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# Overlap between highly suitable habitats and longline gear management areas reveals vulnerable and protected regions for highly migratory sharks

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ABSTRACT: Highly migratory species (e.g. sharks, tunas, turtles, cetaceans) present unique conservation management challenges due to their wide-ranging movements. Consequently, the extent to which management areas protect habitats for highly migratory species is often unknown. Within the southeast region of the USA's exclusive economic zone, highly migratory sharks are target and/or bycatch species in pelagic and bottom longline fisheries. Here, we developed maximum entropy habitat suitability models for great hammerhead sharks *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas* within the southeast region based on satellite tag (n = 96) and remotely sensed environmental data. Modeled highly suitable habitats were compared to longline gear management areas to determine what proportion of these habitats are protected from, and vulnerable to, longline fisheries. The percentages of highly suitable habitats overlapping with longline management areas varied by species and season (78% warm, 36% cool season for great hammerhead sharks; 48% warm, 79% cool for tiger sharks; and 2% warm, 100% cool for bull sharks). Highly suitable great hammerhead and tiger shark habitats were relatively well protected from pelagic longline fisheries yet vulnerable to bottom longline fisheries. Additionally, both species were vulnerable to pelagic and bottom longline fisheries off southwestern Florida; thus, extending gear restrictions to this area may benefit both species. Bull shark highly suitable habitats were only well protected from longline gear during the cool season. These results demonstrate how habitat suitability modeling can be used to help assess the efficacy of spatial management strategies and inform conservation plans for highly migratory species.

KEY WORDS: Sharks · Habitat suitability · Fishing · Satellite telemetry · Highly migratory species · Bycatch · Spatial ecology · Movement ecology



## INTRODUCTION

Many large highly migratory fish species (HMS) such as sharks, tuna, and billfish are economically and ecologically important (Clarke et al. 2006, Heithaus et al. 2008, Estes et al. 2011). As such, the removal of these species can have important socioeconomic, conservation, and management implications (Collette et al. 2011, Ruppert et al. 2013). Due to overexploitation from both targeted and incidental capture, many HMS have undergone varying levels of population decline over the last 50 yr (Neubauer et al. 2013). Accordingly, implementing effective conservation strategies for HMS is a fisheries management priority (Pons et al. 2017).

To effectively implement fishery management plans, policymakers often require an understanding of species-specific habitat use patterns and must be able to identify suitable habitats (Mora et al. 2003, Norse 2010). However, many HMS can be difficult to locate,

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study, and effectively manage due to their wide-ranging movements, often across domestic and international boundaries (Meltzer 1994). Additionally, the habitat use patterns of HMS can vary regionally, so trends observed in one location may not be applicable elsewhere (Lascelles et al. 2014, Schlaff et al. 2014).

Tagging and fisheries capture data are commonly used to assess the distribution of migratory marine species and support management decisions (Hammerschlag et al. 2011a, McGowan et al. 2017). However, these data generally only provide spatial and temporal snapshots of distributions, which may not be sufficient to summarize the diverse habitat use patterns of HMS. Combining species occurrence data with environmental predictors can greatly improve an understanding of species distribution and habitat use patterns. For example, some HMS, such as sharks, spend disproportionately large amounts of time in specific areas due to favorable environmental conditions, such as optimal water temperatures, which promote primary productivity (Queiroz et al. 2016). While many environmental variables are dynamic in nature, consistent patterns in these variables can be used to identify suitable habitats for particular species, which may be strong candidates for place-based management, such as marine protected areas (MPAs) or gear-restricted areas.

In tropical and temperate waters, great hammerhead sharks *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas* often co-occur over parts of their range. Despite this overlap, these species differ in their ecology and associated habitat use patterns, which likely renders them vulnerable to different levels of fisheries exploitation, both as target and bycatch (Gallagher et al. 2012, IUCN 2017). Great hammerhead sharks are considered overfished and are experiencing population declines in the subtropical Atlantic Ocean and Gulf of Mexico (Miller et al. 2014). While tiger and bull shark populations have experienced declines to a lesser extent in the region over the past several decades, presently, their populations appear to be stabilizing (Carlson et al. 2012). However, all 3 species continue to be caught as bycatch in commercial fisheries within US federal waters (NMFS 2016). Given that all 3 species have relatively slow growth rates and low fecundity, understanding spatiotemporal trends in habitat protection from fisheries has important conservation implications (Worm et al. 2013, IUCN 2017).

Within the southeast region (SER) of the USA's exclusive economic zone (EEZ), which extends from the Virginia–North Carolina border to the Texas–Mexico border, several highly migratory shark species are caught as target and/or bycatch in pelagic longline (PLL) and bottom longline (BLL) commercial fisheries (Carlson et al. 2012, NMFS 2016). While the targeted capture of sharks within the SER is restricted and regulated (Carlson et al. 2012), several species remain vulnerable to being caught as bycatch in the PLL fisheries (targeting tuna and swordfish) and the BLL fisheries (targeting sharks and reef fishes; see NMFS 2016 for bycatch and landings estimates for US commercial fisheries). While many species caught as bycatch in US commercial fisheries will be released (NMFS 2016), recent studies have shown that certain shark species, such as great hammerhead sharks, are vulnerable to at-vessel and post-release mortality, and individuals that survive capture may still experience sublethal losses in fitness (Morgan & Burgess 2007, Gallagher et al. 2014a, Whitney et al. 2016). Thus, it has been argued that perhaps the most effective way to conserve sharks susceptible to bycatch-related mortality or fitness loss is to prevent these species from interacting with fishing gear in their essential habitats through gear modifications or spatial closures (Godin et al. 2012, Gallagher et al. 2014a, Gulak et al. 2015).

