul. 2011	4
Shark 99	111550	*Sphyrna mokarran*	195	M	SPOT5	USA	12 Sep. 2011	53

Shark ID	PTT ID	Species	Fork length (cm)	Sex	Tag type	Location tagged	Tagging date	Days-at-liberty
Shark 100*	40460	*Prionace glauca*	140	M	PAT-Mk10	Portugal	09 Jun. 2008	–
Shark 101*	40462	*Prionace glauca*	200	F	PAT-Mk10	Portugal	06 Jun. 2008	–
Shark 102*	40463	*Prionace glauca*	200	M	PAT-Mk10	Portugal	11 Jun. 2008	–
Shark 103*	66937	*Prionace glauca*	110	F	PAT-Mk10	Portugal	12 Oct. 2006	–
Shark 104*	66962	*Prionace glauca*	90	F	SPOT5	Portugal	10 Oct. 2006	–
Shark 105*	66964	*Prionace glauca*	90	M	SPOT5	Portugal	10 Oct. 2006	–
Shark 106*	66965	*Prionace glauca*	95	M	SPOT5	Portugal	11 Oct. 2006	–
Shark 107*	66966	*Prionace glauca*	120	F	SPOT5	Portugal	12 Oct. 2006	–
Shark 108*	66968	*Prionace glauca*	120	F	SPOT5	Portugal	12 Jun. 2008	–
Shark 109*	85698	*Prionace glauca*	240	M	PAT-Mk10	Oceanic	27 Aug. 2011	–
Shark 110*	86406	*Prionace glauca*	165	F	PAT-Mk10	Oceanic	25 Jun. 2010	–
Shark 111*	107088	*Prionace glauca*	220	F	PAT-Mk10	Oceanic	29 Aug. 2011	–
Shark 112*	34107	*Galeocerdo cuvier*	210	F	SPOT5	USA	25 May 2010	–
Shark 113*	98331	*Sphyrna mokarran*	185	F	SPOT5	USA	07 Feb. 2010	–

1.2. Track processing

1.2.1. Pop-off Satellite Archival Transmitters (PSAT)

The movement of PSAT-tagged sharks was estimated using either satellite relayed data from each tag or from archival data after the tags were physically recovered. Positions of each shark between attachment and tag pop-up were reconstructed using software provided by the manufacturer (WC-GPE, global position estimator program suite), where daily maximal rate-of-change in light intensity was used to estimate local time of midnight or midday for longitude calculations, and day-length estimation for determining latitude. Anomalous longitude estimates resulting from dive-induced shifts in the estimated timings of dawn and dusk from light curves were automatically discarded from the dataset using software provided by the manufacturer (WC-GPE); latitude estimates were subsequently iterated for the previously obtained longitudes. An integrated state-space model [unscented Kalman filter – UKFSST (5); using spatially complete NOAA Optimum Interpolation Quarter Degree Daily SST Analysis data] was then applied to correct the raw geolocation estimates and obtain the most probable track. A regular time-series of locations was then estimated using a continuous-time correlated random walk Kalman filter, CTCRW (6) performed in R (*crawl package*). UKFSST geolocations were parameterised with standard deviation (SD) constants (K) which produced the smallest mean deviation from concurrent Argos positions (7).

1.2.2. Argos Satellite Transmitter tags

Location class (LC) Z data (failed attempt at obtaining a position) were removed from the dataset. The remaining raw position estimates (LC 3, 2, 1, 0, A and B) were analysed point-to-point with a 3 m s^{-1} speed filter to remove outlier locations. Subsequently, the CTCRW state-space model was applied to each individual track, producing a single position estimate per day. Argos positions were parameterised with the K error model parameters for longitude and latitude implemented in the *crawl package* (6).

1.3. Spatial density analysis and statistics

As described above, to obtain unbiased estimates of shark space use, gaps between consecutive dates in the raw tracking data were interpolated to one position per day. However, and even though the frequency of long temporal gaps (> 20 days) in the dataset was small (Table S2), any tracks with gaps exceeding 20 days were split into segments prior to interpolation, thus avoiding the inclusion of unrepresentative location estimates (8).

Table S2. Number of temporal gaps of a given length per track for the different species and tag type.

		Frequency of gaps; mean (± SD)			
Species	Tag type	> 5d	> 10d	> 20d	Number of tracks
Prionace glauca	PAT-Mk10	4.3 (4.2)	0.9 (1.1)	0.1 (0.3)	27
	SPOT5	1.4 (1.7)	0.3 (0.6)	0.0	11
Isurus spp.	PAT-Mk10	4.2 (3.9)	1 (1.4)	0.1 (0.3)	12
	SPOT5	0.0	0.0	0.0	3
Galeocerdo cuvier	SPOT5	3.9 (2.4)	1.4 (2.2)	0.1 (0.4)	32
Sphyrna spp.	SPOT5	2.6 (4.5)	0.5 (0.9)	0.1 (0.3)	14

To account for the spatial error around real individual geolocations, these were randomly resampled (100 times) along tag-specific longitudinal and latitudinal Gaussian error fields (7, 9). To reduce tagging location and track length bias, the number of resampled positions per grid cell were normalised by the number of individual sharks within each grid cell (10); thus, an effort-weighted index of residence per unit area (number of mean days per grid cell) was calculated from the initial resampled geolocations using ArcGIS geographical information system (ESRI Inc., CA, USA) (see Fig. S2). We then applied a spatial hotspot analysis, the Getis-Ord Gi* hotspot analysis (11), implemented in ArcGIS to identify objectively the patterns of spatial significance. For a set of weighted features, this analysis identifies clusters of points with higher (hotspot) or lower (coldspot) values in magnitude than expected by random chance (12). Briefly, the procedure analyses spatial data and determines the correlation of a given data point value (in our case mean days per grid cell) with the values in surrounding (neighbour) areas, automatically performing a test of significance (z-score) for each area. At a significance level of 0.05, a z-score would have to be smaller than -1.96 or greater than 1.96 to be statistically significant. Hence, hotspots and coldspots of shark geolocations were defined as high (above the resampled mean days) and low (below the resampled mean days) space use areas, respectively. In the analysis the spatial relationship was conceptualised through a fixed distance band and importantly, the appropriate value was objectively calculated within ArcGIS (*spatial statistics tool*). To test whether serial correlation was an issue in the performed analysis, we applied a spatial hotspot analysis using every fifth location in the observed tracks (Fig. S3).

