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Highly migratory species predictive spatial modeling (PRiSM): an analytical framework for assessing the performance of spatial fisheries management

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Abstract

Spatial management for highly migratory species (HMS) is difficult due to many species' mobile habits and the dynamic nature of oceanic habitats. Current static spatial management areas for fisheries in the United States have been in place for extended periods of time with limited data collection inside the areas, making any analysis of their efficacy challenging. Spatial modeling approaches can be specifically designed to integrate species data from outside of closed areas to project species distributions inside and outside closed areas relative to the fishery. We developed HMS-PRedictive Spatial Modeling (PRiSM), which uses fishery-dependent observer data of species' presence–absence, oceanographic covariates, and gear covariates in a generalized additive model (GAM) framework to produce fishery interaction spatial models. Species fishery interaction distributions were generated monthly within the domain of two HMS longline fisheries and used to produce a series of performance metrics for HMS closed areas. PRiSM was tested on bycatch species, including shortfin mako shark (*Isurus oxyrinchus*), billfish (Istiophoridae), and leatherback sea turtle (*Dermochelys coriacea*) in a pelagic longline fishery, and sandbar shark (*Carcharhinus plumbeus*), dusky shark (*C. obscurus*), and scalloped hammerhead shark (*Sphyrna lewini*) in a bottom longline fishery. Model validation procedures suggest PRiSM performed well for these species. The closed area performance metrics provided an objective and flexible framework to compare distributions between closed and open areas under recent environmental conditions. Fisheries managers can use the metrics generated by PRiSM to supplement other streams of information and guide spatial management decisions to support sustainable fisheries.

Introduction

Highly migratory species (HMS) including tunas, sharks, swordfish and billfishes are, by definition, broadly distributed and have large migratory ranges. Spatial management

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for HMS can be challenging due to their highly mobile habits and the dynamic nature of oceanic habitats (Hyrenbach et al. 2000; Hazen et al. 2018). There are worldwide calls to expand spatial protections for such species, including marine protected areas (MPAs), shark sanctuaries, and other designations; however, there are a number of challenges to delineating appropriate locations and boundaries that will tangibly enhance conservation (Davidson and Dulvy 2017; Derrick et al. 2020). The U.S. National Marine Fisheries Service (NMFS) uses spatial management areas and/or measures (e.g., closed areas, gear-restricted areas, essential fish habitat, etc.) to achieve a variety of conservation goals for HMS (e.g., Charleston Bump Closed Area; NMFS 2019). In general, these areas were designed to reduce bycatch of overfished stocks and/or species protected under the Endangered Species Act (ESA) or Marine Mammal Protection Act (MMPA). However, some of the existing static areas along the U.S. east coast that restrict HMS fishing have been in place for extended periods of time (15–20 years) and the ability to evaluate their continued effectiveness is hampered

by a lack of data, especially fishery-dependent data (e.g., logbooks, at-sea observers) (NMFS 2019). Additionally, the purpose and need for the establishment of certain areas may now be mitigated by additions of newer regulations and changes in fishing techniques or improvements in stock status, creating potential conservation redundancies in regulations or even potentially obviating the need for restrictions on certain static areas.

The NMFS Atlantic HMS Management Division has prioritized pursuing ways to facilitate data collection in existing closed areas (i.e., a form of spatial fisheries management where certain areas are closed to specific fishing activities), possibly including opportunities for fishery-dependent and -independent sampling within these areas (NMFS 2019). However, such efforts can be expensive, time-consuming, and polarizing. Fortunately, spatial statistical tools like species distribution and habitat suitability modeling are available to help address these important management questions without on-the-water field sampling in closed areas (Hobday and Hartmann 2006; Brodie et al. 2018; Welch et al. 2019a). Spatial modeling approaches can be specifically designed to integrate existing species distribution data from outside of closed areas (e.g., observer data, survey data, tagging data) with available environmental covariates (e.g., sea surface temperature, depth, chlorophyll) to project species distributions and habitat suitability (Brodie et al. 2018; White et al. 2019) inside and outside closed areas relative to the fishery. When a data source is fishery-dependent, there is an inherent bias of that data source towards fishermen behavior such as fishing location, fishing depth, gear type and time of fishing (Lynch et al. 2012; Conn et al. 2017; Thorson et al. 2020). Selecting this type of data source that results in the influence of the fishery on model outputs (species–fishery interactions) can be appropriate and possibly preferred when evaluating spatial management that was designed to limit interactions between certain species and that fishery. Therefore, we refer to the models described below as fishery interaction spatial models. In addition to using model outputs from the fishery interaction spatial models for evaluation of HMS spatial management, these types of models could also allow for more dynamic spatial management (Hobday and Hartmann 2006; Brodie et al. 2017; Welch et al. 2019b). Specifically, models can objectively assess the appropriate timing, location, and size of areas that restrict fishing, accounting for short- and long-term environmental changes.

The U.S. Atlantic HMS pelagic longline (PLL) fishery and shark bottom longline (BLL) fishery are two fisheries directly managed by NMFS. The HMS PLL fishery primarily targets swordfish (*Xiphias gladius*) and yellowfin tuna (*Thunnus albacares*), while the HMS BLL fishery targets various coastal shark species. Both fisheries have existing spatial management areas. For example, the Charleston Bump Closed Area (Fig. 1a), implemented in 2001, is closed to the PLL fishery from February through April and was originally designed to reduce bycatch and fishing mortality of undersized swordfish, billfish, and other overfished and protected species within the U.S. PLL fishery (NMFS 2019). The Mid-Atlantic Shark Closed Area (Fig. 1b), implemented in 2005, is closed to the BLL fishery from January through July (with the exception of one vessel that participates in the shark research fishery) to primarily protect juvenile sandbar and dusky sharks from fishing while occupying offshore nursery habitat (NMFS 2019). Given the difficulties in obtaining fishery data inside a closed area, the performance of these management areas for achieving their conservation objectives has not been fully evaluated since implementation. However, long-term changes in stock status, fishing effort and composition, regulatory regimes, gear configurations, and environmental conditions warrant such evaluations as mismatches between species distribution and closed areas can result in negative conservation and/or socioeconomic impacts for affected fisheries. On the other hand, evaluations may validate these time- and area-based restrictions.

At-sea observer programs have been in place for the PLL and BLL fisheries since the early 1990s (Beerkircher et al. 2002; Morgan et al. 2009; Mathers et al. 2018). These observer programs detail fishery practices and catch information for both fisheries from a sample of total trips each year (typically 10–15% for PLL and 5–8% for BLL from 2005 to 2019, except for the BLL shark research fishery which has 100% coverage for a small number of participating vessels and that operates inside and outside the Mid-Atlantic Shark Closed Area). Below we describe HMS-PRedictive Spatial Modeling (PRiSM) that forms the basis for an analytical framework for the assessment of HMS spatial fisheries management. Specifically, PRiSM deliberately uses available fishery-dependent data from both observer programs from the two fisheries to develop fishery interaction spatial models and predictions both within and outside of closed areas to generate a series of spatial fisheries management assessment metrics to evaluate closed areas that impact the fisheries. Here, PRiSM is tested on a subset of bycatch species in each fishery to assess two closed areas, Charleston Bump Closed Area and the Mid-Atlantic Shark Closed Area. The approach could have broad applicability to other regions and fisheries that have static spatial management areas and provide the opportunity for fisheries management to respond more rapidly to changing conditions over time.
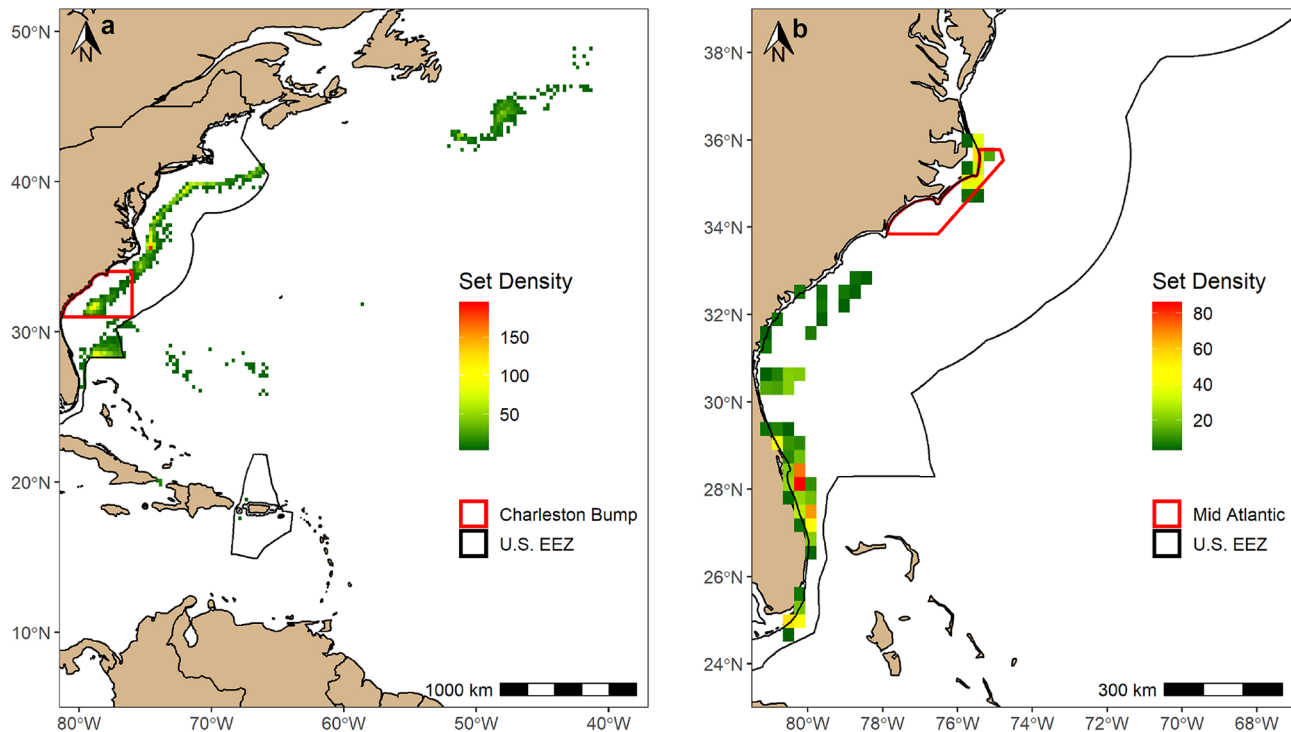
Fig. 1 a Density of Pelagic Longline Observer Program sets from 1997 to 2018 and the Charleston Bump Closed Area. **b** Density of Bottom Longline Observer Program sets from 2005 to 2019 and the Mid-Atlantic Shark Closed Area. Densities were generated for 0.25º grid cells and any grid cells where less than three vessels were pre-sent were removed for confidentiality purposes. Although grid cells are not present in certain areas due to confidentiality, the full latitudinal extent of the pelagic and bottom longline fishery extends from 6° N to 50° N and 24.8° N to 38.4° N, respectively