Several longline gear management areas have been implemented in the SER to reduce fisheries interactions with a variety of species, including (but not limited to) bluefin tuna *Thunnus thynnus*, pilot whales *Globicephala* spp., sandbar sharks *C. plumbeus*, and dusky sharks *C. obscurus*. However, it is presently unclear if, and to what extent, these longline gear management areas protect highly suitable habitats for great hammerhead, tiger, and bull sharks that also co-occur within the SER. Accordingly, this study seeks to fill these knowledge gaps by (1) identifying highly suitable habitats for these 3 species based on environmental variables within their known ranges of the SER, (2) determining what proportion of their highly suitable habitats are currently protected within longline gear management areas versus vulnerable to exploitation in longline fisheries, and (3) comparing the magnitude of these protected and vulnerable habitats at both species-specific and seasonal levels. Understanding when and where these species are vulnerable to PLL and/or BLL gear may assist managers with policy decisions relating to sustainable exploitation, bycatch reduction, and/or assessment of the efficacy of current management strategies for these species. Additionally, the approach developed here can be applied to other HMS to better understand their movement ecology and aid in the evaluation of current conservation management strategies.

## MATERIALS AND METHODS

### General methods overview

Great hammerhead, tiger, and bull sharks were tagged with satellite transmitters to determine their spatial distribution patterns in the study region. Positional data were filtered, interpolated, and regularized to improve spatial accuracy, minimize spatial autocorrelation, and address issues of irregular transmissions and data gaps. The resulting positional data were then used in conjunction with remotely sensed environmental data following a step-wise maximum entropy (MaxEnt) approach to develop habitat suitability models for 3 temporal periods. The resulting models were reclassified to identify highly suitable habitats, which were then overlapped with longline gear management areas to identify regions where the focal species could be vulnerable to longline fishing gear within their range. Details on each step of this procedure are described below.

### Study area

This study was restricted to the SER for 3 reasons: first, all of the satellite-tagged sharks included in this study were present within the SER; second, there are multiple fisheries within this region that use PLL or BLL gear (most notably the HMS PLL, the Gulf of Mexico BLL reef fish fishery, as well as the BLL shark fishery); and third, the SER is a distinct management zone that provided a natural cut-off point between subtropical and temperate zones, which focused analysis to habitats within the known range of the 3 focal species (NOAA 2017).

### Data collection

#### Capturing and handling

Great hammerhead, tiger, and bull sharks were captured using baited circle-hook drumlines in southern Florida, as well as in the northern Bahamas following Gallagher et al. (2014b).

#### Tagging

Each shark was measured, sexed, and tagged with a Smart Position and Temperature Transmitting tag (SPOT5, Wildlife Computers). Since great hammerhead sharks are sensitive to capture and handling stress (Gallagher et al. 2014b), this species was tagged with a towed SPOT5 tag that could be quickly attached via a tether and titanium dart anchored into the musculature at the base of the first dorsal fin. In comparison, tiger and bull sharks were tagged by affixing the tag to the first dorsal fin using titanium bolts, neoprene and steel washers, and high-carbon steel nuts. This gear combination helps protect the shark's fin from metal corrosion while ensuring the tag eventually detaches from the shark when the steel nuts corrode in saltwater (Hammerschlag et al. 2011b). To minimize biofouling, all tags were coated in Propspeed, a non-toxic, non-metallic, anti-fouling agent.

The geographic location of each tagged shark was determined via Doppler-shift calculation made by the Argos Data Collection and Location Service (www.argos-system.org). Location accuracy was dependent on the number of tag transmissions received by Argos satellites.

### Data interpolation and analysis

Satellite tag data were downloaded from Argos and filtered for location accuracy. Argos provides location accuracy using location classes (LC) 3, 2, 1, 0, A, B, and Z (in decreasing accuracy), which are associated with the following error estimates: LC3 < 250 m, 250 m < LC2 < 500 m, and 500 m < LC1 < 1500 m. Tougaard et al. (2008) consider the error estimates associated with LC A and B to be >1 km and >5 km, respectively. LC Z estimates are highly unreliable and as such were removed from the dataset.

Following Graham et al. (2016), filtered points were then interpolated and regularized to minimize spatial autocorrelation and spatial biases that would otherwise exist as a result of the irregular sampling intervals at which SPOT-derived data are acquired. Geopositions were interpolated and regularized to a 12 h frequency up to a 3 d interval following a curvilinear interpolation method developed by Tremblay et al. (2006) based on the piecewise cubic Hermite interpolating polynomial in MatLab (MathWorks).

To investigate for potential differences in seasonal patterns, geopositional data were evaluated with respect to 1 of 3 temporal periods: (1) warm season, representing May through October, (2) cool season, representing November through April, and (3) year-round, representing the entire dataset. Two seasonal periods (warm versus cool) were designated because the study region is mostly subtropical and dominated by 2 distinct seasons, a summer warm/wet season and a winter cool/dry season. Moreover, US fisheries management primarily operates on the temporal scale used in this study.

### Environmental variables

To identify suitable habitats for the focal species based on environmental factors, habitat suitability models were developed using 5 environmental variables likely to impact shark occurrence: bathymetry, bathymetric slope, chlorophyll a (chl *a*) concentration, sea surface temperature (SST), and surface current magnitude (Table 1). These variables were selected based on a review of environmental factors that are known to influence the habitat use of the 3 study species (e.g. Carlson et al. 2010, Queiroz et al. 2016, Guttridge et al. 2017), as well as previous MaxEnt habitat suitability models for sharks, which identified these environmental variables as predictors of shark occurrence (e.g. McKinney et al. 2012, Sequeira et al. 2012). Surface variables (chl *a* concentration: NASA OceanColor, https://oceancolor.gsfc.nasa.gov/data/aqua; SST: NASA PO.DAAC JPL, https://podaac.jpl.nasa.gov; and surface current magnitude: HYCOM, https://hycom.org) were chosen to correspond with the surface locations reported by the SPOT5 tags, as well as the temporal range over which the locations were reported (2010–2015). These surface variables were appropriate as the focal species are all epipelagic, and telemetry studies have demonstrated that within the study region, all 3 study species spend the majority of their time within the upper 50 m of the water column, with considerable time at or near the surface (Carlson et al. 2010, Vaudo et al. 2014, Calich 2016). Geospatial rasters for all environmental variables were downloaded using the MGET toolbox for ArcGIS (Roberts et al. 2010), except for multibeam bathymetry, which was downloaded directly from NOAA (2016), and bathymetric slope, which was derived using the 'surface slope' tool in ArcGIS (version 10.3).