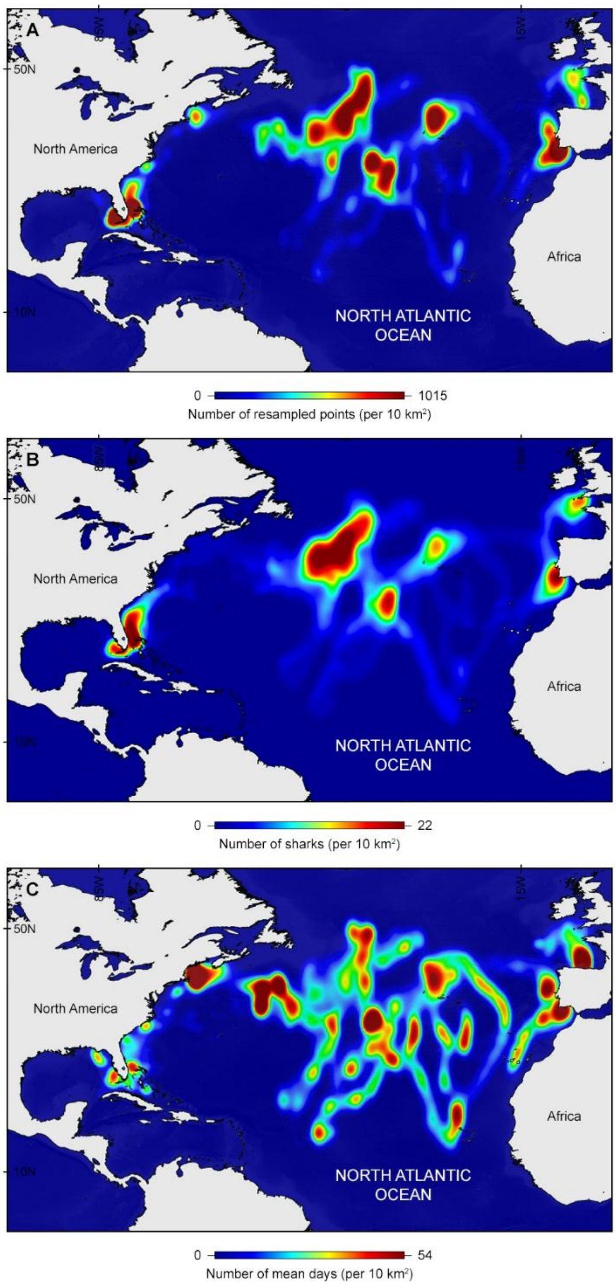

Fig. S2. Tagging location and track length bias reduction procedure; the number of resampled positions per grid cell (A) were normalised by dividing it by the number of tracked sharks (B), thus calculating the number of mean days per grid cell (C); the kernel smoothing parameter was calculated using a smooth cross validation procedure in R and was kept constant to enable the visual comparison of residence probabilities.

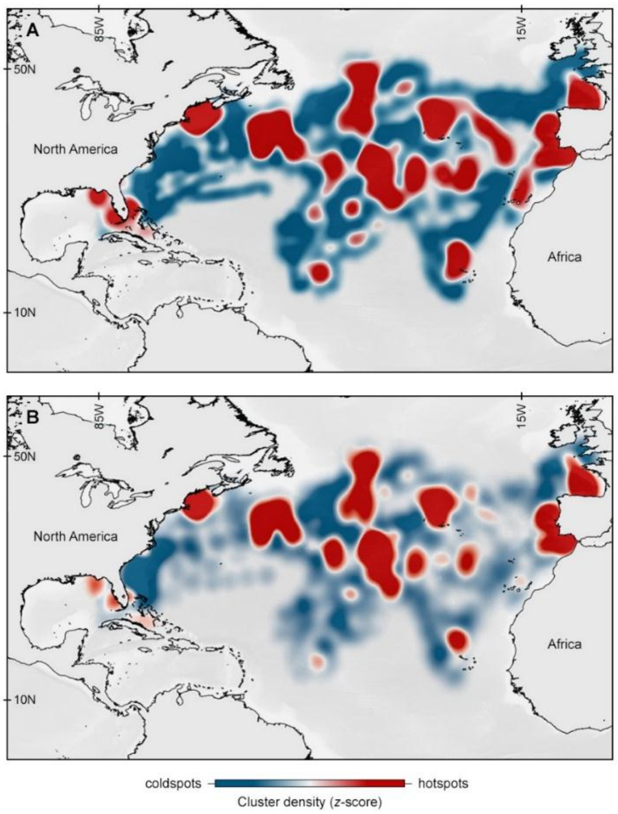

Fig. S3. Map of the estimated high (hotspot; red) and low (coldspot; blue) use habitats of sharks using daily (A) or every fifth location (B).

1.4. Vessel monitoring system data

Vessel monitoring system (VMS) data from 186 Spanish and Portuguese longliners (> 15 m length) operating in the north-east Atlantic were obtained from the respective national fisheries monitoring centres. The Spanish dataset spanned from January 2005 to December 2009, whereas the Portuguese data ranged from January 2003 to December 2005 and January 2009 to December 2011. Each record contained the Global Positioning System (GPS) position of the vessel (accurate to < 500 m), time stamp, and a vessel identification number. All records were anonymous with respect to the vessel registration number, dimensions and administrative ports. Received data duty cycle/reporting frequency ranged from 10 min to two hours. To determine the actual fishing locations where each individual longline was deployed, we developed an algorithm which detected sharp turning angles (> 130º), considered to be the point between longline deployment and retrieval (see Fig. S4). When a possible turn point was found, the inbound leg was retraced until the distance travelled exceeded the longline length (between 80 and 100 km); the prior point was then taken as the start of deployment and the outbound leg was traced until the end-of-deployment point was determined in a similar fashion. A further check was undertaken that the endpoints were within a short distance of each other to confirm that a proper 'V' shape was defined. Subsequently, all movements between fishing locations were ignored (including trips to and from fishing ports), retaining only data pertaining to fishing activity (*n* = 1,063,861 data points). To estimate longliner space-use, fishing data were first normalised by calculating daily centroids and then mapped onto a grid at a spatial resolution of 1° × 1° with fishing effort computed as the number of vessels in each grid cell per day (Fig. 3).

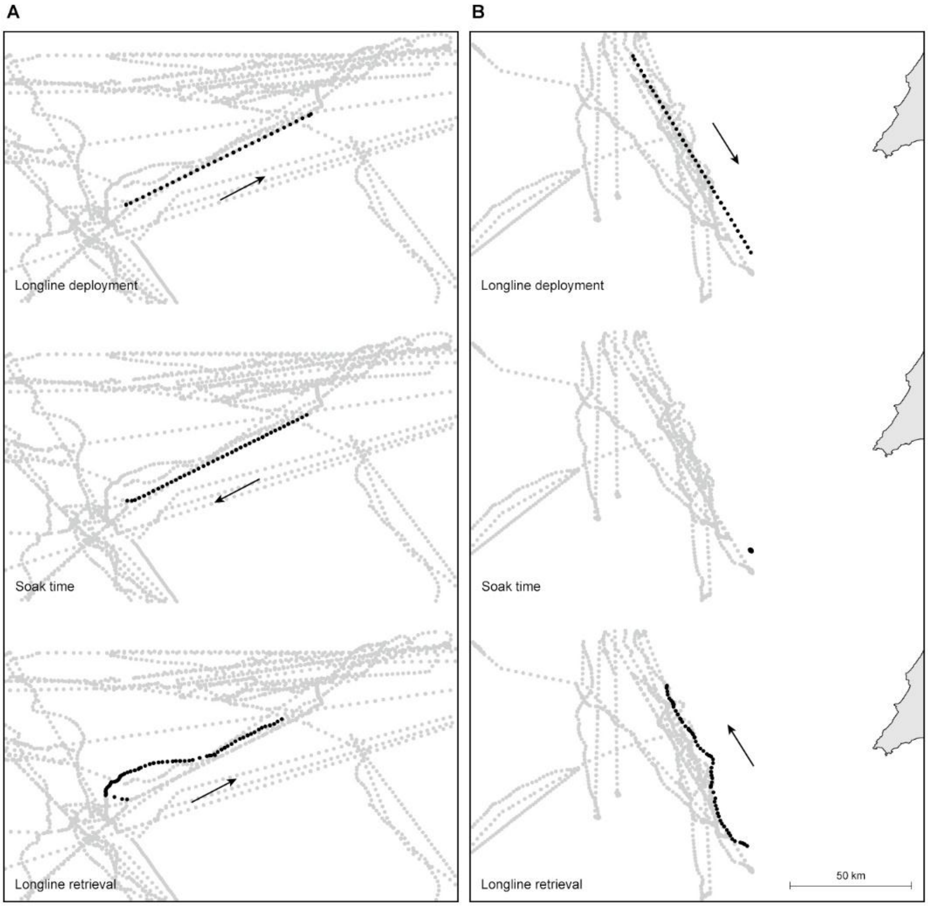

Fig. S4. Examples of area restricted searches with distinct soak time phases in tracked surface longliners, in areas with low (A) and high (B) abundance of targeted prey.