Methods

Observer program datasets

The observer program datasets each consisted of gear, set/haul information, and catch of each species (Fig. 1a, b). Data from the PLL observer program were considered from 1992 to 2018, while the BLL observer program data were limited to 2005–2019 because data prior to 2005 were collected using a different data collection protocol that limited data comparison.

Model species

Three focal species or species groups that are high priorities for the reduction in bycatch or bycatch mortality were selected for initial modeling in each fishery. For the PLL fishery, we selected the billfish group, where the catch of all billfish species (*Makaira nigricans, Kajikia albida, Istiophorus albicans, Tetrapturus pfluegeri, Tetrapturus georgii*) was combined over the dataset (occurrence rate in sets: 40%); shortfin mako shark (*Isurus oxyrinchus*) (27%); and leatherback sea turtle (*Dermochelys coriacea*) (6%).

Billfish were selected because the possession of billfish on PLL vessels is prohibited (50 C.F.R. § 635.71(c)(1) 2021) and they are an important group of species to the recreational fishing community. Aggregation of the billfish species was necessary and appropriate to improve sample size. We selected the shortfin mako shark because the species is currently overfished and overfishing is occurring (NMFS 2020a). Also, PLL fishermen can only keep a shortfin mako shark if it is dead at haul back and the haul is observed by an in-person observer or via electronic monitoring (50 C.F.R. § 635.21(c)(1)(iv) 2021). Leatherback sea turtles were selected because they are listed as endangered under the ESA (35 F.R. 8491 1970), and are thus subject to ESA protections in the PLL fishery (NMFS 2020b).

For the BLL fishery, three shark species were selected: sandbar shark (*Carcharhinus plumbeus*) (occurrence rate in sets: 78%), dusky shark (*Carcharhinus obscurus*) (23%), and scalloped hammerhead (*Sphyrna lewini*) (29%). All three species are overfished (NMFS 2020a). In addition, the Mid-Atlantic Shark Closed Area was designed specifically to protect juvenile sandbar and dusky sharks (68 F.R. 74746 2004).

Gear covariates

To account for the behavior of fishermen whose use of fishing gear may have differed (e.g., hook type, hook size, bait type, hook depth, set time, etc.) based on target species or gear and bait regulations, a series of gear-related covariates were incorporated into the PLL models. A hook configuration covariate was created with five categories based on the number of hooks at each hook type and size (i.e., using natural breaks in the data): J hook, where all hooks in a set were J hooks; smaller than or equal to 16/0 circle hooks; larger than 16/0 circle hooks; mixed circle hook, where all hooks in a set were circle hooks of various sizes; and mixed, where both J and circle hooks were present in a set. A bait type covariate was also created with four categories: squid, when only squid was used in a set; fish, when only fish were used in a set; other, when fish or squid were not used as bait in the set (e.g. artificial); and mix, when a combination of the previous three bait types were used on a set. The maximum hook depth and the hour the set began were assigned to each set and were also considered in the models.

A series of gear-related covariates were also generated and considered in the BLL models. A hook configuration covariate was developed with four categories using natural breaks in the data: smaller than 12/0 J hook; larger than or equal to 12/0 J hooks; smaller than or equal to 16/0 circle hooks; and larger than 16/0 circle hooks. Similar to above, a bait type covariate was also created with three categories: teleost, elasmobranch, or unknown. Mean set depth and the hour the set began were also considered in the models.

Environmental covariates

Environmental covariates selected for the PLL models have been used to describe habitat distributions of similar pelagic species in past studies (Hazen et al. 2013; Brodie et al. 2018; Farchadi et al. 2019). Three static covariates were used, including, bathymetry, rugosity, and lunar illumination. Bathymetry data were obtained from ETOPO1 (https://www.ngdc.noaa.gov/mgg/global/global.html) at a 1 min resolution. Rugosity was calculated as the standard deviation of bathymetry over a 0.25º square. Lunar illumination was extracted from the *oce* package v.1.2 in R v.3.6.1 (Kelley and Richards 2020) and represented the fraction of the moon's visible disk that is illuminated. Lunar illumination was selected because it has been known to impact the vertical distribution of swordfish (Lerner et al. 2013). Most dynamic environmental covariates were extracted as daily fields from a Copernicus Marine Environmental Monitoring Service (CMEMS) Global Ocean Physics Reanalysis product over 1993–2018 at a 1/12º resolution. Environmental covariates chosen from CMEMS included sea surface temperature (SST), sea surface height (SSH), ocean mixed layer

depth (MLD), and northward and eastward seawater velocity. SST standard deviation (SST SD) was calculated from SST over a 0.25º square. Chlorophyll-a (Chla) was extracted from the ERDDAP ESA CCI Ocean Colour Product at an eight-day mean instead of daily to reduce contamination by cloud cover/weather conditions. Chla data spanned from 1997 to 2018 and had a resolution of 0.04º. All environmental covariates were extracted over the entire spatial domain (described below) of the PLL (5º N to 51.5º N; 98º W to 37º W).

The majority of environmental covariates selected for the BLL models are known to impact the habitat use of coastal shark species (Conrath and Musick 2008; Froeschke et al. 2010; Ward-Paige et al. 2015; Crear et al. 2020). Two static covariates were used, including bathymetry and rugosity. Data from both covariates were obtained using the methods described above. Most dynamic environmental covariates were extracted as daily fields from HYCOM + NCODA Global 1/12 Analysis over 2005–2019 at a 1/12º resolution (Ferris 2019) rather than using CMEMS because HYCOM had sea surface and bottom salinity from the same product. Environmental covariates chosen from HYCOM included SST, sea surface salinity (SSS), bottom temperature, bottom salinity, and SSH. Similar to above, SST SD and bottom temperature SD were calculated from SST and bottom temperature, respectively. Turbidity in the units of Secchi disk depth (m) was extracted from a CMEMS product at a 4 km resolution from 1997 to 2019. Lastly, Chla was extracted using the same methods described above. Environmental covariates were extracted over the same spatial domain as those for the PLL.

Each environmental covariate was matched to each set/haul of the PLL or BLL dataset based on the date and location. Data for PLL were matched from 1997 to 2018 (10,116 sets/hauls) due to the limited temporal range of Chla, whereas data for the BLL were matched from 2005 to 2019 (1123 sets/hauls), due to data limitation pre-2005. The matched datasets were checked for positive bathymetry values and to ensure the environmental covariates and set/haul data were matched correctly. A small number of outliers were removed when a species occurred in an unlikely environment, which may have resulted from species misidentification. Fishing effort was calculated as the number of hooks multiplied by soak time.