Since SST, chl *a* concentration, and surface current magnitude all vary seasonally, these rasters were averaged for each temporal period under analysis (warm and cool seasons, and year-round) using the 'cell statistics' tool in ArcGIS.

All rasters were then projected to North American Datum 1983 (NAD83) and Universal Transverse Mercator (UTM) Zone 17N and resampled for consistency in spatial extent and resolution. To preserve the accuracy of the high-resolution bathymetry data, all rasters were resampled to 1 km resolution prior to developing each habitat model. However, as this step artificially increased the resolution of some of the rasters, the original resolution of the data should be considered when reviewing each model and associated environmental ranges (Table 1).

Table 1. Environmental variables used to create preliminary MaxEnt habitat suitability models. na: not applicable, SST: sea surface temperature

| Variable | Unit | Spatial resolution | Temporal resolution | Source |
|---|---|---|---|---|
| SST | °C | 4 km | Monthly[a] | NASA PO.DAAC JPL |
| Chl *a* concentration | mg $m^{-3}$ | 4 km | Monthly[a] | NASA OceanColor |
| Surface current magnitude | m $s^{-1}$ | 1/12° | Daily[a] | HYCOM |
| Multibeam bathymetry | m | ~500 m[b] | na | NOAA |
| Bathymetric slope | % rise | 1 km | na | ArcGIS-derived |

[a]Temporal range extended from March 1, 2010 to May 31, 2015, based on data availability
[b]The multibeam bathymetry raster was filled with ETOPO1 data (www.ngdc.noaa.gov/mgg/global) with 1 arc-minute resolution in locations where multibeam data were unavailable

### Habitat suitability models

A MaxEnt approach was used to develop habitat suitability models for each of the study species (MaxEnt version 3.3.3k; Phillips et al. 2006). MaxEnt has been used extensively for modeling species distributions and it is competitive with other high-performing models (Elith et al. 2006, 2011). MaxEnt has been previously used to create habitat suitability models for highly migratory sharks, including whale sharks *Rhincodon typus* (McKinney et al. 2012, Sequeira et al. 2012), basking sharks *Cetorhinus maximus* (Siders et al. 2013), and blue sharks *Prionace glauca* (Sousa 2009).

The MaxEnt approach uses machine learning to create habitat suitability models based on presence-only data and environmental covariates. While multiple model outputs are possible, the 'raw' model output was used in this study because it estimates the relative suitability of one location over another in terms of the expected relative number of presences per unit area (Merow et al. 2013, Yackulic et al.

2013), without making assumptions about a species occupancy rate, which is currently unknown for the focal species (Elith et al. 2011, Yackulic et al. 2013).

A presence-only modeling approach was chosen for this study because SPOT5 tags only report presence data. Simulated pseudo-absence data were not developed for this study because the absence of shark data in a specific location does not mean a shark was not there. For example, the tag may not have broken the surface of the water, or perhaps an Argos satellite was not available to record the location. Accordingly, developing simulated pseudo-absence data was not possible. As such, we felt it was most appropriate to follow a presence-only modeling approach and to use the results of the raw output to describe habitat suitability instead of occupancy rates.

Initial analyses were run to ensure that each model only included relevant variables that significantly improved model performance. To accomplish this, correlation analysis was first run in ArcGIS to ensure no highly correlated variables were included in any models. Next, the models were evaluated following a step-wise procedure developed by Yost et al. (2008). Each model was initially created with all 5 explanatory environmental variables (Table 1). Models were then run in replicate (n = 10) using randomly chosen, non-repeating (cross-validated) background samples to allow for statistical comparisons between model variations. At this stage, 25% of the samples were retained for model validation to ensure that the majority (75%) of the data were used to identify important habitat variables within the SER, which is a spatially dynamic region that encompasses a wide range of habitat variation. Duplicate data points were allowed, as the data had already been filtered and interpolated to ensure only reliable data were used in analysis. Once all replicates of the 5-variable models were completed, jackknife tests were run to identify the variable that contributed the least to the overall training gain of each model variation. This variable was then eliminated and the model was re-run with the remaining variables. This procedure was repeated until only 1 variable remained. Once all of the model variations were complete, the models were evaluated based on their area under the receiver operating characteristic curve (AUC) values, which is an index of model performance that provides a single measure of model accuracy (Yost et al. 2008). Multiple, pairwise Mann-Whitney *U*-tests were used to determine which model variation resulted in the highest AUC score with the least number of variables, to avoid overfitting the model (our Tables S1–S3 in the Supplement at www.int-res.com/articles/suppl/m602p183_supp.pdf; see also Yost et al. 2008).

Once the most influential variables were identified, final habitat suitability models were developed for each species by temporal period (warm season, cool season, and year-round) to account for species and seasonal variations. To ensure robust statistical evaluation, the final models were validated using a random test percentage of 50%.

Lastly, each model (n = 9) was reclassified in ArcGIS based on natural breaks to identify areas that were predicted to have a high, moderate, and low probability of species presence based on environmental preferences. Natural breaks were chosen over alternative methods (e.g. manually setting thresholds), because the habitat use patterns of these species are not directly comparable, and using natural breaks allowed us to highlight patterns in each species individual habitat use patterns. Areas with a high probability of species presence were exported for further analysis and are referred to as 'highly suitable habitats'. To determine the potential ranges of environmental variables experienced by each species during each season, the relevant variables (as identified by the habitat models) and associated interpolated locations were added to ArcGIS and variable values were extracted using the 'extract multi values to points' tool.