For a subset of 50 longliners, fishing data was further analysed to identify areas of restricted search, or spatial clusters of longline deployment locations. Briefly, when searching for fish species, longliners move from and back to the start position in three distinct phases:

line deployment, soak time and line retrieval (Fig. S4A). However, when sufficient numbers of target fish are found, the vessel remains stationary during soak time, thus allowing the longliners to target the same areas repeatedly (Fig. S4B), which results in (i) higher spatial concentration of fishing locations (data points), (ii) a higher number of turn points per grid cell, and (iii) increased number of hours between turn points, which were identified by the filtering algorithm as area-restricted spatial clusters. Environmental field data (section 1.5) were then extracted for the spatial clusters (see Fig. S5).

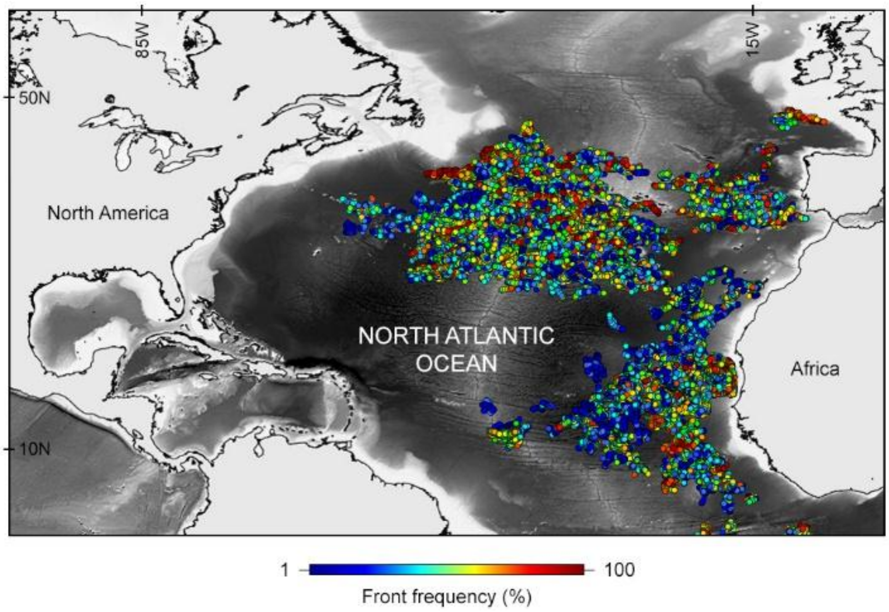

Fig. S5. Area restricted searches spatial clusters of longline deployment locations associated with frontal boundaries in the ocean.

1.5. Null model simulations and environmental preferences

1.5.1. Simulations of shark movements

To test shark associations with oceanographic features (a measure of habitat selection) quasi-realistic ‘null’ shark tracks, based on a random-walk model, were generated using custom-written R code. At the start of each simulated track, the null shark was placed at a random position within the actual tagging location error field (7, 9) and the initial turning angle derived from a 360° uniform distribution. The movement path of each shark comprised a sequence of discrete steps (each representing one day) and turning angles, with the former limited by the actual number of individual steps recorded for each real shark. In each iteration, the step length and angle were drawn from species-specific step length/angle distributions estimated from the tracked sharks, and a move was performed. After computing a new position, a check was made to ensure that it did not fall within land masses, in which case the position was rejected and a new step length and angle were redrawn. The simulated walks were also restricted to occur within the area defined by the minimum convex polygon (MCP) that encompassed all observed locations of each species.

For each tracked shark a total of 200 simulation runs were completed (for examples see Fig. S6). Simulated random walks were then combined with satellite-derived environmental data. The environmental data used were daily (i) sea surface temperature, SST and (ii) SST anomalies derived from NOAA Optimum Interpolation Quarter Degree Daily SST Analysis (OISST) data; based on the OISST data we also calculated (iii) daily SST maximum gradient maps by calculating for each pixel a geodetic–distance-corrected maximum thermal gradient (ºC/100 km), and (iv) thermal front frequency (Ffreq) seasonal maps (0.1° spatial resolution), derived from a front-following algorithm (13); (v) monthly merged chlorophyll *a* levels (0.25° spatial resolution), acquired from GlobColour (European Space Agency – ESA); and finally, (vi) weekly merged sea surface height (SSH) anomalies (0.33° spatial resolution) obtained from AVISO satellite altimetry data. To determine the optimal number of simulated pseudo-absences we calculated, for each environmental variable, the mean and standard deviation of increasing numbers of 'null' tracks were computed. Calculated statistics stabilised with sample sizes of about 50 to 75 simulated tracks for each observed track (Fig. S7A-D), and thus, we set our sample size at 75 'null' tracks per shark track.

Oceanographic variables were also sampled for real tracks; however, to account for estimated error distribution around individual geolocations, we calculated a spatially weighted average of the environmental data for each location using 75 randomly resampled locations (from section 1.3).