Model design

Fishery interaction spatial models were designed strictly for the Western North Atlantic Ocean, excluding the Gulf of Mexico, so all sets west of the southern tip of Florida (80.5º W) were removed from each species or species group datasets. We used a generalized additive model (GAM) framework for the fishery interaction spatial models because of

its ability to handle nonlinear relationships with habitat data (Hastie and Tibshirani 1990; Wood 2006). Following similar habitat modeling studies (Brodie et al. 2018; McHenry et al. 2019), we used species presence/absence as the response variable and thus a binomial distribution. In addition to the above environmental and gear covariates, month, year, day of year, latitude, and longitude were considered as covariates for the fishery interaction spatial models. The log of effort was included as an offset variable in the model so that the model could take into account each set's effort. The equations for the full models considered for PLL and BLL species are below in (1) and (2), respectively:

$$
\begin{aligned}
Y \sim {}& \text{factor(month)} + \text{factor(year)} \\
& + s(\text{doy}) + s(\text{lat, lon}) \\
& + \text{factor(hook config)} + \text{factor(bait)} \\
& + s(\text{max hook depth}) \\
& + s(\text{set time}) + s(\text{lunar}) + s(\text{bat}) \\
& + s(\text{rug}) + s(\text{sst}) + s(\text{ssh}) + s(\text{chla}) + s(\text{mld}) \\
& + s(\text{vo}) + s(\text{uo}) + s(\text{sstsd}) + \log(\text{effort})
\end{aligned} \tag{1}
$$

$$
\begin{aligned}
Y \sim {}& \text{factor(month)} + \text{factor(year)} + s(\text{doy}) \\
& + s(\text{lat, lon}) + \text{factor(hook config)} + \text{factor(bait)} \\
& + s(\text{mean set depth}) + s(\text{set time}) + s(\text{bat}) \\
& + s(\text{rug}) + s(\text{sst}) + s(\text{bot temp}) + s(\text{sss}) \\
& + s(\text{bot sal}) + s(\text{ssh}) + s(\text{chla}) + s(\text{sstsd}) \\
& + s(\text{bot temp sd}) + s(\text{turb}) + \log(\text{effort})
\end{aligned} \tag{2}
$$

where doy is day of year, bat is bathymetry, rug is rugosity, bot temp is bottom temperature, bot temp sd is bottom temperature standard deviation, vo is northward current velocity, uo is eastward current velocity, and turb is turbidity. All analyses were conducted in R v.3.6.1 (R Core Team 2020).

All diagnostics described below were conducted on the full model (i.e., all covariates were included, see Eqs. 1 and 2). When two covariates were collinear, one of those covariates was removed. For example, maximum hook depth was not included in the PLL models because it was collinear with sea surface height. The smoothing functions for the covariates were thin plate regression splines. Temporal autocorrelation was assessed through auto-correlation function (acf) plots and variance inflation factors (VIF), and spatial autocorrelation was evaluated through variograms for each species fishery interaction spatial model. When temporal autocorrelation was present in various species' models, we tried to reduce or eliminate it by switching the year covariate to a random effect and often replaced month with day of the year of each set in the model with a cubic regression spline. We attempted to include the 2D smooth term of latitude and longitude to reduce the spatial autocorrelation present. However, concurvity, which is when a smooth term

can be estimated by another smooth term, was often present between the spatial term and other environmental covariates. Because of the presence of concurvity and an often weak spatial autocorrelation trend in the models, for the majority of species, we did not include the 2D smooth term for space.

Model selection was divided into two steps. In the first step, models were developed and run that consisted of various combinations of environmental covariates while leaving the gear covariates out. The best model was selected for the first step using Akaike information criterion (AIC), which evaluates relative model performance while penalizing for additional model parameters, or when appropriate, expert opinion (e.g., the authors' biological expertise applied in rare instances where modeled distributions extended into areas beyond a species' known range). In the second step, models were developed and run that consisted of the environmental covariates from the best model from step one and different combinations of gear covariates. The overall best model was selected from the second step using AIC. Once the best combination of covariates was identified, the number of knots within each smoother was adjusted to remove unrealistic noise in the marginal response output, while also optimizing the model's deviance explained. If models were overdispersed, the quasibinomial family was used, which allows overdispersion to be modeled (McCullagh and Nelder 1989). All models were fit using the *mgcv* package v.1.8.33 in R v.3.6.1 (Wood 2011). Predictions over each covariate were generated using marginal means (Searle et al. 1980) and estimates of uncertainty were produced from 1000 bootstrapped samples (Efron and Tibshirani 1993).

Fishery interaction spatial models were evaluated using three different cross-validation approaches (random, spatial, and temporal) using the *dismo* package v.1.3.3 in R v.3.6.1 (Hijman et al. 2017; Roberts et al. 2017). The first was a tenfold cross-validation, where the observations were randomly divided into ten equally sized groups. One group was selected as the test dataset and used for prediction while the other nine were used to train the model. This process was repeated so that each group served as the test dataset. Area under the receiver operating curve (AUC) and true skill statistic (TSS) were used to assess the predictive performance of the models on new data. AUC values range from 0 to 1, where a value of 0.5 indicates the prediction is no different than random, whereas a value closer to 1 indicates perfect model prediction (Fielding and Bell 1997). TSS ranges from −1 to 1, where a value of 0 means the model performed no better than random and a value of 1 indicates perfect model performance (Allouche et al. 2006).

The second approach was a spatial validation method to ensure the model was adequate at predicting over all areas throughout the model domain. Spatial blocks were generated over the domain of the fishery and systematically assigned a group number using the *blockCV* package v.2.1.1 in R

v.3.6.1 (Valvi et al. 2019). The size of the spatial blocks and the number of groups (i.e., folds) were selected so that the amount of presences and absences were similar among the groups. Similar to above, one group was selected as the test dataset and used for prediction while the other groups were used to train the model. The process was repeated so that each group served as the test dataset and AUC and TSS were used to assess the predictive performance of the model.

The third approach was a temporal validation method to ensure the model was accurately predicting over the projected time period (2016–2018; see the next section for explanation). Temporal groups (i.e., folds) were assigned to each year and similar to above, cross-validation was performed so that each group was identified as the test dataset once. AUC and TSS were averaged over projected time period years.

Habitat projection

Species fishery interaction distributions were projected over recent mean historical conditions (2016–2018) each month to best represent present conditions. Each of the dynamic environmental covariates used in the fishery interaction spatial models for PLL and BLL species was averaged each month from 2016 to 2018 at each grid cell. The resolution of all environmental covariates was rescaled to match that of the covariate with the coarsest resolution (1/12º). Fishery interaction spatial models were then applied to their respective mean environmental covariates for each month, which generated monthly species fishery interaction distribution outputs (herein referred to as 'occurrence probabilities'), ranging from 0 to 1.

Closed area performance metrics

To aid fishery managers in evaluating the performance of HMS closed areas, we developed four objective metrics that utilized the monthly occurrence probabilities of each species. All metrics described below were intended to provide a framework within PRiSM that fishery managers may use to make further determinations of a closed area. These metrics and their results are not indicative of what fishery managers may or may not do in the future; rather they only present additional information that managers could use.

Prior to calculating each metric, we reduced the monthly occurrence probabilities domain to likely fishing areas. This was done using the 95% kernel utilization distribution (KUD) of the fishery over the entire PLL or BLL observer program dataset. Due to the large extent and range of the PLL fishery (Fig. 1a), the domain resulted in a continuous polygon that engulfed the U.S. exclusive economic zone (EEZ) along the U.S. east coast. Any areas inside the KUD that occurred in estuaries, 1 km from the

U.S. coastline, within other countries' EEZs, or extended beyond the maximum extent of the fishery were removed because fishing by U.S. PLL vessels did not occur in those areas. Unlike the PLL fishery, the BLL fishery strictly occurs inside the U.S. EEZ and primarily occurs off of North Carolina and Florida (Fig. 1b). Therefore, a separate 95% KUD was calculated to represent the BLL fishery domain, which was a continuous polygon that extended between those two states. Any areas inside the KUD that occurred outside the U.S. EEZ, inside an estuary, or deeper than 500 m were removed because fishing did not occur in those areas. Monthly occurrence probabilities that occurred inside their respective 95% KUDs were deemed inside the fishery domain and were used for the metrics.

The first metric compared the monthly mean occurrence probability of each species inside the closed area (Charleston Bump Closed Area for PLL species and Mid-Atlantic Shark Closed Area for BLL species) to the observed occurrence rate of that species in the fishery domain outside the closed area (Metric 1). This metric was only assessed during the months the closed areas were in effect (Charleston Bump: February–April; Mid-Atlantic Shark Area: January–July) because during the other months, actual occurrence rates inside the closed areas could be determined. This metric allowed evaluation of the closed areas for the species when fishing was prohibited. Under this metric, a closed area may be considered effective at protecting a species or species group if the estimated occurrence probabilities in the closed area are higher than the observed occurrence rate outside the closed area.

