10-2018

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Recommended Citation

Dell'Apa, Andrea; Grazia Pennino, Maria; Bangley, Charles W; and Bonzek, Christopher F., A Hierarchical Bayesian Modeling Approach for the Habitat Distribution of Smooth Dogfish by Sex and Season in Inshore Coastal Waters of the US Northwest Atlantic (2018). *Marine And Coastal Fisheries*, 10(6), 590-605.
10.1002/mcf2.10051

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 10:590–605, 2018

ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10051

ARTICLE

A Hierarchical Bayesian Modeling Approach for the Habitat Distribution of Smooth Dogfish by Sex and Season in Inshore Coastal Waters of the U.S. Northwest Atlantic

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Abstract

The Smooth Dogfish *Mustelus canis* is an abundant, small coastal shark occurring along the U.S. Atlantic coast. Despite being targeted by a directed fishery and having recently undergone a stock assessment that found the population neither overfished nor experiencing overfishing, little is known about the spatial and temporal distribution of this species. Here, we used catch data from the spring and fall Northeast Area Monitoring and Assessment Program's fishery-independent trawl surveys conducted between 2007 and 2016 and various environmental factors to perform hierarchical Bayesian modeling as a first attempt to spatially predict adult Smooth Dogfish CPUE in U.S. northwest Atlantic Ocean waters by sex and season. Relevant environmental variables differed between both sexes and seasons. Male and female CPUEs were similarly associated with lower salinity and shallower depth in the spring. During fall, male CPUE was associated with sea surface temperature and bottom rugosity, and female CPUE was associated with chlorophyll-*a* concentration, bottom rugosity, and year. Habitat modeling results predicted that areas of high male and female CPUEs would overlap during spring but strongly diverge during fall, when greater predicted CPUEs for males were distributed considerably farther north. These results suggest sexual segregation among Smooth Dogfish during fall, with the springtime overlap in distribution coinciding with the pupping and mating season in this population. This difference in distribution during fall may allow for a male-only directed fishery for Smooth Dogfish in the northern extent of the species' range in waters near southern New England and Georges Bank.

Subject editor: Kenneth Rose, University of Maryland Center for Environmental Science, Cambridge

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Received May 30, 2018; accepted October 9, 2018

Globally, fishery management for elasmobranch populations and stocks has proven to be particularly challenging due to the life history traits (e.g., slow growth rate, late age of maturity, low fecundity, and long gestation period) of the majority of these species (Cortés 2004; Barker and Schluessel 2005; Stevens et al. 2005), resulting in documented decreases in some populations (Robbins et al. 2006; Dulvy et al. 2008; Ferretti et al. 2010). Nonetheless, evidence suggests that if managed properly, elasmobranch fisheries can be sustainable (Peterson et al. 2017; Simpfendorfer and Dulvy 2017). The U.S. Atlantic population of Smooth Dogfish *Mustelus canis* (also called the Dusky Smoothhound or Smoothhound) is among the stocks that have been considered to be fished at sustainable levels and for which a science-based fishery management plan has been put in place (Simpfendorfer and Dulvy 2017).

The Smooth Dogfish is a small (<2 m TL) coastal shark that is more commonly found in waters less than 20 m in depth (Heemstra 1997; Castro 2011), although it has also been reported at maximum depths of 460 m (Kiraly et al. 2003). In the northwest Atlantic Ocean, its habitat range encompasses coastal waters from the Bay of Fundy, Canada (where it is only occasionally caught), to the western Gulf of Mexico (though many records need to be verified due to potential misclassification with the Gulf Smoothhound *M. sinusmexicanus*; Castro 2011) off the Texas–Mexico border (Kiraly et al. 2003). The population is characterized by seasonal migration in response to changes in water temperatures. The species overwinters off the Carolinas and as far south as the central Atlantic Florida coast, while in the summer it is more commonly found in coastal waters between Cape Cod, Massachusetts, and Delaware Bay (Kiraly et al. 2003; Castro 2011; SEDAR 2015a).