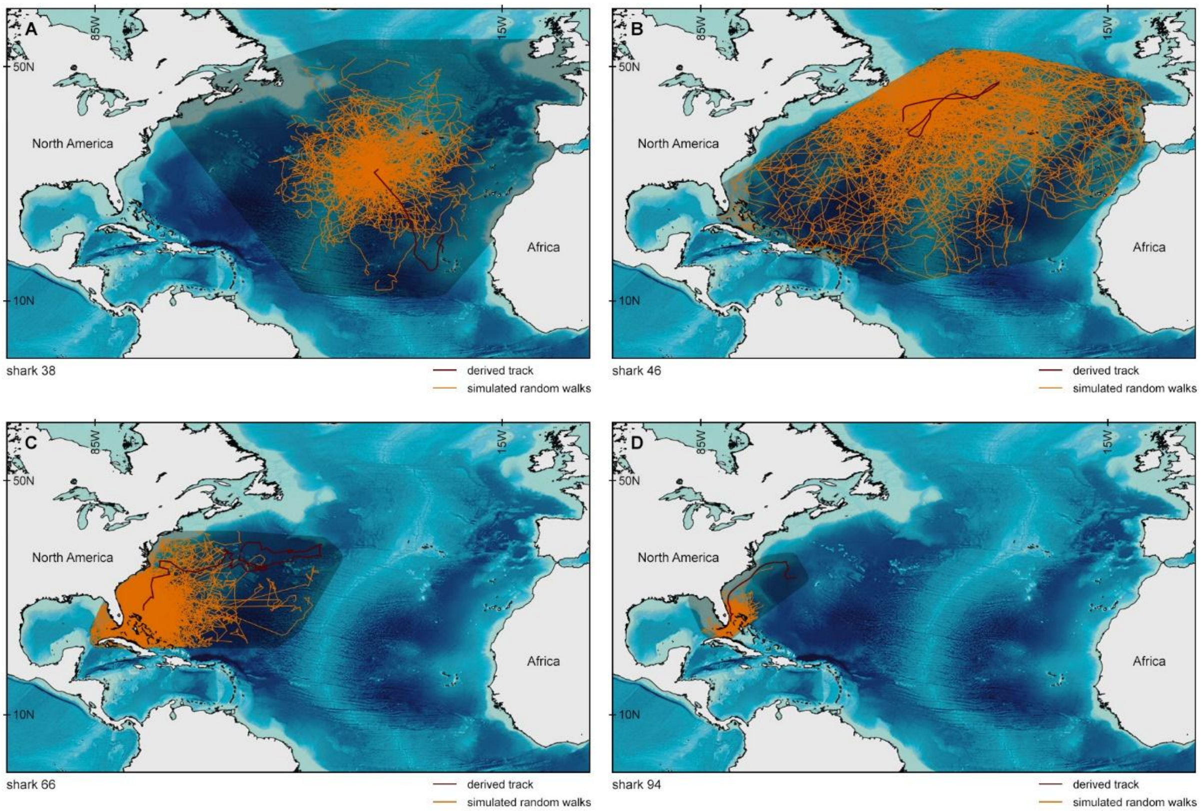

Fig. S6. Examples of random walk simulations for the different shark species; blue (A), mako (B), tiger (C) and hammerhead (D). Red lines are tagged shark movements; orange lines are 75 replicate random-walk model sharks.

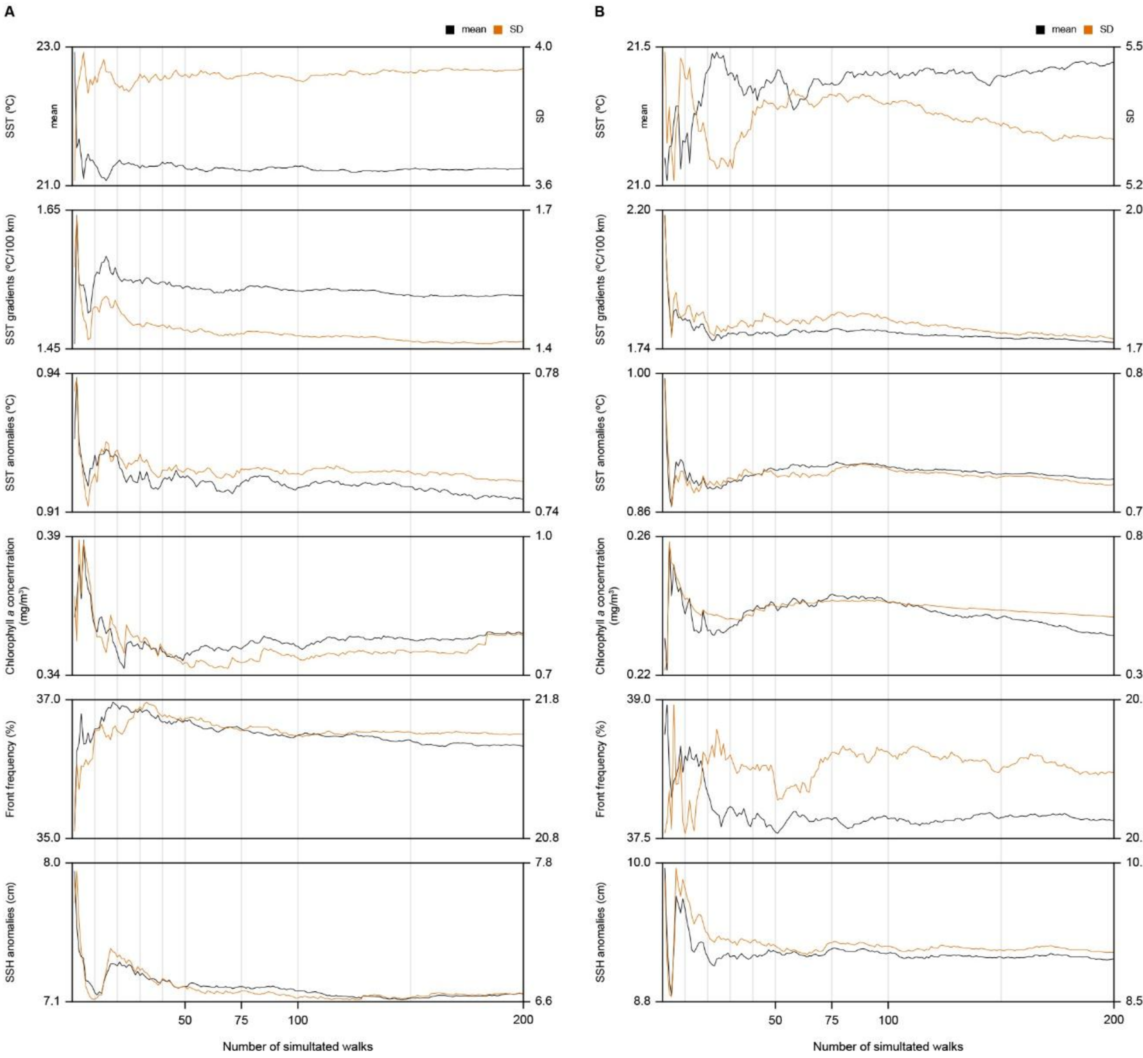

Fig. S7. Effects of different number of pseudo-absence locations on the mean and SD variation for the different environmental variables, shark species and longliners; blue (A), mako (B), tiger (C), hammerhead (D) and longliners (E); SST, sea surface temperature; SSH, sea surface height.