The next three metrics are related to species' "high-risk" area or habitat. High-risk area represented areas where the top x% of occurrence probabilities for a species occurred (i.e., high-risk areas defined as areas where fishery interactions are most likely to occur within the fishery domain). First, we determined the occurrence probability that represented the high-risk area value threshold. For example, if x was 25%, then the occurrence probability threshold was the value when 25% of all occurrence probabilities over all months were greater than or equal to that value. High-risk area each month was defined as areas where occurrence probabilities were equal to or greater than the occurrence probability threshold. Defining a value for x allowed us to place a weight on each species based on the level of management importance, where the higher the x, the more of that species' occurrence probabilities we would incorporate as 'high risk.' We determined the value of x based on the status of each species or species group and listed the corresponding occurrence probability threshold (Table 1). The value of x for species listed as endangered or threatened under the ESA was 50 and 40%, respectively, because ESA listing implies a greater management importance and more risk-averse approach. The

Table 1 The six species statuses used to determine the top $x\%$ of occurrence probabilities and corresponding occurrence probability threshold needed to calculate each species' high-risk area

Species	Species status	$x\%$	Probability threshold
Leatherback Sea turtle	ESA/endangered	50	0.03
Mako shark	MSA/overfished/ overfishing	25	0.54
Billfish species Group	MSA/community importance	25	0.37
Dusky shark	MSA/overfished / overfishing	25	0.51
Sandbar shark	MSA/overfished / overfishing	25	0.9987
Scalloped Hammerhead	MSA/overfished / overfishing	25	0.83

Acronyms are Endangered Species Act (ESA) and Magnuson–Stevens Fishery Conservation and Management Act

value for x of species that fall under the Magnuson–Stevens Fishery Conservation and Management Act (MSA) and where overfishing is occurring, that are overfished, and/or have high community importance was 25%.

The first of the three metrics related to individual species high-risk area compared high-risk area that occurred inside the closed area to areas outside the closed area (Metric 2). The ratio between the median high-risk area occurrence probability within the closed area and the median high-risk area occurrence probability outside the closed area was calculated each month. It was assumed that if the closed area is doing well at protecting the highest risk area for a species', then the ratio would be > 1 when the closed area was closed. For the next metric, we calculated the percent area of individual species high-risk area that occurred inside the closed area each month (Metric 3). For the final metric, we calculated the percent of the closed area with individual species high-risk area each month (Metric 4). It is assumed that if the closed areas are effectively protecting these species, Metrics 3 and 4 will be maximized while the areas are closed. For these two metrics, all values inside the high-risk area were treated equally, meaning the occurrence probabilities were ignored and only the presence of high-risk area in a grid cell was considered.

Results

For PLL models, the best model for billfish, mako shark, and leatherback sea turtle had a deviance explained of 34.3, 20.3, and 14.1%, respectively. For BLL models, the deviance explained for the best models were 49, 38.3, and 47.2% for sandbar shark, dusky shark, and scalloped hammerhead, respectively (Table 2). For all six species and for the three

validation approaches (random, spatial, and temporal), the predictive performance of the models was considered to be either fair (AUC > 0.70) or good (AUC > 0.80) (Swets 1988; Buckley et al. 2011) (Table 2). Marginal mean prediction plots indicate the relationship between species probability of occurrence and each covariate, while all other covariates are at their mean. Marginal mean predictions of the probability of occurrence for the billfish species group in the PLL and the dusky shark in the BLL at each covariate in the respective species' best model are in Figs. 2 and 3, respectively. An example of a monthly occurrence probability map (trimmed to the fishery domains) for a PLL (billfish species) and BLL (dusky shark) species on average between 2016 and 2018 is in Fig. 4a, b, respectively. Monthly maps of upper and lower bounds of occurrence probability (using standard errors) for each species were also examined and indicated uncertainty was relatively low within the fishery domains. All species' marginal means plots and monthly occurrence probability maps (including upper and lower bounds maps) can be found in Supplementary Information 1 Figs S1–S4 and Supplementary Information 1 Figs S5–S10, respectively.

Closed area performance metrics

Performance metrics described below in the context of both closed areas were used solely to demonstrate the PRiSM framework. These results do not represent definitive assessments of either closed area, nor are they indicative of what fishery managers may or may not do in the future.

Performance metrics often showed similar trends but varied from species to species in the PLL fishery for the Charleston Bump Closed Area. In Metric 1 (comparing mean occurrence probabilities inside versus observed mean occurrence rates outside the closed area during closure months), mako sharks had a higher mean occurrence probability inside Charleston Bump Closed Area compared to the observed mean occurrence rate outside during all three months Charleston Bump Closed Area was closed (Fig. 5b). On the other hand, for the billfish species group, the observed mean occurrence rate outside the closed area was higher during all three months (Fig. 5c). For leatherback sea turtles mean occurrence probability inside was very similar to the observed mean occurrence rate outside in February and March, but in April the observed mean occurrence rate was higher (Fig. 5a).

Species' high-risk area varied from month to month which ultimately impacted the three metrics calculated from the high-risk area. An example of mapped species high-risk area for the PLL species for a given month is in Fig. 6a–c, while maps for all months can be found in the Online Resource 1 Fig S11. For example, there was no high-risk area within the PLL fishery domain for the billfish group in November or December. For Metric 2, ratios between

Table 2 Information about the observed occurrence rate of each species in their respective fishery, as well as the best model covariates (with the exception of temporal covariates, e.g. year), deviance explained from the best model, and predictive performance metrics from the three validation approaches for each species

Species	Occurrence (% of sets)	Best model covariates	Deviance explained (%)	Validation approach	AUC	TSS
Billfish group	40	sst, ssh, chla, mld, vo, uo, sstsd, hook, bait, set hour	34.4	Random	0.85	0.56
				Spatial	0.81	0.52
				Temporal	0.82	0.51
Mako shark	27	lunar, bat, rug, sst, chla, ssh, mld, vo, sstsd, bait, set hour	20.3	Random	0.80	0.48
				Spatial	0.72	0.35
				Temporal	0.81	0.51
Leatherback sea turtle	6	bat, rug, sst, chla, ssh, vo, uo, set hour	14.1	Random	0.77	0.44
				Spatial	0.71	0.33
				Temporal	0.70	0.43
Sandbar shark	78	bat, bt, bs, sst, ssh, chla	49.0	Random	0.87	0.65
				Spatial	0.81	0.55
				Temporal	0.88	0.71
Dusky shark	23	bat, bt, bs, chla, btsd, sstsd, set hour set lat, set lon	38.3	Random	0.79	0.51
				Spatial	0.72	0.38
				Temporal	0.72	0.48
Scalloped hammerhead	29	bat, bt, bs, turb, ssh, btsd, sstsd, set hour, bait, set lat, set lon	47.2	Random	0.78	0.48
				Spatial	0.75	0.40
				Temporal	0.70	0.42

The actual covariate names are as follows: *lunar* lunar illumination; *bat* bathymetry; *rug* rugosity; *sst* sea surface temperature; *chla* chlorophyll a; *ssh* sea surface height; *mld* mixed layer depth; *vo* vertical current velocity; *uo* horizontal current velocity; *sstsd* sea surface temperature standard deviation; *bt* bottom temperature; *bs* bottom salinity; *btsd* bottom temperature standard deviation; *turb* turbidity; *hook* hook configuration; *bait* bait type; *set hour* hour the set began; *set lat* begin set latitude; *set lon* begin set longitude

median occurrence probabilities for species high-risk area inside and outside the closed area were calculated, where a value > 1 meant that the high-risk area was higher risk inside the closed area compared to outside the closed area. In addition, the closer the ratio was to 1 the closer the median values were to each other. For the leatherback sea turtle and mako shark, ratios were > 1 for all three months Charleston Bump Closed Area was closed (Feb–Apr; Fig. 7a, b). On the other hand, the ratios from Feb–Apr for the billfish group equaled zero, meaning there was no high-risk area inside Charleston Bump Closed Area during those months (Fig. 7c).

Metric 3 (the percent of high-risk area found inside the closed area) varied substantially among months and species. While the Charleston Bump Closed Area was closed, 3–4.6%, 1.7–3.8%, and 0% of leatherback sea turtle, mako shark, and the billfish species group high-risk areas occurred inside the closed area, respectively (Fig. 9a). Billfish's high-risk area did not occur inside the closed area until after it was opened. Increases in percent of high-risk area in the Charleston Bump Closed Area for multiple species began in November and continued through January and then began to decrease in March and April. For Metric 4, the percent of closed area with high-risk area, ranged from 0 to 100%, where 100% would mean that all of the closed area represented high-risk area. During the closure of Charleston Bump Closed Area, high-risk area of leatherback sea turtle, mako shark, and the billfish species group covered between 28 and 90%, 42 and 45%, and 0% of the closed area, respectively (Fig. 10a). A large percentage of the closed area (> 80%) was also covered by leatherback high-risk area during November, December, and January.