One important consideration of using MaxEnt models is that the accuracy of the models can be strongly influenced by bias in sampling effort (Baldwin 2009), which in this case applied to the area where the sharks were tagged and tracked (our Figs. S1 & S2 in the Supplement). Accordingly, we restricted our interpretation of the MaxEnt outputs to the SER, which has similar environmental conditions to areas where our tagged sharks have been tracked as well as areas that have been identified as essential fish habitat for these species based on multiple data sources (NOAA 2017).

### Longline gear management areas

Areas where the use of PLL and/or BLL gears are prohibited (including seasonal and conditional prohibitions) throughout the SER were identified using the US Code of Federal Regulations. An area was only included in the analysis if it had an established fisheries management boundary, and regulations prohibited (or restricted, in the case of the Cape Hatteras Gear Restricted Area) the use of PLL and/or BLL gears during a portion of each year; areas that met these requirements are henceforth referred to as 'management areas'. The types of management areas chosen for analysis included: MPAs, marine sanctuaries, special management zones, closed areas, gear-restricted areas, and habitat areas of particular concern (see Table S4 in the Supplement for a complete list of all management areas included in the analysis). Shapefiles of these areas were either downloaded from federal websites or constructed in ArcGIS using coordinates provided in the US Code of Federal Regulations. In total, 85 areas that prohibit PLL and/or BLL gears were identified (Fig. 1, Table S4).

Management areas were categorized as occurring during the warm or cool season depending on when using longline gear was prohibited within each area. Management areas that occurred during the warm and cool seasons were placed into the year-round category, even if they did not prohibit longline gear over the entire year. For example, the mid-Atlantic shark closure, which runs from January 1 to July 31, is included in the year-round model because it occurs during both the warm and cool seasons.

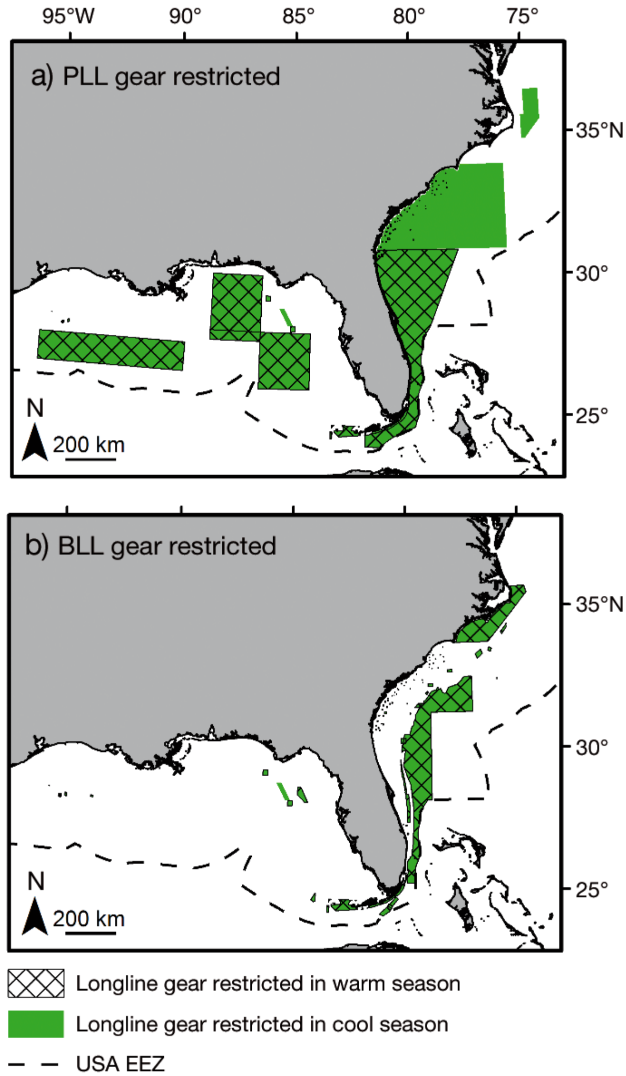


Fig. 1. Areas where (a) pelagic longline (PLL) and/or (b) bottom longline (BLL) gears are prohibited in the southeast region of the USA's exclusive economic zone (EEZ). These areas were categorized into the warm season or cool season based on when they restricted longline gear use (May–October or November–April, respectively). Areas with closure dates in both the warm and cool seasons were placed in a year-round category, even if they did not prohibit longline gear over the entire year. This figure is displayed using the projected coordinate system North American Datum 1983 (NAD83) and Universal Transverse Mercator (UTM) Zone 17N

### Identifying protected suitable habitat

Once highly suitable habitats were identified, they were intersected with longline gear management areas to identify where habitats with a high probability of species presence are protected from PLL and/or BLL gear. Analysis was restricted to within the SER (i.e. highly suitable habitats and management areas within state waters were excluded from analysis) to ensure analyses were run over a consistent area, to eliminate any potential problems associated with data variability near the shoreline, and to restrict analysis to locations where commercial longline fishing occurs. Note that the spatial extent of state waters only accounted for 7.84 % of the EEZ within the SER.

Analysis of warm and cool seasonal trends included both the locations where some form of longline gear was prohibited during a specific season as well as the year-round closures. Locations with a high probability of species presence that overlapped with gear management areas were identified as 'protected areas' because PLL and/or BLL gear cannot be used in these habitats during a specified time and thus the animals are protected from 1 or both of these gear types when occupying these areas. In cases where a region is only protected from 1 longline gear type, it is important to consider that the other longline fishery may still be operating and thus the species may remain vulnerable to a form of longline fishing (see Fig. 1 for specific fishery management areas).