Inhabiting mostly shallow and estuarine coastal waters, the Smooth Dogfish is considered a nocturnal bottom feeder, primarily consuming crustaceans, including crabs, shrimps, and lobsters, and more opportunistically feeding on molluscs, bony fishes, cephalopods, and polychaete worms (Gelsleichter et al. 1999; Kiraly et al. 2003; Castro 2011). However, the species' feeding habits vary based on the geographic area and prey availability and distribution such that it is considered both an opportunistic feeder and a scavenger depending on the prey species that are available (Kiraly et al. 2003; Castro 2011).

At the federal level, fishery management for the Smooth Dogfish in the U.S. Atlantic has gone through several key changes over the last decades (for a detailed history of U.S. Atlantic Smooth Dogfish fishery management at the federal and state levels, refer to SEDAR 2015b). Historically, and due to identification issues, the Smooth Dogfish stock has been managed as a complex of three species: Smooth Dogfish, Florida Smoothhound *M. norrisi*, and Gulf Smoothhound. Hence, the term "Smooth Dogfish" within U.S. Atlantic fishery management has been used to refer more generally to these three species combined.

The Smooth Dogfish has not been of particularly high economic value for the U.S. Atlantic commercial shark fishery (though it is the second most abundant shark species in U.S. Atlantic coastal waters after the Spiny Dogfish *Squalus acanthias*). At the federal level, in 1999 the Smooth Dogfish was included on the list of shark species that were protected from finning and for which all landed sharks must have a fin-to-carcass-weight ratio of not more than 5%; in 2003, the species was further included on the list of species protected under the Shark Finning Prohibition Act (SFPA). The first commercial quota for the species was set by the National Marine Fisheries Service (NMFS) in 2009. In 2010, the U.S. government issued the Shark Conservation Act (SCA) to further protect sharks and close regulatory loopholes in the preceding SFPA. The SCA was intended to protect all shark species from finning and made it illegal to remove any fins of a shark at sea. An exception was introduced for the commercial fishery of Smooth Dogfish within 92.6 km (50 nautical miles) of each state's coastline. The new law increased the fin-to-carcass-weight ratio limit for Smooth Dogfish from 5% to 12%, with Smooth Dogfish making up at least 25% of the catch onboard a vessel when landing. In 2015, the first benchmark stock assessments for the U.S. Atlantic and Gulf of Mexico Smooth Dogfish complexes were conducted separately. The results of the U.S. Atlantic assessment indicated that the stock is likely neither overfished nor experiencing overfishing, although the review panel recommended caution due to uncertainty in the catches as well as uncertainty associated with the stock–recruitment relationship that resulted from the analysis (SEDAR 2015c).

Additionally, the review panel's recommendations included the need to increase efforts for monitoring and recording of various environmental variables (e.g., bottom water temperature and salinity) in fishery-independent surveys (SEDAR 2015a). In turn, this information may be used to enhance indices of relative abundance that serve as proxies for the CPUE, which is commonly used as the index in stock assessment modeling and in the process of determining stock abundance status. Currently, there is a lack of information on the influence of environmental variables or abiotic factors (e.g., water depth) on the spatiotemporal distribution of Smooth Dogfish. Moreover, despite the knowledge that many shark populations have been observed to be or are suspected to be characterized by the presence of sexual segregation (Pratt and Carrier 2001; Sims 2005; Wearmouth and Sims 2008; Mucientes et al. 2009; Dell'Apa et al. 2014), there is a paucity of studies that have investigated the spatiotemporal distribution of Smooth Dogfish by sex—information that may be used to enhance fisheries management of the species. For example, the U.S. Atlantic population of Spiny Dogfish has a long history of commercial exploitation and associated fishery management. Recently, results from several studies (Dell'Apa et al. 2014, 2017; Sagarese et al. 2016; Haugen et al. 2017) have drawn attention to the possibility of exploring the potential for alternative, separate management measures for the two sexes in order to enhance Spiny Dogfish fishery sustainability (e.g., area- or region-specific, male-only directed fishery). A similar fishery management scenario may be envisioned for Smooth Dogfish due to the many similarities between the two species in terms of biology, ecology, habitat use, and reproductive behavior (e.g., size, feeding habits, north–south seasonal migration, and sexual dimorphism, with adult females being larger than adult males).