Similar to PLL, the four performance metrics showed similar patterns, but varied for the three species in the BLL fishery for the Mid-Atlantic Shark Closed Area. Metric 1 showed that the mean occurrence probability inside the Mid-Atlantic Shark Closed Area was higher than the observed mean occurrence rate outside the closed area for all seven months of the Mid-Atlantic Shark Closed Area for all three species (Fig. 5d–f).
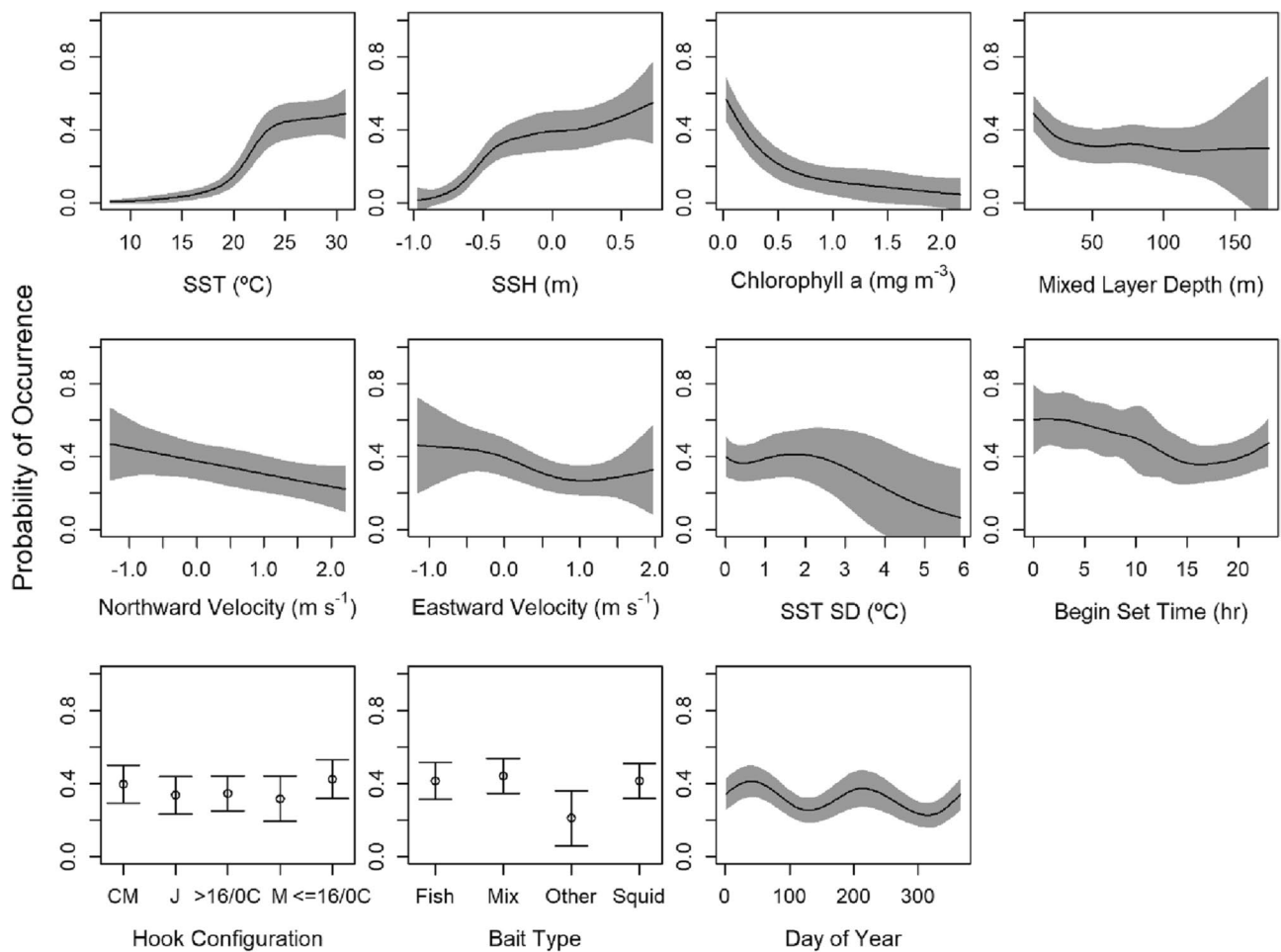
Fig. 2 Marginal mean predictions of probability of occurrence for the billfish species group in the pelagic longline at each covariate in the best model. The black line shows the actual marginal means for each covariate, while the grey area (and error bars for Hook Configuration and Bait Type) represents the 95% confidence intervals generated through bootstrapping. Hook configurations abbreviations are circle hook mixed (CM), J hook (J), larger than 16/0 circle hook (> 16/0C), mixed of circle and J hooks (M), and smaller than or equal to 16/0 circle hook (< = 16/0C). Abbreviated covariates are SST—sea surface temperature; SST SD—sea surface standard deviation; SSH—sea surface height

Unlike for the PLL species, for all BLL species, there was species high-risk area for every month within the BLL fishery domain. An example of mapped individual species high-risk area for the BLL species for a given month is in Fig. 6d–f, while maps for all months can be found in the Online Resource 1 Fig. S12. Metric 2 (ratios of median values) showed that dusky shark high-risk area inside the Mid-Atlantic Shark Closed Area was better than high-risk area outside the closed area for five of the seven months the closed area is closed (Fig. 8a). During two of the seven months, scalloped hammerhead high-risk area was better inside the closed area compared to outside (Fig. 8c). For

sandbar sharks, a lot of the fishery domain had very high occurrence probabilities across months (> 0.99), which resulted in a very high occurrence probability threshold (0.9987; Table 1). This likely occurred because sandbar sharks were more abundant in the bottom longline and were targeted in the shark research fishery. This resulted in similar median values for each month and thus ratios very close to one for sandbar shark (Fig. 8b).

While the Mid-Atlantic Shark Area was closed, 6.0–25.3%, 5.3–12.6%, and 12.1–50.9% of dusky shark, scalloped hammerhead, and sandbar shark high-risk areas occurred inside the closed area, respectively based on
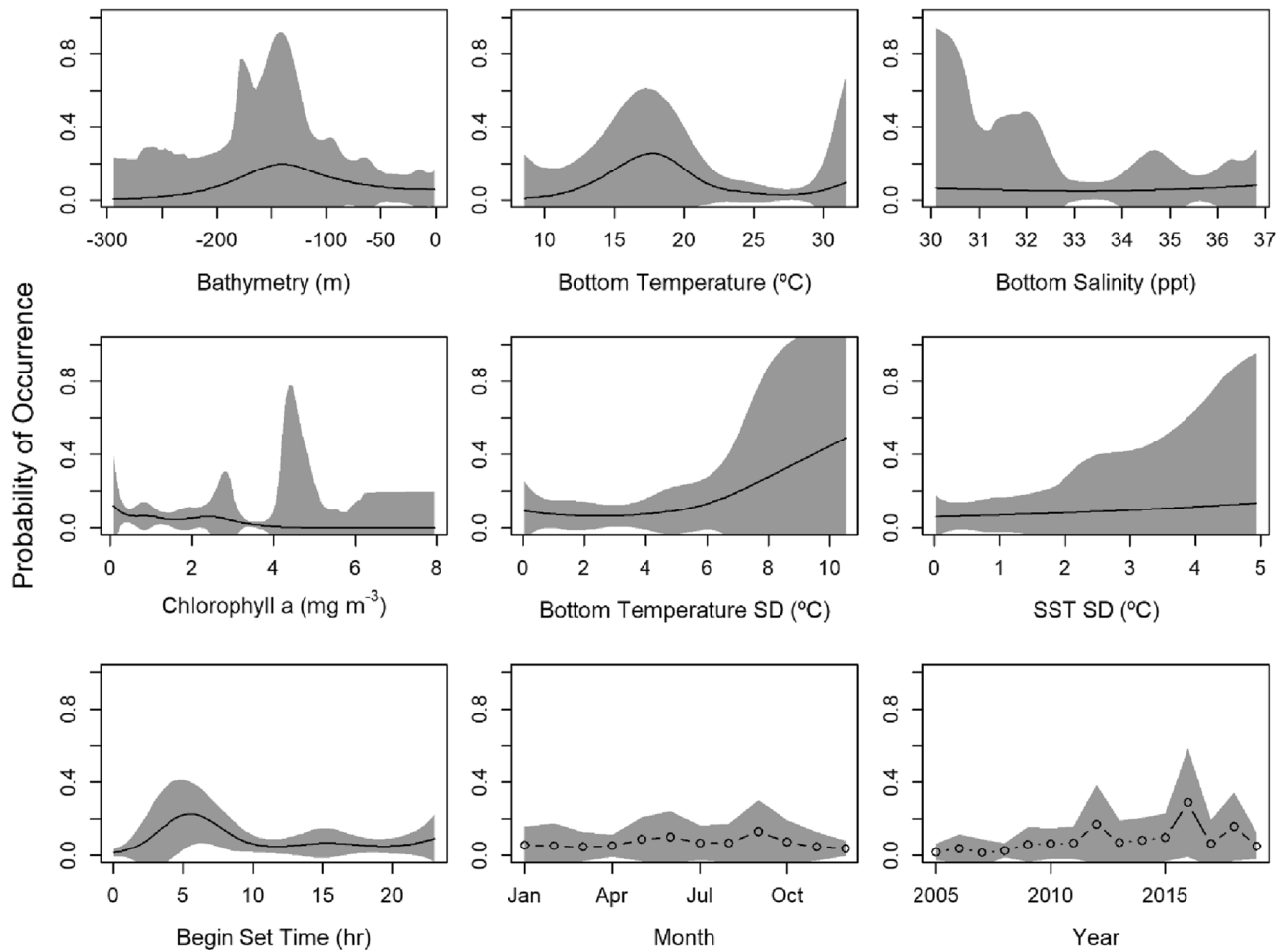
Fig. 3 Marginal mean predictions of probability of occurrence for the dusky shark in the shark bottom longline at each covariate in the best model. The black line shows the actual marginal means for each covariate, while the grey area represents the 95% confidence intervals generated through bootstrapping. Bottom temperature SD stands for bottom temperature standard deviation and SST SD stands for sea surface temperature standard deviation