To determine how much of each species' highly suitable habitat was protected from longline fishing gear, the spatial extent of the protected areas (in $km^2$) was divided by the total modeled habitat area

Table 2. Summary statistics of the sharks included in this study. Note that some sharks were present in both seasons. STL: stretch total length

| Species | No. of sharks (no. of interpolated locations) | | | Sex (F:M) | STL (cm) |
|---|---|---|---|---|---|
| | Year-round | Warm season | Cool season | | |
| Great hammerhead shark *Sphyrna mokarran* | 25 (557) | 16 (272) | 14 (285) | 10:15 | 124–450 |
| Tiger shark *Galeocerdo cuvier* | 45 (3310) | 35 (2321) | 28 (989) | 37:8 | 175–403 |
| Bull shark *Carcharhinus leucas* | 26 (793) | 12 (326) | 23 (467) | 18:8 | 170–269 |

with a high probability of species presence (in km$^2$). This result was then converted to a percentage to indicate the percentage of habitat with a high probability of species presence that is protected from PLL and/or BLL gear.

## RESULTS

In total, 23 great hammerhead, 65 tiger, and 29 bull sharks were captured and tagged between March 2010 and December 2015. Following filtering and interpolation, 4660 data points from 96 animals were used to create habitat suitability models (Fig. S1, Table S5 in the Supplement, Table 2).

MaxEnt models were created for the study species during each temporal period, for a total of 9 individual models (Fig. S3 in the Supplement, Fig. 2). All models performed better than random and would be classified as 'good' ($0.7 < AUC \leq 0.9$) or 'very good' ($AUC > 0.9$), indicating the models are useful and informative (see our Table 3 for AUC scores; Swets 1988, Baldwin 2009). While the combination of variables that were incorporated into each model varied, the most commonly included environmental variable was bathymetry, which was included in each of the models, while bathymetric slope, which did not significantly improve any of the models, was not included in any model (Tables 3 & S1–S3).

Habitats with a high probability of great hammerhead, tiger, or bull shark presence varied by season (Fig. 3, Table 4). Similarly, highly suitable habitats where the focal species were protected from PLL and/or BLL fishing gear also varied by season, and within these protected areas, the level of protection varied by gear type (Fig. S4 in the Supplement, Fig. 3).

While 78% of highly suitable great hammerhead habitats were protected from PLL and/or BLL gears in the warm season, only 36% were protected in the

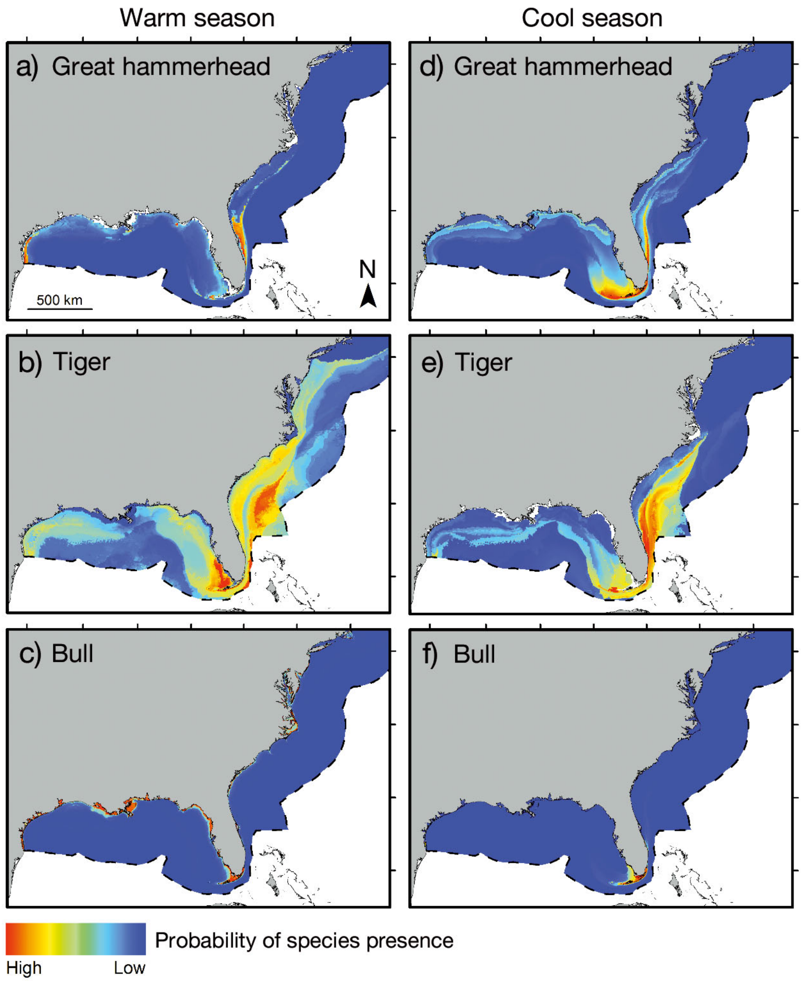


Fig. 2. Probability of great hammerhead shark *Sphyrna mokarran*, tiger shark *Galeocerdo cuvier*, and bull shark *Carcharhinus leucas* presence within the southeast region of the USA's exclusive economic zone in the (a–c) warm (May–October) and (d–f) cool season (November–April). See Fig. 1 for reference grid

Table 3. Environmental variables used to create each of the final MaxEnt habitat suitability models, for great hammerhead sharks *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas*. AUC: area under the receiver operating characteristic curve, SST: sea surface temperature