Similarly, due to the nature of the market's demand and processing needs, the commercial fishery for U.S. North Atlantic Spiny Dogfish has evolved mainly into a size-selective fishery targeting primarily larger individuals (i.e., females) in inshore coastal waters (adult females tend to inhabit shallower inshore coastal waters compared to adult males). This size-selective fishery resulted in lower numbers of females over time and an increasingly skewed male : female ratio in fishery-independent surveys used to assess the stock status (for a detailed history of the Spiny Dogfish commercial fishery, exploitation, and fishery management, refer to Dell'Apa et al. 2015). Therefore, given the recent development of commercial quotas for Smooth Dogfish, an increased understanding of the species' spatiotemporal distribution along the U.S. northwest Atlantic coastal area for the two sexes and the environmental and abiotic factors that influence their distribution and abundance may enhance the development and implementation of more sustainable fishery management strategies over the long term.

The objective of this study was to model the abundance of Smooth Dogfish by sex and season in inshore coastal waters of the U.S. Atlantic by considering oceanographic (i.e., sea surface temperature [SST], sea surface salinity [SSS], and chlorophyll-*a* concentration [chl-*a*]) and topographic (i.e., depth, slope, distance to land, and rugosity) characteristics as predictive variables for CPUE, which is used as a proxy for species abundance. This is the first study to use a large, fishery-independent database as a source of data for analysis and prediction of the habitat distribution of Smooth Dogfish along the U.S. northwest Atlantic inshore coastal area. The results of this study provide information on the spatial distribution of adult Smooth Dogfish by sex and season, which can be used by fishery managers to identify and adopt enhanced fishery management strategies for this species in the U.S. Atlantic.

METHODS

Data collection.— Data on Smooth Dogfish individuals were collected during the Northeast Area Monitoring and Assessment Program's (NEAMAP) fishery-independent trawl surveys conducted between 2007 and 2016. The NEAMAP surveys are conducted twice per year in spring (April–May) and fall (September–October) in coastal waters of the U.S. mid-Atlantic, covering the western edge of Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. A detailed description of the NEAMAP mid-Atlantic surveys was provided by Dell'Apa et al. (2017).

Calculation of CPUE.— The Smooth Dogfish CPUE by sex for each trawl haul was calculated as the total number of individuals for each 20 min of trawling. For each sex, the present analysis included only adults. For the purpose of this analysis, we opted to use size at maturity calculated from maturity data collected by the same NEAMAP trawl survey (Virginia Institute of Marine Science [VIMS], data available upon request) for this species in the U.S. northwest Atlantic (length at maturity for males [n = 3,788] = 64.4 cm precaudal length [PCL]; length at maturity for females [n = 1,686] = 73.5 cm PCL). We used the NEAMAP survey-derived data rather than the most commonly used size-at-maturity data reported by Conrath and Musick (2002), even though the latter data had been recommended as references for Smooth Dogfish in this area by Southeast Data, Assessment, and Review (SEDAR 2015b). The sizes at maturity by Conrath and Musick (2002) were calculated from a limited number of individuals (166 males and 277 females) collected from a larger area (Massachusetts to Florida) compared to our analysis, and there was no clear indication of how the collected samples were dispersed in terms of numbers, locations, and time (e.g., years or seasons). Therefore, we consider the reproductive data calculated from the NEAMAP survey (2007–2016) to be a more updated data source for male and female Smooth Dogfish size at maturity in U.S. northwest Atlantic coastal waters.