Metric 3 (Fig. 9b). For Metric 4, approximately 10.4–86.8%, 2.5–61.1%, and 0.8–90.6% of the Mid-Atlantic Shark Area was covered by dusky shark, scalloped hammerhead, and sandbar shark high-risk area, during the closure respectively (Fig. 10b). Starting in June and July (last 2 months of closure), the percentages substantially drop compared to prior months. November or December was the first month where the percentages began to increase again (Fig. 10b).

Discussion

Species distribution and habitat modeling methods have a growing number of applications in marine resource management (Hobday and Hartmann 2006; Becker et al. 2016; Welch et al. 2019b). Such modeling, which takes advantage of more widely accessible machine learning and high-performance computing platforms, has the potential to aid a variety of fisheries management goals in a dynamic and shifting ocean environment (Holsman et al. 2019). PRiSM is directly applicable because it produces models that reflect spatial interaction potential in a fishery (by only using fishery-dependent data and incorporating detailed gear information specific to the fishery) and then directly linking it to the spatial management area for that corresponding fishery. This internal consistency could allow managers to use PRiSM results to supplement other streams of information and guide current and future spatial management decisions in each unique fishery.

Based on the three model validation metrics conducted and the applicability of the closed area metrics, we have demonstrated the utility of PRiSM for fishery managers to
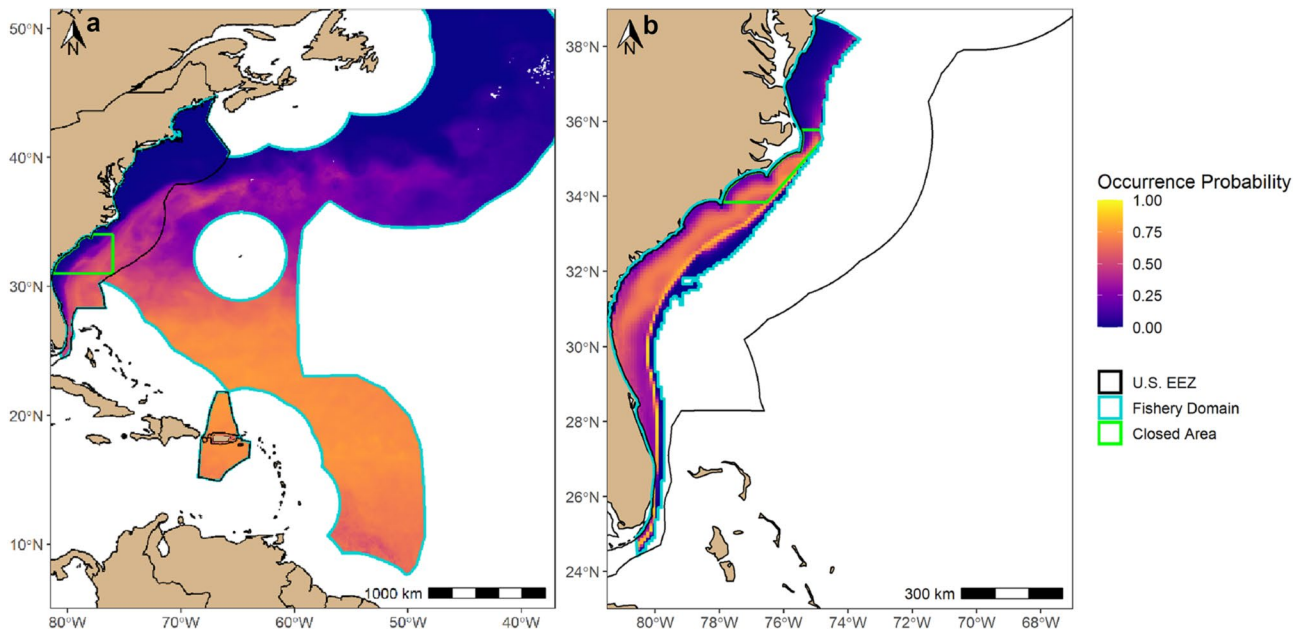
Fig. 4 a Estimated billfish fishery interaction distribution outputs (occurrence probabilities) during average February conditions from 2016 to 2018 within the pelagic longline fishery domain (light blue). The closed area (green) is Charleston Bump. **b** Estimated dusky shark fishery interaction distribution outputs (occurrence probabilities) during average February conditions from 2016 to 2018 within the bottom longline fishery domain (light blue). The closed area (green) is the Mid-Atlantic Shark Closed Area

assess the performance of multiple closed areas on a subset of species. Three cross-validation approaches demonstrated fair to good model performance for all six species that were robust to temporal and spatial structure in the data. The closed area metrics provide an objective way to assess various areas while incorporating the fishery domain, species high-risk areas, and the location of the closed area. PRiSM can be expanded or adapted to more species and regions as well as other fisheries. For example, PRiSM could be applied to multiple target and non-target species caught in the PLL and BLL fisheries (e.g., yellowfin tuna, silky shark, loggerhead turtle), and other regions such as the Gulf of Mexico. As long as there are sufficient fisheries data and corresponding spatial management areas, the framework of PRiSM can be applied to other regions and fisheries.

The metrics for the species used in this study and closed areas under recent environmental conditions suggests that the closed areas may be performing adequately during some times for some species, but also that there may be opportunities for improvement. Using multiple metrics, there appear to be months and areas within the Charleston Bump and Mid-Atlantic Shark Closed Areas that offer protection for the species considered. In contrast, results also suggest that protections could be improved with shifts in the timing, size, and/or location of these closed areas. Generating these metrics for other relevant species and areas may provide a

standardized approach for evaluating current and future spatial management efforts. It is important to note that the species and closed areas used in this study are intended to demonstrate PRiSM as a proof of concept, and that no results or interpretations are definitive. Ultimately, PRiSM is one of several techniques that provide managers with information that they could use to assess the performance of closed areas. It is important, given historical and projected impacts of climate change on fisheries/fishing communities (Rogers et al. 2019; Champion et al. 2021), changes in fishing techniques and regulations, and other long-term environmental and socioeconomic shifts, that these static closed areas be assessed regularly to ensure that their purported benefits are maintained without resulting in unnecessary harm to fishing communities.