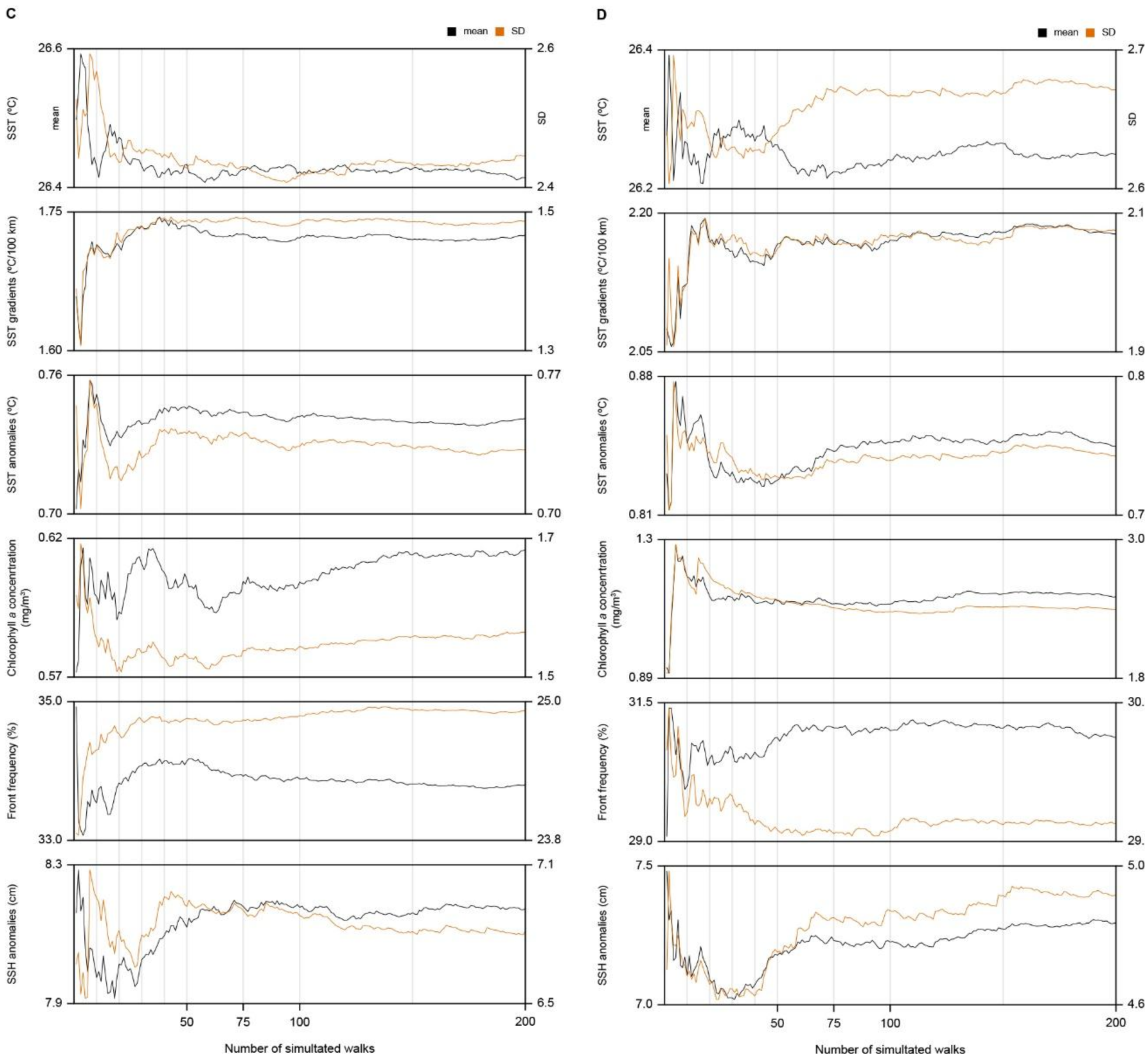

Fig. S7 (cont'd). Effects of different number of pseudo-absence locations on the mean and SD variation for the different environmental variables, shark species and longliners; blue (A), mako (B), tiger (C), hammerhead (D) and longliners (E); SST, sea surface temperature; SSH, sea surface height.

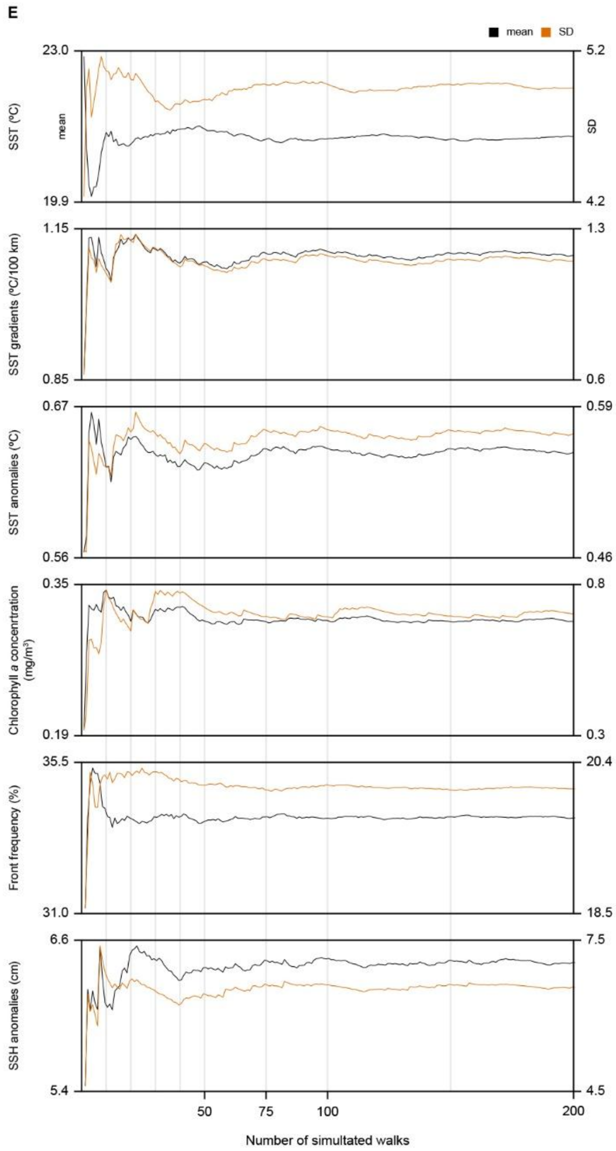

Fig. S7 (cont'd). Effects of different number of pseudo-absence locations on the mean and SD variation for the different environmental variables, shark species and longliners; blue (A), mako (B), tiger (C), hammerhead (D) and longliners (E); SST, sea surface temperature; SSH, sea surface height.

1.5.2. Simulations of longliner movements

Similarly, to test longliner associations with oceanographic features quasi-realistic 'null' vessel tracks were generated for a subset of 300 vessel/year combinations [selected amongst the vessels with both (i) the highest number of data points (days) in a year and (ii) largest fishing area]. At the start of each simulated track, the null vessel was placed at a random position within the daily estimated standard deviation of fishing locations (latitude SD: 0.19º; longitude SD: 0.30º) and the initial turning angle derived from a 360º uniform distribution.

All subsequent simulation steps were similar to those described in section 1.5.1 with simulated tracks also restricted to occur within defined MCP area defined by all observed longliner locations (for examples see Fig. S8). Given that environmental statistics for vessels also stabilised at about 75 simulated tracks (Fig. S6E) we set our sample size at 75 ‘null’ tracks per vessel.

Oceanographic variables were sampled for both the simulated and real tracks; however, to account for the daily dispersion in fishing locations, we averaged the environmental data for all fishing points in a given day, and assigned the mean value to the daily centroid (calculated in section 1.4).

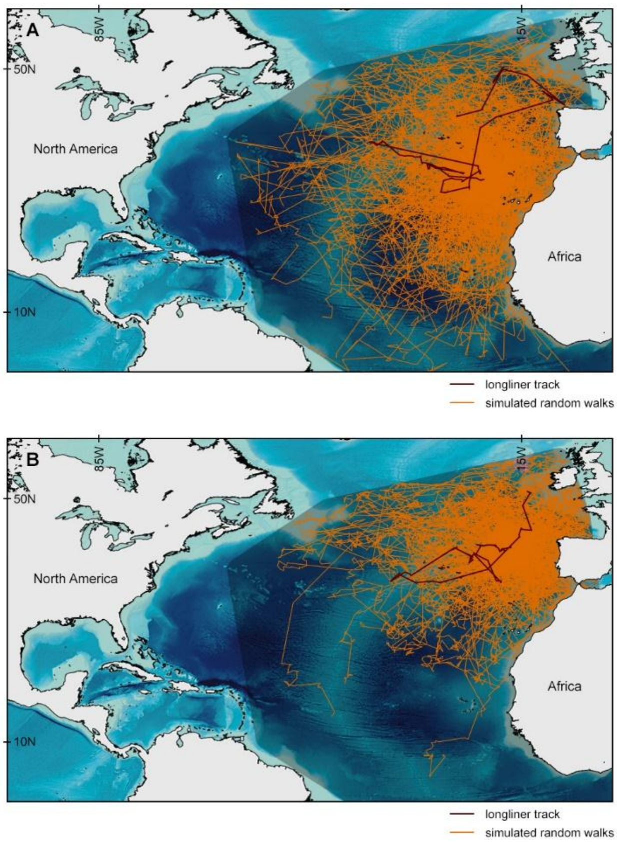

Fig. S8. Examples of random walk simulations for two different longliners.