The lengths of individuals were converted from PCL (cm) to TL (cm) by using a conversion factor (TL = 3.507 + [1.192 × PCL]) that was calculated from the VIMS longline survey (n = 795) conducted between 1980 and 2015 (VIMS, data available upon request). The resulting size at maturity after conversion from PCL to TL was over 91 cm TL for adult females and over 80.3 cm TL for adult males. For each sex, to determine whether there was any significant difference in the total number of adult sharks caught during spring versus fall, we compared all of the CPUEs by season through a nonparametric Wilcoxon–Mann–Whitney test because the data were nonnormally distributed (Kolmogorov–Smirnov test: $P > 0.05$).

Environmental variables.— Seven environmental variables were considered as potential predictors of Smooth

Dogfish CPUE (Table 1). These included two oceanographic variables (SST, °C; and SSS, practical salinity units [psu]), chl-*a* (mg/m^3), distance to shore (m), and three bathymetric features (depth, m; slope, % grade; and seabed rugosity). Rugosity is used as an index of benthic terrain complexity, accounting for variations in seafloor topography; values of rugosity range between 0 (no terrain variation) and 1 (complete terrain variation), and it is commonly used as a proxy for benthic diversity in the absence of more detailed information on sediment type and structure (Lauria et al. 2015). Low rugosity values correspond to unconsolidated substrate, such as mud and sand, while high rugosity values are associated with rocky substrate (Fonseca et al. 2017).

Monthly average means for years of SST, SSS, and chl-*a* data were extracted from the National Aeronautics and Space Administration (NASA) Earth Observations project (http://neo.sci.gsfc.nasa.gov) with a 0.1° × 0.1° grid cell resolution. Bathymetry was derived from the same NASA Earth Observations Web site by using the General Bathymetric Chart of the Oceans (GEBCO) grid. Moreover, data for bathymetry were collected at each haul location during the NEAMAP trawl surveys. These data were used to correct and check the information on final mean depth. When a discrepancy occurred between the GEBCO data and the survey data, the mean of the two data sets was calculated and used for the analysis.

Other environmental features—distance to shore, slope, and rugosity—were derived from the bathymetry map using the Near tool (World Equidistant Cylindrical coordinate system), the Slope Spatial Analyst tool, and the Terrain Ruggedness (Vector Ruggedness Measure) tool, respectively, in ArcGIS version 10.2.2 (ESRI, Redlands, California).

TABLE 1. Summary of variables included in the Bayesian spatial model as potential fixed effects influencing Smooth Dogfish distribution in the U.S. mid-Atlantic (SST = sea surface temperature; chl-*a* = chlorophyll-*a* concentration; SSS = sea surface salinity; psu = practical salinity units).

Variable	Description	Units
Bathymetry	Mean fishing depth of haul	m
Slope	Seabed slope at the sampling station	% grade
Distance to shore	Distance from the coast at the sampling station	m
Rugosity	Seafloor topography at the sampling station	0 to 1 scale
SST	SST monthly value of haul	°C
Chl-*a*	Chl-*a* monthly value of haul	mg/m^3
SSS	Salinity of the water	psu
Year	Year when haul was sampled	Numeric

All variables were aggregated at a spatial resolution of 0.25° × 0.25° using the "raster" package (Hijmans et al. 2016) in R version 3.1.2 (R Development Core Team 2018). Variables were checked for collinearity, correlation (Pearson's product-moment correlation coefficient [Pearson's *r*]), outliers, and missing data before their use in modeling (Zuur et al. 2010). Distance to coast was highly correlated (Pearson's $r > 0.75$) with depth as well as chl-*a* and SSS. For this reason, these variables were used alternatively in the models. Specifically, separate model runs were performed including only one of the highly correlated variables (distance to coast or depth, chl-*a*, or SSS) to determine which would explain more of the variance.