Like any other spatial model, there are limits to this approach, such as the level of uncertainty in the model as well as in the environmental data used to generate the model and ultimately to predict over. Model uncertainly can be influenced by many factors, including low sample size (i.e., number of positive occurrences) and the absence of covariates in the model that may be important in driving the occurrence rate of species in a fishery. Specifically, for species that do not occur enough in a fishery or whose model performance is low, PRiSM would not be an appropriate technique to apply. In addition, the temporal period over which species
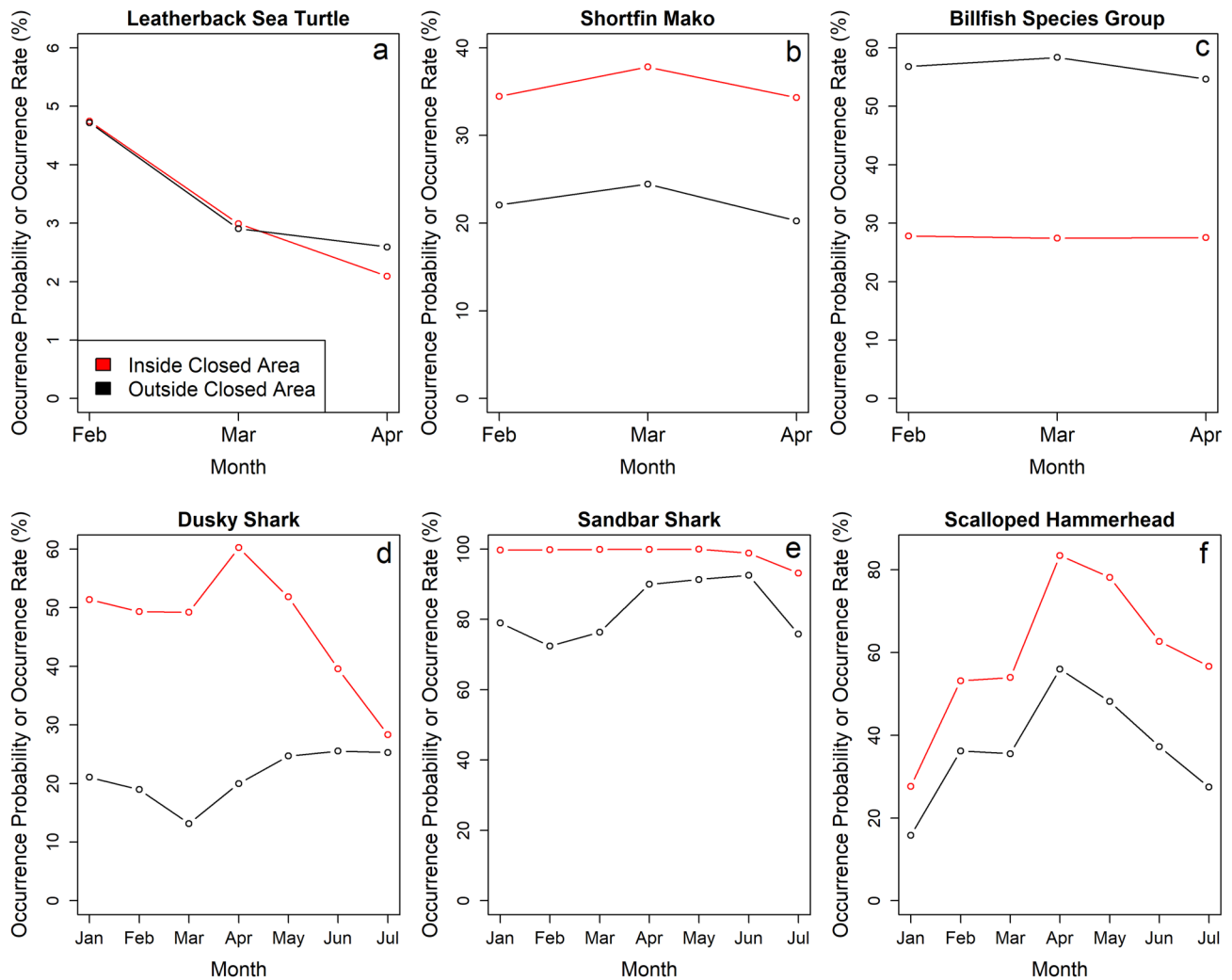
Fig. 5 Monthly mean occurrence probability inside the closed area (red line) and the observed mean occurrence rate outside the closed area (black line) during the months the areas were closed (Metric 1). For leatherback sea turtle (**a**), mako shark (**b**), and the billfish group (**c**) the referred closed area is the Charleston Bump Closed Area which is closed to the pelagic longline from Feb–Apr. For dusky shark (**d**), sandbar shark (**e**), and scalloped hammerhead (**f**) the referred closed area is the Mid-Atlantic Shark Closed Area which is closed to bottom longline from Jan–Jul

occurrence probability is predicted will directly impact the assessment metrics. For example, occurrence probabilities may drastically differ when predicting over monthly average conditions over three recent years (used in this study) compared to over one recent year or compared to over weekly averages. Therefore, it is important that the temporal period selected is justified. This should be based on the temporal resolution (e.g., month) the area is managed under, when area assessment is needed, and when (if any) adjustments are made to the area.

Further model validation could occur if enough data inside closed areas are able to be collected either through fishery-dependent or fishery-independent methods such as surveys, tagging studies, or cooperative research with fishing vessels. Although tagging studies provide insight into actual species habitat use and distribution, it does lack the fishery component (e.g., fishermen decisions: hook type/ size, bait type, set time, and depth of set), which certainly impacts whether an individual organism is caught or not. Despite these differences, it is still good practice to test or compare model output and performance on other data if possible (Chatfield 1995; Thorne et al. 2019). For example, mako shark fishery interaction distributions from our model shifted latitudinally with season, a pattern also observed in satellite-tagged mako sharks (Vaudo et al. 2016). Also, it appears that dusky sharks may prefer areas within the
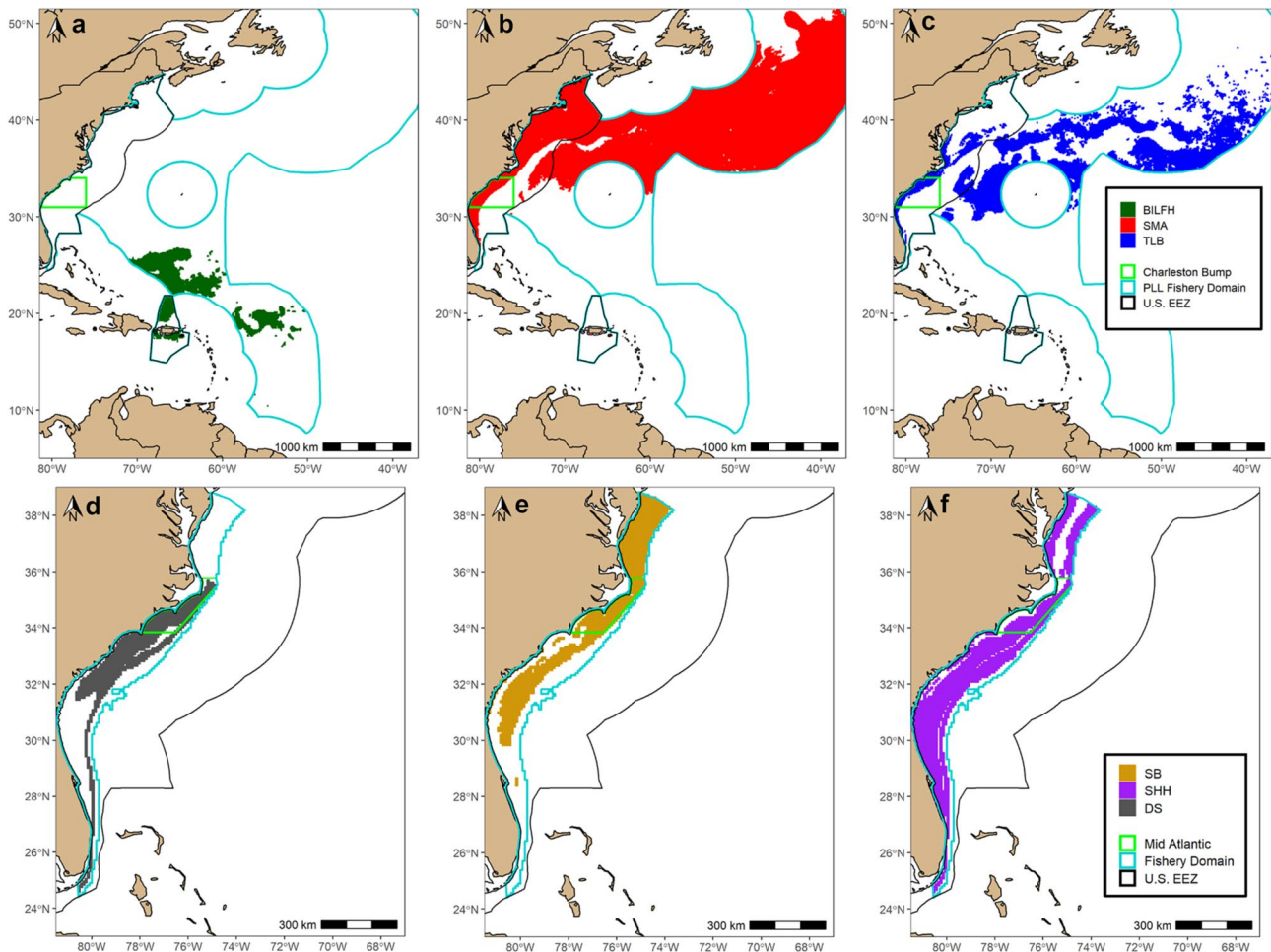
Fig. 6 Individual species high-risk area (top *x*% of occurrence probabilities) within their respective fishery domains (95% kernel utilization distribution) in light blue for the month of April for the pelagic longline species; billfish species group (BILFH, **a**), shortfin mako shark (SMA, **b**), and leatherback sea turtle (TLB, **c**) and for the bottom longline species; dusky shark (DS, **d**), sandbar shark (SB, **e**), and scalloped hammerhead (SHH, **f**). The fishery domain for the pelagic longline also includes the U.S. EEZ. The Charleston Bump Closed Area and Mid-Atlantic Shark Closed Area are indicated by the light green outline on their respective maps

Mid-Atlantic Shark Closed Area 1–2 months prior to the closure, a similar observation found in an acoustic tracking study on juvenile dusky sharks (Bangley et al. 2020). It is important to note, similar to the PLL closed area metrics, observed catch rates of PLL bycatch species (mako shark and leatherback sea turtle) from 2016 to 2018 were often relatively high between December and January inside the Charleston Bump Closed Area. The observed catch rates for the species considered for the BLL were relatively high in December inside the Mid-Atlantic Shark Closed Area, following similar trends found in the BLL closed area metrics. These similarities found in the observer data for both fisheries and in datasets of a different nature (tagging datasets), validates PRiSM further.

