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

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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*).

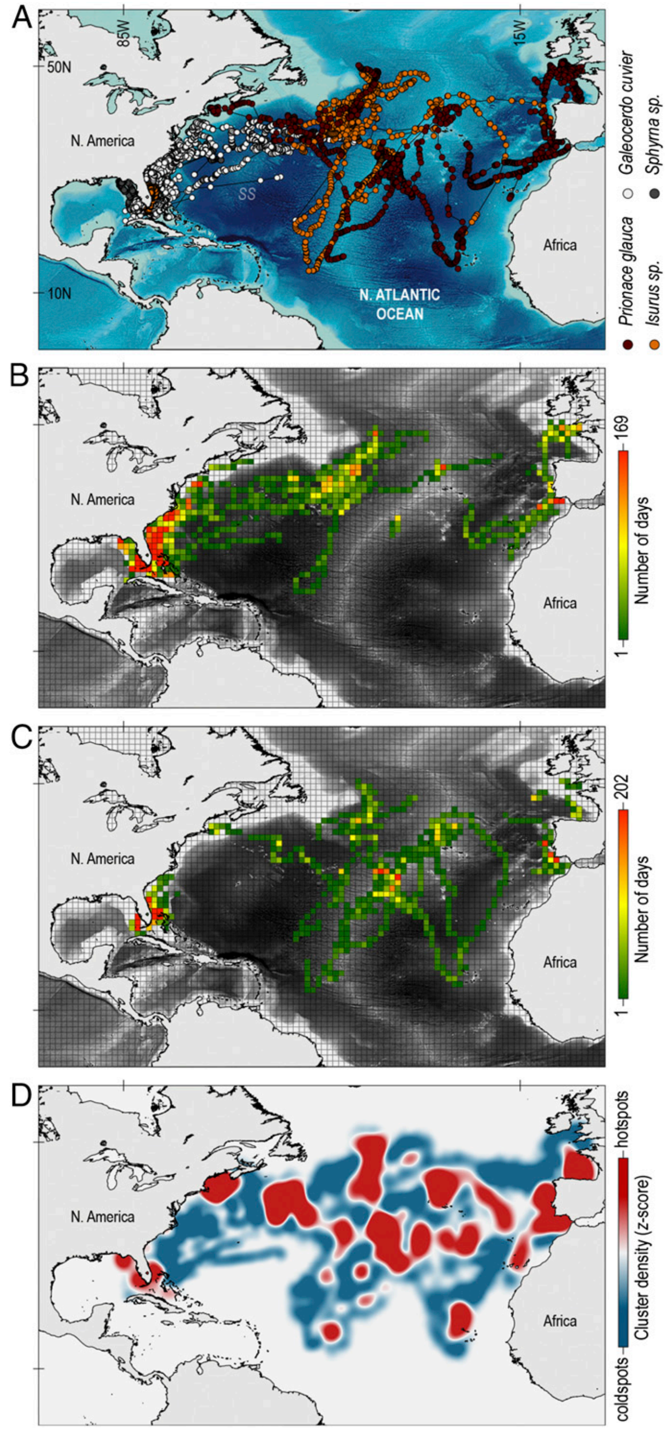

Fig. 1. Spatial distributions of satellite-tracked pelagic sharks. (*A*) Fishery-independent satellite track geolocations of oceanic and coastal/pelagic sharks in the North Atlantic Ocean, 2006–2012. Space use shift between spring-summer (March–August) (*B*) and autumn-winter (September–February) (*C*) 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

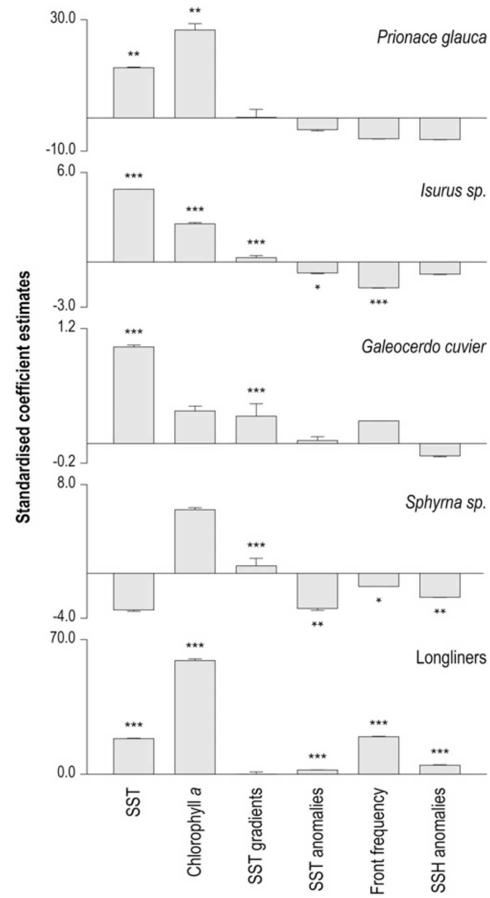

Fig. 2. Habitat selection of pelagic sharks and longliners. Standardized RSPF model coefficient estimates and SEs for the different environmental variables, shark species, and longliners. Note that higher positive values indicates stronger selection for that particular habitat type. Selection indices 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.