1.5.3. Habitat modelling

To investigate habitat preferences we tested associations of individual sharks and vessels with oceanographic features by comparing real with simulated random tracks using Resource Selection Probability Functions (RSPFs; 14, 15, 16, 17). Before running the analyses, records with incomplete environmental information, e.g. where remotely sensed data were not available due to cloud cover, were removed from the datasets. Also, to avoid pseudo-replication and spatial auto-correlation of oceanographic data, locations within a radius of 0.33^o (lowest spatial resolution of satellite-derived environmental data – AVISO SSH anomalies) of the previous position were removed. Predictor variables were subsequently checked for co-linearity using Spearman's rank correlation matrix; however, none of the variables exceeded the 0.75 correlation coefficient (18; see also Table S3) and thus all variables were considered in the same candidate model.

RSPFs are models used to compare the amount of used habitat with the amount of available habitat (15). Furthermore, logistic regression has become one of the most common statistical approaches to estimate habitat selection models (19). We estimated logistic RSPF models [implemented in R (*ResourceSelection package*); (16, 17)] under a use-availability framework. The obtained variable estimates were post-hoc standardised based on standard deviations (20) which allowed for comparisons between the relative influence of variables and habitat use, regardless of the measurement scale quantifying the resource. As a result, the explored habitat (defined by used/real locations) was analysed in contrast to available (random) locations. RSPF models were estimated using maximum likelihood methods with the final model form and covariates selected using Bayesian information criterion (BIC). Habitat modelling can be affected by serial correlation in telemetry data (21). However, the 0.33^o spatial reduction performed previously, also resulted in significant sub-sampled temporal datasets (mean temporal gaps in real tracks: 5.02 days; mean temporal gaps in simulated tracks: 5.64 days). Therefore no further temporal sub-sampling was performed.

Table S3. Spearman's rank correlation coefficient matrix for predictor variables; SST – sea surface temperature; Chl. *a* conc. – chlorophyll *a* concentration; SSH – sea surface height.

Species	Variable	SST gradients	SST anomalies	Chl. *a* conc.	Front frequency	SSH anomalies
Prionace glauca	SST	-0.37	-0.11	-0.36	-0.11	0.04
	SST gradients	–	0.18	0.20	0.20	0.09
	SST anomalies	–	–	0.07	0.06	0.13
	Chl. *a* conc.	–	–	–	-0.15	-0.07
	Front frequency	–	–	–	–	0.02
Isurus sp.	SST	-0.35	-0.18	-0.29	-0.27	0.04
	SST gradients	–	0.33	0.20	0.29	0.09
	SST anomalies	–	–	0.18	0.14	0.15
	Chl. *a* conc.	–	–	–	0.04	-0.01
	Front frequency	–	–	–	–	0.00
Galeocerdo cuvier	SST	-0.42	-0.30	0.01	-0.11	-0.04
	SST gradients	–	0.39	0.12	0.15	0.00
	SST anomalies	–	–	0.21	0.01	0.00
	Chl. *a* conc.	–	–	–	-0.04	-0.07
	Front frequency	–	–	–	–	0.02
Sphyrna sp.	SST	-0.45	-0.54	-0.05	-0.22	-0.19
	SST gradients	–	0.53	0.15	0.21	0.10
	SST anomalies	–	–	0.32	0.14	0.09
	Chl. *a* conc.	–	–	–	-0.11	0.00
	Front frequency	–	–	–	–	0.06
longliners	SST	-0.29	-0.12	-0.15	-0.24	-0.01
	SST gradients	–	0.32	0.19	0.26	0.18
	SST anomalies	–	–	0.10	0.11	0.17
	Chl. *a* conc.	–	–	–	0.04	0.00
	Front frequency	–	–	–	–	-0.01

1.6. Overlap between sharks and longlines

The spatial overlap (%) between sharks and longliners irrespective of time was calculated by counting the total number of $1^{o} \times 1^{o}$ grid cells where both sharks and longliners occurred at least once, as a function of the total number of grid cells. To quantify the spatial and temporal co-occurrence of longlines and sharks in the same geographic grid cell at the same time, the sum of the number of days with shared occupancy (overlap frequency, i.e. presence of both vessels and sharks in a 1º × 1º grid cell on the same day) was determined. A fixed 1º × 1º geographic grid cell was chosen because it encompassed the length of the longlines which typically range between 80 and 100 km in total length. Because there was a mismatch between Portuguese and Spanish data and both fleets target different oceanic regions, VMS data was reorganised in a total of 30 fishing scenarios which resulted from all the possible combinations of five years of Spanish with six years of Portuguese fishing data. The different fishing scenarios enabled descriptive statistics (e.g. mean, standard deviation) to be calculated for temporal co-occurrence for each scenario allowing us to confirm the similarity in estimates of overlap frequency between scenarios. Specifically, within each scenario, and for each day of the analysis, each vessel track was examined to determine whether a longline fishing point existed for that date. If so, grid coordinates were calculated and the grid cell vessel count updated. If the next point in the vessel track was one day later, then the vessel was considered to be fishing for the 24 h between those points and therefore all grid cells encountered while moving between the start and end fishing points were updated. Once all vessel tracks were processed, shark tracks were analysed in a similar way, with interpolated grid cells updated with occupancy and with counts made of the number of cells containing both longlines and sharks from which the numbers of 'days-at-risk' for each shark were calculated.

2. Supporting Results and Discussion

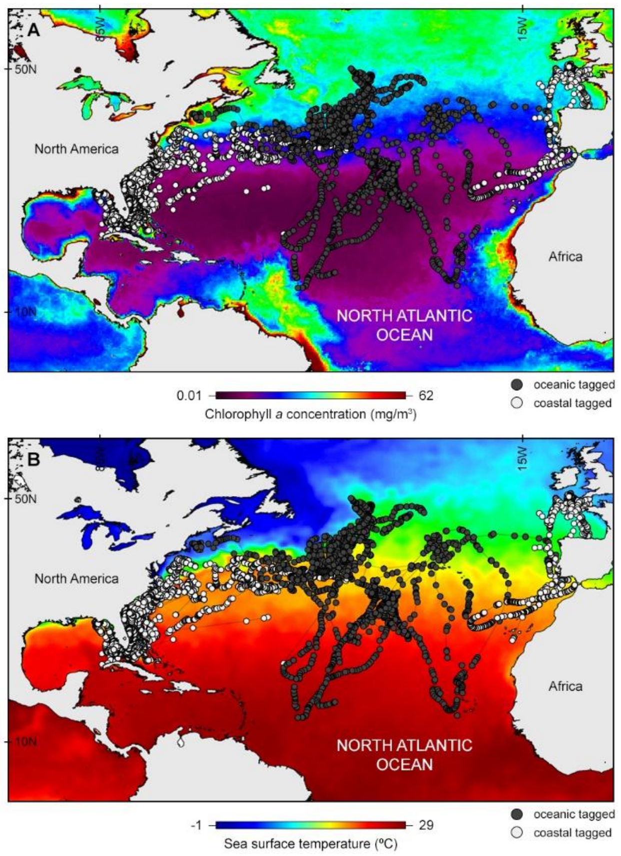

Fig. S9. Processed satellite tag geolocations of six pelagic sharks overlaid on a six-year average of chlorophyll *a* concentration (A) and sea surface temperature (B).