Modeling of species abundance.— The spatial variation of the CPUE values for Smooth Dogfish by sex and season was modeled using hierarchical Bayesian zero-inflated Poisson (ZIP) intrinsic conditional autoregressive (iCAR) models in order to account for both zero inflation and spatial autocorrelation (Latimer et al. 2006). This type of model integrates two processes: (1) the suitability process for which the species is present ($z_i = 1$) or absent ($z_i = 0$) in a particular location; and (2) the process determining the number of individuals observed at suitable locations (CPUE process). The suitability process is modeled using a binomial distribution, while the CPUE process is modeled with a Poisson distribution.

In addition to the environmental variables, both processes include a temporal component of year as a factor and an iCAR model (Besag 1974) for spatial autocorrelation between observations. The iCAR component assumes that the probability of the species' presence and CPUE at one site depends on the probability of the species' presence and CPUE at neighboring sites. Specifically, it follows that

$$\text{Suitability process:} \quad z_i \sim \text{Bernoulli}(\pi_i)$$
$$\text{logit}(\pi_i) = X_i\beta + \rho_{j(i)}$$

$$\text{CPUE process:} \quad y_i \sim \text{Poisson}(z_i, \lambda_i)$$
$$\log(\lambda_i) = X_i\beta' + \rho_{j(i)}\,,$$

where X_i is the matrix of covariates; β and β' represent the vector of the regression coefficients (for the suitability process and CPUE process, respectively); and ρ and ρ' represent the spatial random effect of location *i* at grid cell *j* (for the suitability process and CPUE process, respectively). Each grid cell (0.25° × 0.25°) is considered a spatial entity defined by eight neighbors. For the suitability process, a logit link function is used, while for the CPUE, an exponential link function is used.

Following Bayesian reasoning, the parameters are treated as random variables, and prior knowledge has to be incorporated via the corresponding prior distributions of the said parameters. In particular, for the parameters involved in both the suitability and CPUE processes, we used uninformative Gaussian priors centered at zero with a fixed large variance of 100. The prior distribution for the variance of the spatial effects followed a uniform distribution on the interval (0, 1,000). For each model, 50,000 Gibbs iterations were used for three chains, with a thinning interval of 5 and a burn-in of 5,000 iterations. These models were fitted using the "hSDM.ZIP.iCAR()" function of the "hSDM" package (Vieilledent et al. 2014) in R version 3.1.2 (R Core Team 2018).

All possible combinations of the candidate covariates were tested using both backward and forward approaches in order to select the relevant ones. We selected the model that had the lowest deviance information criterion (DIC; Spiegelhalter et al. 2002) and that contained only relevant predictors (i.e., those predictors with 95% credibility intervals [CrI] not including zero). Lower values of DIC represent the best compromise between fit and the estimated number of parameters.

Model validation.— Following Dell'Apa et al. (2017), we used two different approaches to assess the predictive accuracy of the selected model. First, the predicted and observed values from the full data set were compared. Second, a 50-fold cross-validation based on a random half of the data set was performed to build the model, and the remaining data were used to test the prediction (Fielding and Bell 1997). For both approaches, three statistics were calculated: Pearson's r, root mean square error (RMSE), and average error (Dell'Apa et al. 2017).

RESULTS

Males

During 2,870 trawl hauls, adult male Smooth Dogfish were present in 665 tows, of which 604 occurred in spring and 61 occurred in fall (Figures 1, 2). In total, 3,055 males were caught during spring, and 311 males were caught during fall ($W = 608{,}468.5$, $P < 0.001$).

For the spring season, the final selected model retained SSS and bathymetry as relevant predictors (Table S1 available separately online in the Supplement). In particular, the expected CPUE showed a negative relationship with SSS (posterior mean = −3.75; CrI = −2.53 to −0.02) as well as with bathymetry (posterior mean = −2.39; CrI = −3.92 to −1.95). Male CPUE decreased continuously from an SSS value of about 30 psu and reached a minimal value at a depth of approximately 250 m (Figure 3A).