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).

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).

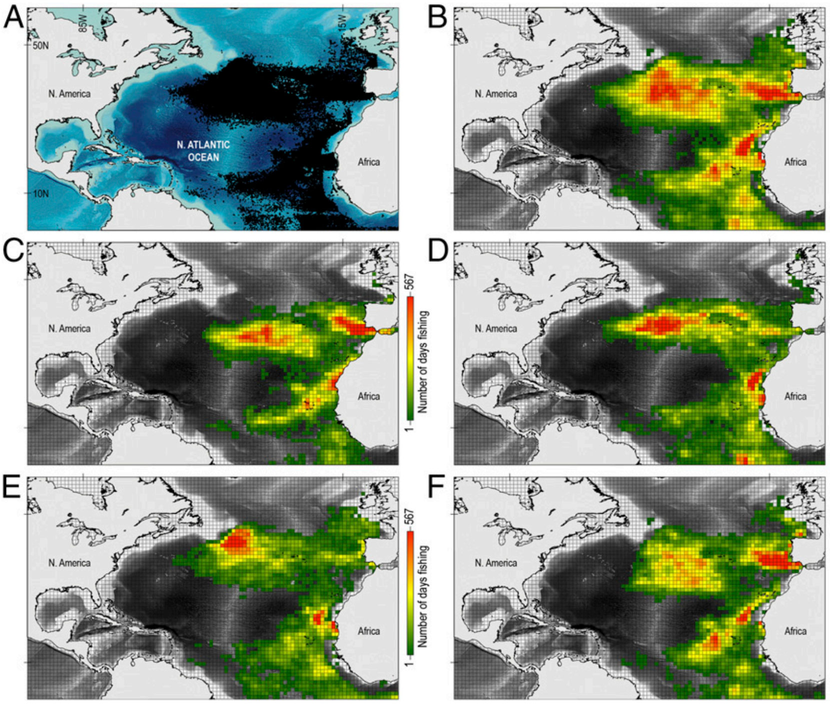

Fig. 3. Annual and seasonal distributions of Spanish and Portuguese longline fishing effort. (*A*) Distribution of longline deployment locations by 186 Spanish and Portuguese vessels, 2003–2011. (*B*) Map showing core fishing areas of the combined fleets. Seasonal shifts and stability in spatial coverage 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

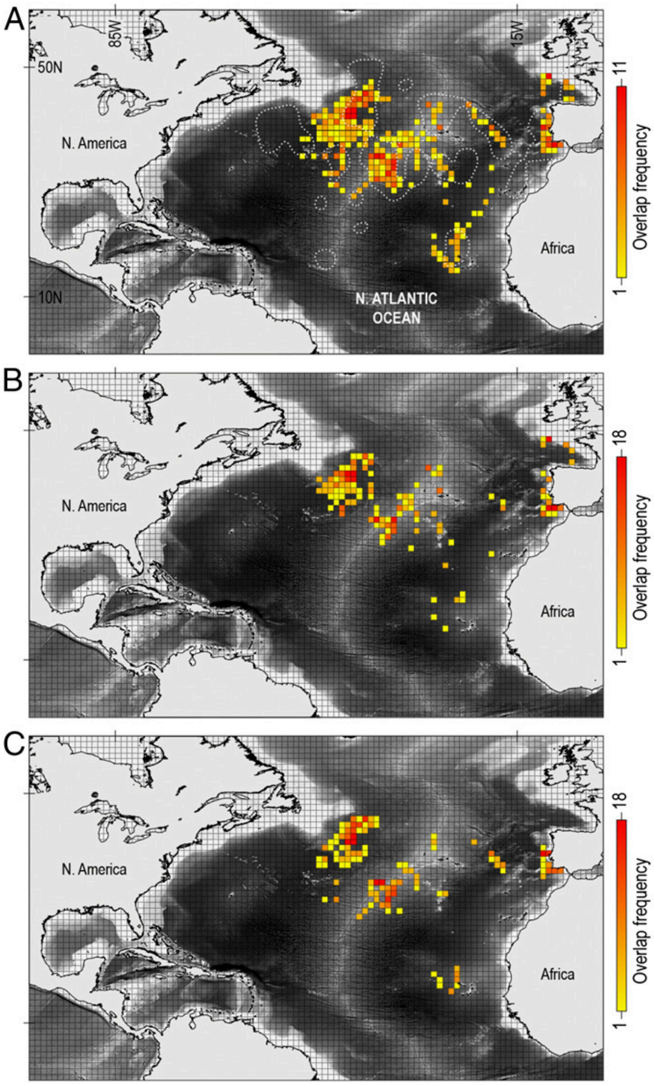

Fig. 4. Oceanic shark spatial and temporal overlap with longline vessels. (*A*) Distribution of the temporal cooccurrence (shared grid cell) between satellite-tracked oceanic sharks and Spanish and Portuguese pelagic longliners. Dotted white lines denote edges of space-use hotspots in Fig. 1*D*. Temporal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