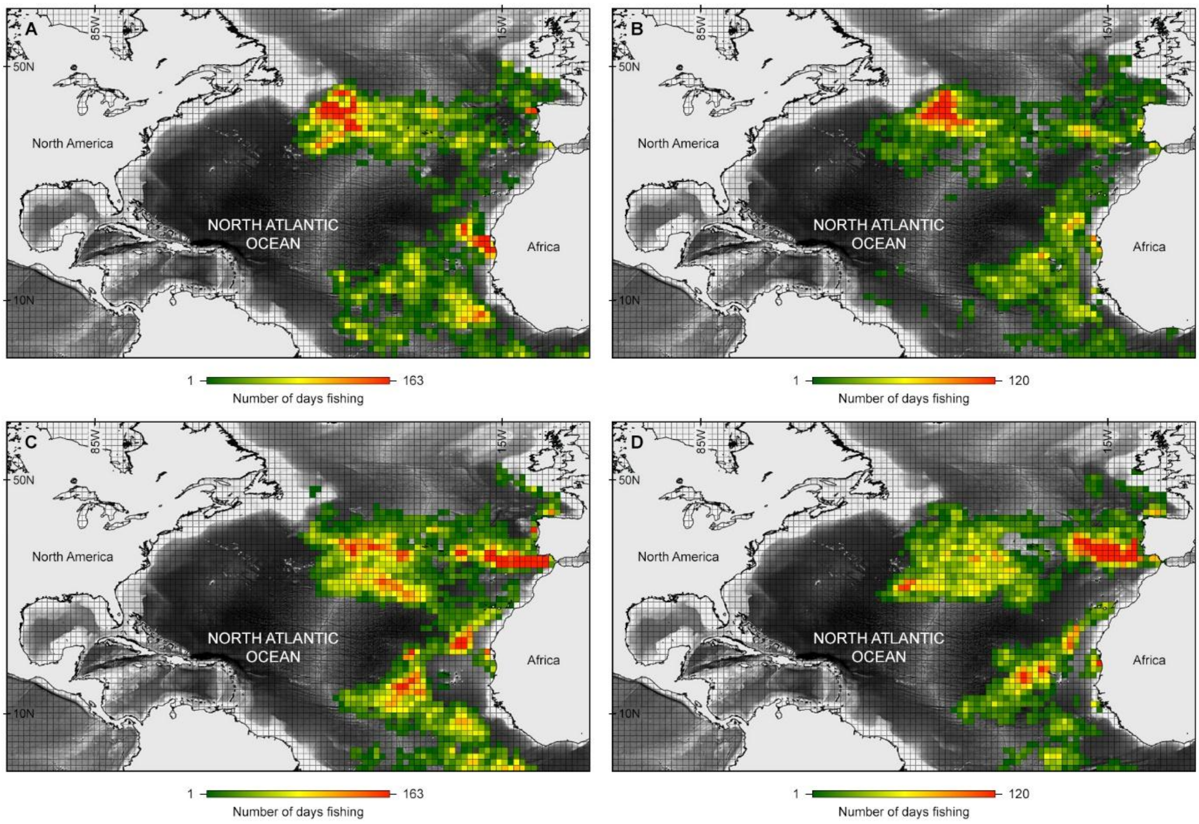

Fig. S10. Temporal persistence in fishing patterns. Spatial distribution of longline fishing intensity is conserved between seasons across years: (A) summer (Jun – Aug) 2005 and (B) summer 2009; and (C) autumn (Sep – Nov) 2005 and (D) autumn 2009. (B).

2.1 Reducing hotspot bias

Defining space use ‘hotspots’ of sharks is one way of exploring shark/environment relationships, however, designating spatial hotspots can be biased due to several factors. For instance, a hotspot could be inaccurately assigned from tracking data if tags are deployed at a single location, the tracks are all of short duration, and no account is taken of re-weighting the geolocations with respect to tagging locations. In the present study we attempted to reduce each of these potential spatial biases. First, we spread deployments of tags across seven release locations spanning the North Atlantic (Fig. S1), and with tags attached to all species (except the one longfin mako tagged) in multiple locations (Table S1). Our efforts to spread tagging locations is consistent with other broad-scale tracking studies of large pelagic fish where hotspots and interactions have been investigated (e.g. 8, 22). Secondly, to our knowledge we have tagged the largest number of sharks in a single electronic tagging study to be undertaken in the North Atlantic Ocean (*n* = 113). Tagging this number of sharks for 3 months on average per individual broadens the range of possible shark habitats recorded so that the spatial ‘hotspot’ analysis may be more representative of actual shark space use patterns. Lastly, and as with other similar studies (8, 10), we used a hotspot mapping technique that statistically assigns greater weight on tag geolocations that are further away from tagging locations to further reduce the effects of tagging bias. Whilst it would be desirable to track many more sharks for longer periods to define hotspots even more accurately, it should be recognised that our study is a first step in exploring fine-scale shark/environment/fishery spatial and temporal co-occurrence across the broad scale.

2.2. Species-specific high-use areas

The tagging location and track length bias-reduction procedure was applied to tracking data of each species separately, to evaluate the presence of species-specific high-space-use areas and their contribution to the identification of hotspots (Fig. 1D). Even though tagged sharks generally occupied large oceanographic regions limited by temperature (Fig. 2B), areas with high shared space-use were observed (Fig. S10), for example in the western and eastern coastal and continental shelves of the North Atlantic (including the Canary and Cape Verde islands) and oceanic areas including the Gulf Stream, NLCZ and west and south-west of the Azores. These regions were also identified as areas of high seasonal fishing effort (Fig. 3) and were also where the highest shark-vessel overlap frequencies were observed (Fig. 4).

Noticeably, areas of high blue shark residency were observed south of Nova Scotia (Gulf Stream) and south of the Azores (Fig. S10A), which were also classified as hotspots (Fig. 1D). Likewise, higher space-use/abundance of mako sharks in the Gulf Stream, the NLCZ and the Azores and mid-Atlantic Ridge areas were also identified with tracking data (Fig. S10B). The distribution of tiger and hammerhead sharks was generally restricted to coastal shelf areas (Fig. S10C,D) which contributed to the identification of coastal hotspots (Fig. 1D).