PRiSM may have the capacity to be extended into other uses and applications beyond the assessment of existing closed areas. It could be used, along with other fisheries information, to determine locations of monitoring areas or help optimize the location, size, and timing of potential new or modified closed areas. Proposed spatial management areas can be run through PRiSM's metrics with species' PRiSM model occurrence probabilities until the metrics are optimized while ensuring significant target species habitat is available to the fishery. An approach like PRiSM can be used to help improve essential fish habitat designations and assess the impacts of various marine uses on HMS, such as offshore energy development (Friedland et al. 2021).
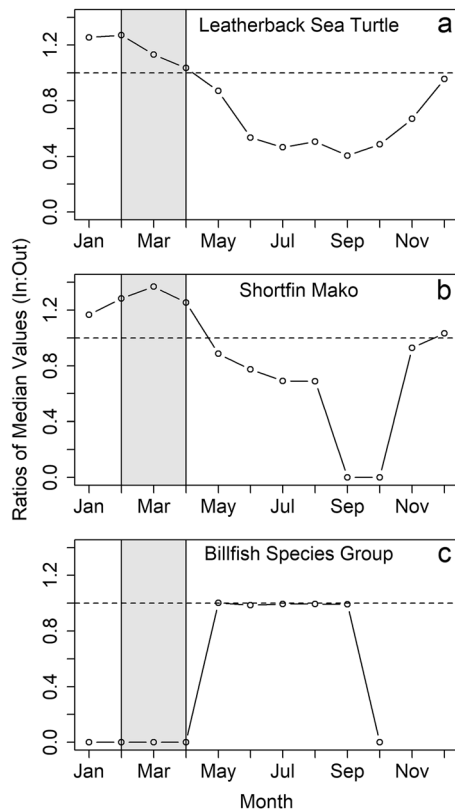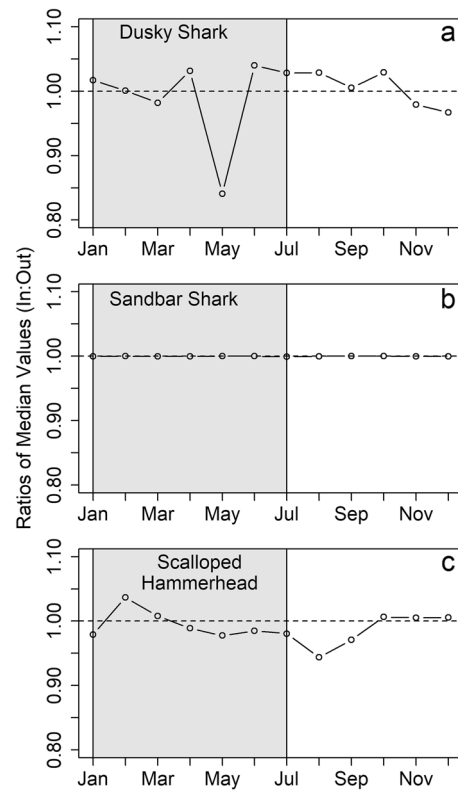
Fig. 7 Ratios of median values each month inside and outside the Charleston Bump Closed Area (Metric 2). Species monthly ratios are calculated as (median high-risk area occurrence probability inside the closed area)/(median high-risk area occurrence probability outside the closed area). Values above 1 (the dashed line) indicate when high-risk area was even higher risk inside the closed area compared to outside the closed area. The shaded grey area indicates the months the Charleston Bump Closed Area is closed to pelagic longline. Months where there are no values indicate when no high-risk area occurred inside the fishery domain

Fig. 8 Ratios of median values each month inside and outside the Mid-Atlantic Shark Closed Area (Metric 2). Species monthly ratios are calculated as (median high-risk area occurrence probability inside the closed area)/(median high-risk area occurrence probability outside the closed area). Values above 1 (the dashed line) indicate when high-risk area was higher inside the closed area compared to outside the closed area. The shaded grey area indicates the months the Mid-Atlantic Shark Closed Area is closed to bottom longline

Techniques like PRiSM create the opportunity for evaluation of more dynamic management approaches that allow for the refinement of managed areas to the temporal and spatial scales of the dynamic ocean (Lewison et al. 2015; Dunn et al. 2016). For example, dynamic management tools such as EcoCast use habitat modeling techniques similar to PRiSM to generate real-time maps that indicated areas where fisheries bycatch was minimized and fisheries target catch was maximized (Hazen et al. 2018; Welch et al. 2019a). Hazen et al. (2018) estimated that dynamic closures could achieve comparable bycatch risk reduction at a fraction of the size (2–10× smaller) of static closed areas. In the Eastern Tuna and Billfish Fishery in Australia, habitat modeling was used to generate three spatial management zones based on the probability of southern bluefin tuna occurrence

every 2 weeks (Hobday and Hartmann 2006). Fishermen had access to these zones based on observer coverage and available share of southern bluefin tuna quota. Seasonal forecasts (3–4 month lead time) were also created and used to help managers and fishermen prepare for potential habitat shifts (Hobday et al. 2011). PRiSM has the capability to assess and recommend spatial management areas at finer temporal resolutions and potentially project spatial management areas months in advance if needed by fishery managers. With that being said, a number of criteria have to be met first, including, skillful physical forecasts that exist and ecological skill relative to the skillful physical variables. As oceanographic data increase in accuracy and resolution, and our understanding of the relationships between fish and their environment improve, it becomes more appropriate to account for shifting ocean dynamics in how fish are managed. This could benefit both species in need of conservation
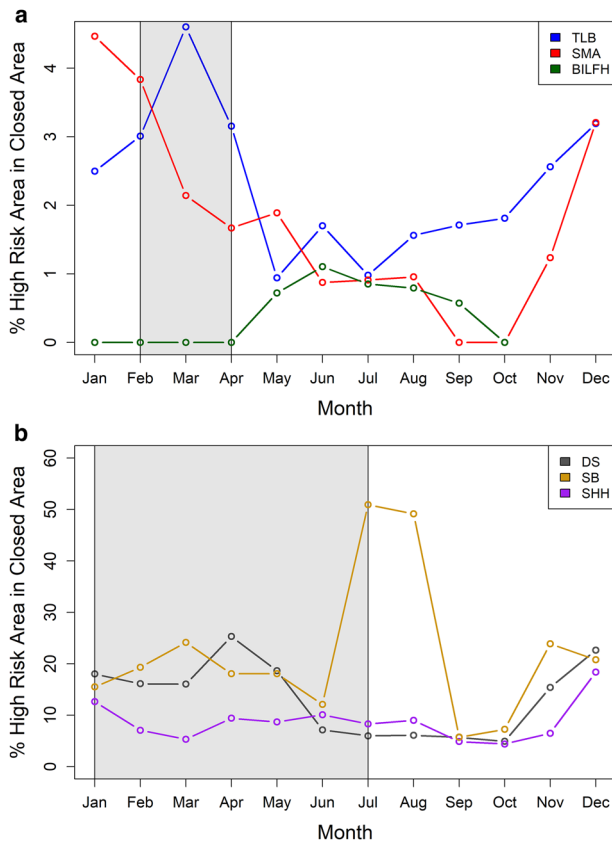
Fig. 9 Percent of high-risk area inside **a** the Charleston Bump Closed Area for pelagic longline species and **b** the Mid-Atlantic Shark Closed Area for bottom longline species (Metric 3). Months where there are no values indicate when no high-risk area occurred inside the fishery domain. The shaded grey area indicates the months the closed areas are in effect. Species abbreviations are as follows: *BILFH* billfish species group; *SMA* shortfin mako shark; *TLB* leatherback sea turtle; *SB* sandbar shark; *SHH* scalloped hammerhead; *DS* dusky shark

Fig. 10 Percent of the **a** Charleston Bump Closed Area or **b** Mid-Atlantic Shark Closed Area covered by high-risk area of their respective species (Metric 4). The shaded grey area indicates the months the closed areas are in effect. Species abbreviations are as follows: *BILFH* billfish species group; *SMA* shortfin mako shark; *TLB* leatherback sea turtle; *SB* sandbar shark; *SHH* scalloped hammerhead; *DS* dusky shark

and fishermen who already use these types of data to inform their fishing locations.

The PRiSM framework we have developed provides an approach to rapidly assess spatial management areas for two different HMS fisheries using widely available modeling techniques and routinely collected fishery-dependent data from outside of closed areas. Given the ongoing need to balance the conservation of HMS stocks and bycatch species with the long-term sustainability of fisheries that catch them, PRiSM provides an adaptable framework to optimize marine spatial management to achieve multiple objectives. With longstanding static spatial management in need of evaluation and potential change within U.S. HMS fisheries, PRiSM represents a useful approach that could help guide spatial management and support sustainable fisheries.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval Not applicable.

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