| | Mean | SD | 95% CI | Range |
|---|---|---|---|---|
| **Year-round** | | | | |
| **Great hammerhead** (test AUC = 0.94) | | | | |
| Bathymetry (m) | 75.43 | 336.51 | 46.94–103.93 | 1–3939 |
| Current magnitude (m $s^{-1}$) | 0.258 | 0.171 | 0.242–0.274 | 0.061–1.441 |
| SST (°C) | 25.69 | 1.35 | 25.58–25.80 | 21.42–28.42 |
| **Tiger** (test AUC = 0.786) | | | | |
| Bathymetry (m) | 549.42 | 834.1 | 520.87–577.97 | 1–5280 |
| Chl *a* (mg $m^{-3}$) | 0.713 | 1.366 | 0.666–0.76 | 0.077–13.614 |
| Current magnitude (m $s^{-1}$) | 0.476 | 0.346 | 0.464–0.488 | 0.047–1.566 |
| SST (°C) | 25.17 | 2.35 | 25.09–25.25 | 13.59–28.09 |
| **Bull** (test AUC = 0.954) | | | | |
| Bathymetry (m) | 29.52 | 120.77 | 19.47–39.57 | 1–929 |
| **Warm season** | | | | |
| **Great hammerhead** (test AUC = 0.962) | | | | |
| Bathymetry (m) | 31.23 | 65.63 | 23.18–39.27 | 1–870 |
| Current magnitude (m $s^{-1}$) | 0.313 | 0.205 | 0.284–0.343 | 0.1–1.51 |
| SST (°C) | 28.41 | 0.81 | 28.31–28.51 | 27.02–29.61 |
| **Tiger** (test AUC = 0.812) | | | | |
| Bathymetry (m) | 579.55 | 889.97 | 543.3–615.8 | 1–5280 |
| Chl *a* (mg $m^{-3}$) | 0.656 | 1.23 | 0.606–0.706 | 0.048–15.89 |
| SST (°C) | 27.73 | 2 | 27.65–27.81 | 19.15–30.7 |
| **Bull** (test AUC = 0.958) | | | | |
| Bathymetry (m) | 23.55 | 103.13 | 10.32–36.77 | 1–929 |
| **Cool season** | | | | |
| **Great hammerhead** (test AUC = 0.927) | | | | |
| Bathymetry (m) | 116.17 | 458.82 | 62.19–170.14 | 1–3939 |
| SST (°C) | 22.76 | 2.22 | 22.5–23.02 | 18.53–26.22 |
| **Tiger** (test AUC = 0.879) | | | | |
| Bathymetry (m) | 476.91 | 676.02 | 434.16–519.66 | 1–4742 |
| Current magnitude (m $s^{-1}$) | 0.542 | 0.366 | 0.518–0.565 | 0.081–1.5 |
| SST (°C) | 23.73 | 1.55 | 23.63–23.83 | 17.36–26.02 |
| **Bull** (test AUC = 0.98) | | | | |
| Bathymetry (m) | 33.92 | 132.23 | 19.4–48.44 | 1–787 |
| SST (°C) | 24.48 | 0.92 | 24.39–24.56 | 18.57–27.02 |

cool season (see Table 4 for habitat area calculations for all species). Within these protected areas, 78% and 36% of great hammerhead shark habitats were protected from PLL gear in the warm and cool seasons, respectively, while 9% and 13% of great hammerhead shark habitats were protected from BLL gears, respectively. Thus, the highly suitable habitats of great hammerhead sharks are more vulnerable to BLL fisheries than PLL fisheries (Figs. 1 & 3).

In comparison, 48% of highly suitable tiger shark habitats were protected from PLL and/or BLL gear in the warm season, while 79% were protected in the cool season. Within these seasons, tiger shark habitats were predominantly protected from both PLL and BLL gears in the cool season (78% and 39% of highly suitable tiger shark habitats were protected from PLL and BLL gears, respectively), leaving these habitats more vulnerable to both fisheries in the warm season (where only 37% and 27% of these habitats were protected, respectively).

Lastly, only 2% of highly suitable bull shark habitats were protected from PLL or BLL gears in the warm season, while 100% and 89% of highly suitable habitats were protected from PLL and BLL gears, respectively during the cool season (though it is important to consider the relatively low amount of highly suitable bull shark habitat identified in this study). While the magnitude of protected habitat varied by season, both great hammerhead and tiger shark highly suitable habitats were vulnerable to PLL and BLL fishing gear west of southwestern Florida during the cool season (Fig. 4).

## DISCUSSION

MaxEnt modeling was used to identify and characterize habitat suitability for great hammerhead, tiger, and bull sharks within the SER and subsequently determine what proportion of their habitats are protected from PLL fisheries, where they are captured as bycatch, as well as from BLL fisheries, where they are captured as both target (in the shark BLL fishery) and bycatch (in the reef fish BLL fishery).

Overall, despite being sympatric species, great hammerhead, tiger, and bull sharks exhibited clear interspecific differences in habitat suitability (e.g. Fig. 2). The highly suitable habitats of great hammerhead and tiger sharks exhibited a relatively high level of overlap, though the tiger shark habitats were more widespread than those of great hammerhead sharks (Fig. 2). These findings are consistent with previously published studies on the distribution and movements of these species in the region (NOAA 2017). In comparison, most highly suitable bull shark habitats were restricted to shallow, inshore waters (<30 m; see Table 3) and there was