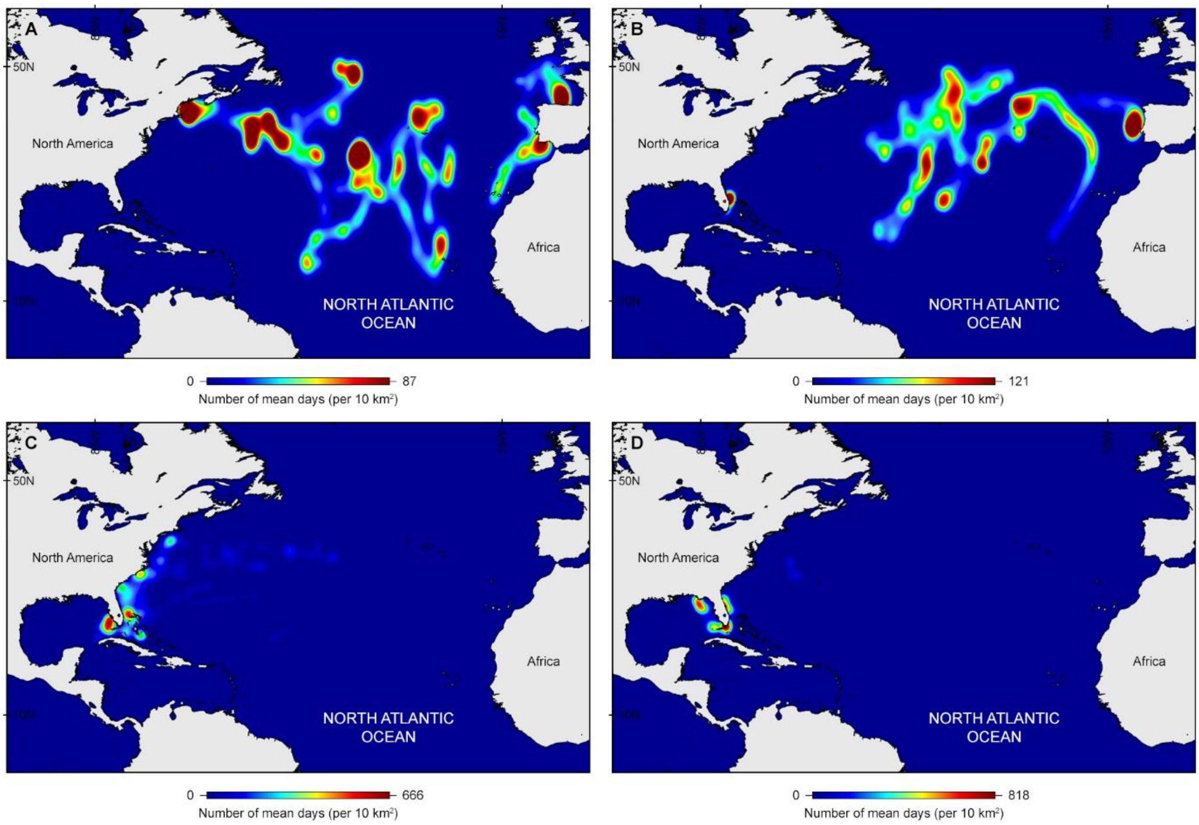

Fig. S11. High species-specific space-use areas calculated for blue (A), mako (B), tiger (C) and hammerhead (D) sharks. The kernel smoothing parameter was kept constant to enable the visual comparison of residence probabilities.

2.3. Environmental preferences

As previously mentioned (section 1.5.3), we used RSPF models to test associations of individual sharks with oceanographic features. The analysis showed that, overall, sharks prefer frontal boundary habitats characterised by steep temperature or productivity gradients (from remote-sensing images of sea surface temperature, SST, or Global colour, Chl ‘a’) (see Fig. 1). Preferences for areas identified with the thermal front frequency (Ffreq) algorithm were, when significant, low. It is possible that (i) the seasonal scale of the Ffreq metric calculation and/or (ii) the 76.5 km spatial scale of the smoothing Gaussian Ffreq filter were inadequate for comparing with shark tracks, since daily position estimates were used in the analysis. This seems to be supported by general higher preferences observed for the daily, higher spatial resolution, SST thermal gradient fields we used. Therefore, it seems likely that tagged sharks were responding at a smaller temporal and spatial scale than possible to measure with the automated front detection filter we implemented, whereas longliners selected SST and productivity boundaries with much greater temporal persistence, i.e. front frequency (Fig. 2). The use of a higher resolution front frequency product may have further improved indication of shark habitat preferences for the movement analysis (e.g. 23).

We found that the risk from fisheries differed between tagged blue and mako sharks, with blue sharks spending on average 2.6 days-at-risk/month and makos 3.0 days-at-risk/month (Mann-Whitney *U*-test = 163.5; $p < 0.05$), which was likely related to differing habitat preferences in mako sharks. For example, RSPF analysis shows that longliners prefer productive habitats characterised by high frontal frequencies, thermal and SSH anomalies for longline deployment (Fig. 2). Hence, similar habitat preferences of sharks and longliners are likely driving co-occurrence, potentially leading to higher probability of shark capture on longlines through increased encounter rates (see also Figs. 4, 5E,F).

Even though tiger and hammerhead sharks displayed similar overall levels of environmental preferences to oceanic sharks, their high space-use of coastal and shelf areas (Fig. S10C,D) – where they were tagged – meant that no overlap with the longlining fleets for which we have data, was observed for hammerhead sharks. In addition, for only two tiger sharks (#66 and #67; Table S1) was co-occurrence recorded during offshore movements into deep water (west of the Azores). Both sharks spent on average 0.4 and 1.0 days-at-risk during the 309 and 122 d tracks, respectively.

2.4 Species-specific differences and exploitation

Species differences in habitat selection and a high degree of spatio-temporal overlap between sharks and longliners combined with different life-history traits may help in part to explain observed pelagic shark catch trends. For example, we found that shortfin mako sharks actively select frontal habitats and overlap the most with longliners. Moreover, they have amongst the lowest fecundity of any shark (~10-12 young every second or third year). In contrast, blue sharks are not only less strongly associated with steep SST gradients thereby overlapping less with longliners, but it also has relatively high fecundity (~80 young per year). This predicts greater susceptibility of makos for capture by longliners compared with blues, and consequently due to lower fecundity, a more rapid potential decline of mako population abundance compared with blue sharks in the North Atlantic. However, although regional analyses of catch per unit effort (CPUE) data from U.S. longliners in the western north Atlantic indicates significant declines for both species, declines were apparently greater for blues than makos (24). The 2009 Atlantic shark stock assessments do not provide any support for regional declines previously reported; they suggest that current North Atlantic blue shark biomass appears to be well above the biomass that would support maximum sustainable yield and close to an unfished biomass (25, 26), whereas despite initially reporting declines for makos, recent estimates now show no evidence for declines (27). These trends are clearly at odds with reported regional declines for blue and mako sharks (24, 28, 29) and in addition with species predictions arising from our space use study. Overall the apparent contradictions in CPUE trends of some oceanic sharks and with our predictions argue for full disclosures of accurate spatial catch data because without them sustainable management will not be possible. Many countries exploiting North Atlantic oceanic habitats do not make, or do not have, full high-quality catch or landings data available for scientific assessments (30). Hence, CPUE trends for blue and mako sharks in the North Atlantic are difficult to interpret because despite VMS technology, the precise location and composition of catches is lacking, therefore it is challenging to determine if the observed trend variability is more closely related to variations in the area targeted or the changing sharks' spatial distributions.

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4. Data Access

The Vessel Monitoring System (VMS) data used in this paper are freely available for non-profit, scientific use from the national government departments given below.

Access to the Portuguese VMS data should be directed to:

Direção Geral de Recursos Naturais, Segurança e Serviços Marítimos
www.dgrm.mam.gov.pt/
Av. Brasilia
1449-030 LISBOA - PORTUGAL
Phone: +351 21 3035700
Fax: +351 21 3035702
dgrm@dgrm.mam.gov.pt

Access to the Spanish VMS data should be directed to:

Ministerio de Agricultura, Alimentación y Medio Ambiente
www.magrama.gob.es
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28014 MADRID - SPAIN
Phone: +44 91 347 45 80
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