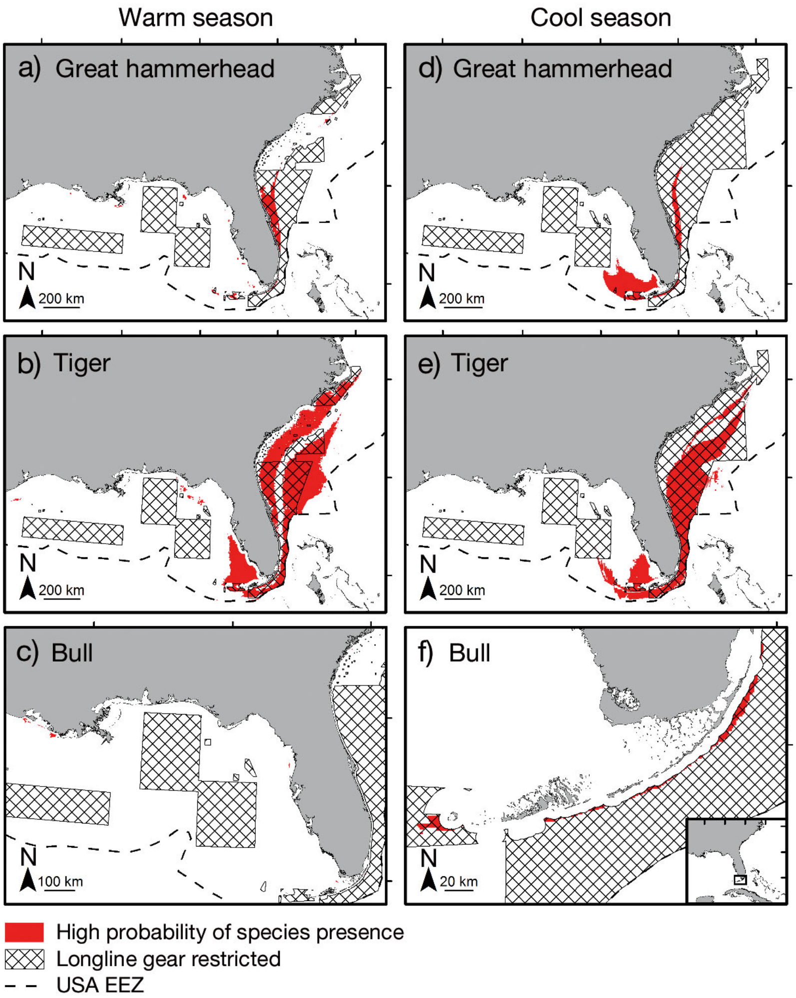


Fig. 3. Locations where highly suitable great hammerhead shark *Sphyrna mokarran*, tiger shark *Galeocerdo cuvier*, and bull shark *Carcharhinus leucas* habitats are protected from longline fishing gear in the southeast region of the USA's exclusive economic zone (EEZ) in the (a–c) warm (May–October) and (d–f) cool season (November–April). See Fig. 1 for reference grid

Table 4. Area of highly suitable habitat and protected habitat in the southeast region of the USA's exclusive economic zone for great hammerhead sharks *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas*, year-round and in the warm (May–October) and cool (November–April) seasons

| | Highly suitable habitat (km$^2$) | Protected highly suitable habitat (km$^2$) | Protected highly suitable habitat (%) |
|---|---|---|---|
| **Year-round** | | | |
| Great hammerhead | 55 012.40 | 24 990.36 | 45.43 |
| Tiger | 257 563.52 | 168 814.37 | 65.54 |
| Bull | 500.82 | 11.98 | 2.39 |
| **Warm season** | | | |
| Great hammerhead | 23 272.02 | 18 262.93 | 78.48 |
| Tiger | 207 757.95 | 100 407.89 | 48.33 |
| Bull | 500.82 | 11.98 | 2.39 |
| **Cool season** | | | |
| Great hammerhead | 46 609.67 | 16 988.09 | 36.45 |
| Tiger | 165 435.72 | 130 215.08 | 78.71 |
| Bull | 418.10 | 418.09 | 100.00 |

only a small proportion of highly suitable bull shark habitat identified within the SER. This is also consistent with the regional habitat use and movement patterns that have been documented for bull sharks (Carlson et al. 2010).

While the models developed in this study identified highly suitable habitats within the range of the focal species previously revealed through satellite tagging (e.g. Graham et al. 2016), our models also identified some suitable habitats in regions that our satellite-tagged sharks did not occupy, such as those identified in the Gulf of Mexico (e.g. compare Figs. 2 & S1). While most of these habitats fall within the essential habitats identified by NOAA (2017), some of the habitats identified here do not. These locations warrant further exploration because if a preferred set of environmental parameters are present in these regions, these areas could be previously undocumented high-use areas for our focal species. In addition to identifying these habitats, the modeled results designate the importance of acknowledging seasonal trends in habitat suitability, which are not indicated in the essential habitat designations of the study species in NOAA (2017).

Despite variations in habitat use patterns of great hammerhead, tiger, and bull sharks, there are specific management areas that appear to protect large proportions of highly suitable habitats for these species, despite not necessarily being implemented specifically for this purpose. In terms of PLL management areas,

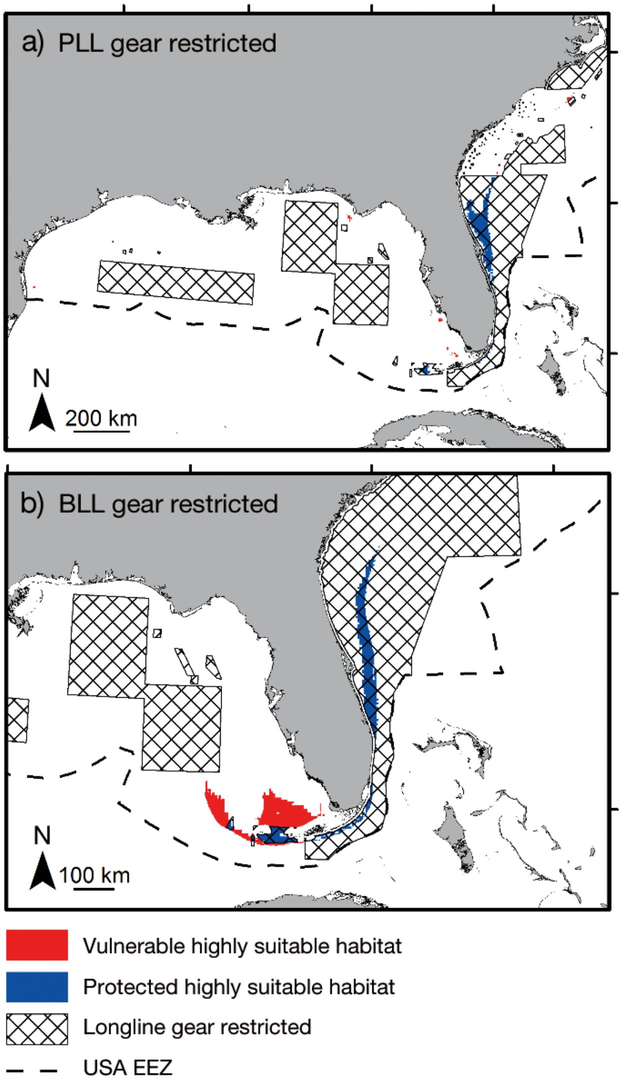


Fig. 4. Locations where highly suitable great hammerhead *Sphyrna mokarran* and tiger shark *Galeocerdo cuvier* habitats are vulnerable to, and protected from, longline fishing gear in the southeast region of the USA's exclusive economic zone (EEZ) in the (a) warm (May–October) and (b) cool season (November–April). See Fig. 1 for reference grid

the East Florida Coast Closed Area largely overlapped with highly suitable habitats of great hammerhead and tiger sharks, and also provided protection to bull shark highly suitable habitats in the cool season. As both great hammerhead and tiger sharks are caught as bycatch in the US Atlantic PLL fishery (Gallagher et al. 2014a), protecting these habitats from PLL gear is possibly providing a significant benefit to these species. In terms of BLL management areas, the Stetson–Miami Terrace Habitat Area of Particular Concern, which was implemented to protect deep-water corals, offers some protection to the highly suitable habitats of tiger sharks, but does not provide substantial protection to the highly suitable habitats of great hammerhead sharks.

As all 3 of the focal species may be retained in the directed shark BLL fishery (NOAA 2018), evaluating the extent to which BLL fishing occurs in highly suitable habitats for these species is important for informing ongoing management decisions. Additionally, the relatively small area of highly suitable bull shark habitat vulnerable to PLL and BLL gears during the warm season suggests that a closure in this area during this period would likely provide beneficial protection if deemed necessary (bull shark populations in the study region appear to be stable at this time; Carlson et al. 2012).

Lastly, there is an area of federally managed waters west of southwestern Florida where highly suitable habitats of both great hammerhead and tiger sharks are vulnerable to PLL and BLL gears in the cool season (Fig. 4). While this region is only an approximation because both models were based on different data, our analysis suggests that this general area is highly suitable for both species and is currently vulnerable to longline gears. As such, further research into the potential impacts of extending restrictions on longline gear to this region is warranted, as this may have positive outcomes for both species (Fig. 4).

The primary limitation of this study is that identification of suitable habitats was based on modeling data. While MaxEnt modeling has been used in a wide variety of studies, including those focused on sharks (McKinney et al. 2012, Sequeira et al. 2012, Siders et al. 2013, Hacohen-Domené et al. 2015), this technique still results in predicted outcomes. While the habitats identified here are consistent with where our tagged animals traveled, as well as where these species have been previously reported (NOAA 2017), the models could be validated with other fishery-dependent and -independent data.

When interpreting our results, additional considerations include sample size, possible sampling bias, extrapolating from the study area, and satellite-tag spatial errors. In terms of sample size, MaxEnt models can be developed with anywhere from 5 to 50 presence locations, and little benefit may be seen by adding additional locations above 50 (Baldwin 2009). Given we used a minimum of 272 and a maximum of 3310 locations per model, sample size is not likely a major limitation within the spatial domain of the models. However, as all of the individuals tracked were sub-adults and adults, our results should be considered with respect to adults. When considering sampling bias, it is important to note that all of the sharks included in this study were tagged in the same general region of the SER. Given that spatial biases can influence model output, the background points used in this study were selected from a random sample of existing presence locations, which can help improve model output when sampling effort is biased (as recommended by Phillips & Dudík 2008). Additionally, within this region, population and sub-population ranges are not fully known. Thus, sample selection bias is a limitation of this study and the results presented here may be skewed towards animals that spend the majority of their time in the tagging area. For this reason, and as suggested by Baldwin (2009), we do not attempt to extrapolate our results beyond where the animals were originally located, tracked, or known to occur within the SER. We also note that our analysis was restricted to federal waters where the majority of commercial longline fishing occurs. Thus, interpretation of our results should not be extended to inshore state waters, although some states allow variations on longline gear to be used in their waters. Satellite-tag spatial errors are always a concern when tag data of this kind is incorporated into a study. However, MaxEnt is relatively resilient to spatial errors in location data up to 5 km (Baldwin 2009). While it is possible some locations may have originally had spatial errors above 5 km, all of the location data used in this study were filtered and interpolated to help minimize spatial autocorrelation as well as any impact unreliable locations may have had on the results.

Queiroz et al. (2016) recently examined the pelagic movements of 6 shark species in the northwest Atlantic Ocean using satellite tags to identify areas of high space use within international waters. These pelagic shark 'hotspots' were then compared to Spanish and Portuguese longline fishing vessels operating in the high seas based on GPS vessel-tracking data. Queiroz et al. (2016) found high levels of shark and vessel co-occurrence that were spatially and temporally persistent between years, demonstrating that Spanish and Portuguese longline vessels were able to follow these pelagic sharks within their hotspots year-round, leading to high exploitation rates within international waters. While a subset of individual great hammerhead and tiger shark tracks used here were also included in Queiroz et al. (2016), our study differs in overall objective, approach, study area, and results. Specifically, we used shark tracking data to model habitat suitability within US waters of the SER and compared these locations to management areas where PLL and/or BLL gear is prohibited. This allowed us to identify potential locations where the focal sharks were both protected from, and vulnerable to, longline gear within the SER.

While the gear management areas in this study region were not necessarily implemented specifically to protect great hammerhead, tiger, or bull sharks, the modeling approach employed suggests these management zones are protecting a relatively large proportion of their highly suitable habitats from either PLL and/or BLL fisheries within the SER. However, there exists a relatively large area of modeled highly suitable habitat shared by great hammerhead and tiger sharks that remains vulnerable to longlining west of southwestern Florida. This zone could be investigated for consideration of future spatial conservation management efforts for great hammerhead and tiger sharks in the SER. We suggest that the approach used here can be applied to other HMS including other species of sharks, tunas, marine mammals, turtles, billfish, and cetaceans, and may also be valuable in conjunction with future predictions of SST to determine how habitat suitability and relative levels of protection will vary under future climate-change scenarios.

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