No relevant interannual differences were found in male CPUE variability during the spring. Higher estimated values of adult male CPUE were found for the area between Long Island Sound and the continental shelf northeast of

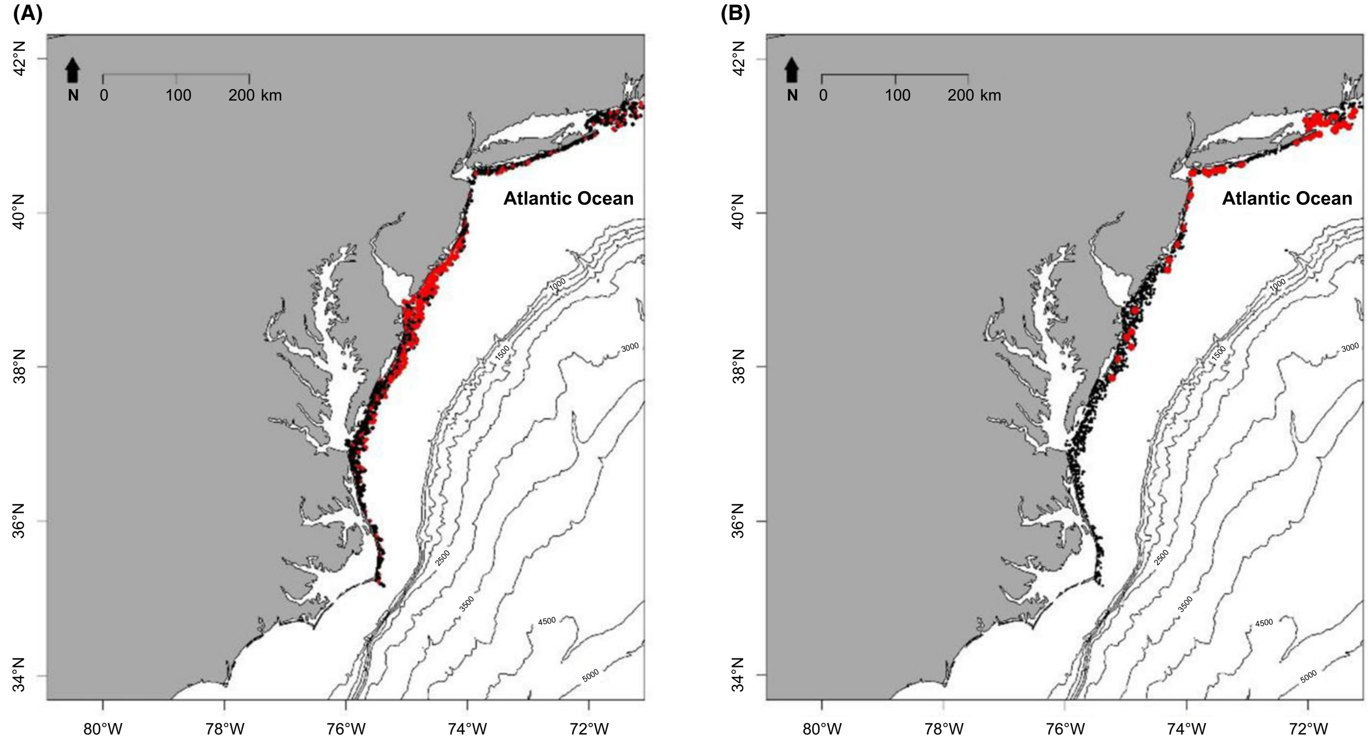

FIGURE 1. Sampling stations of the Northeast Area Monitoring and Assessment Program surveys (2007–2016) in **(A)** spring and **(B)** fall seasons, indicating male Smooth Dogfish presence (red dots) or absence (black dots).

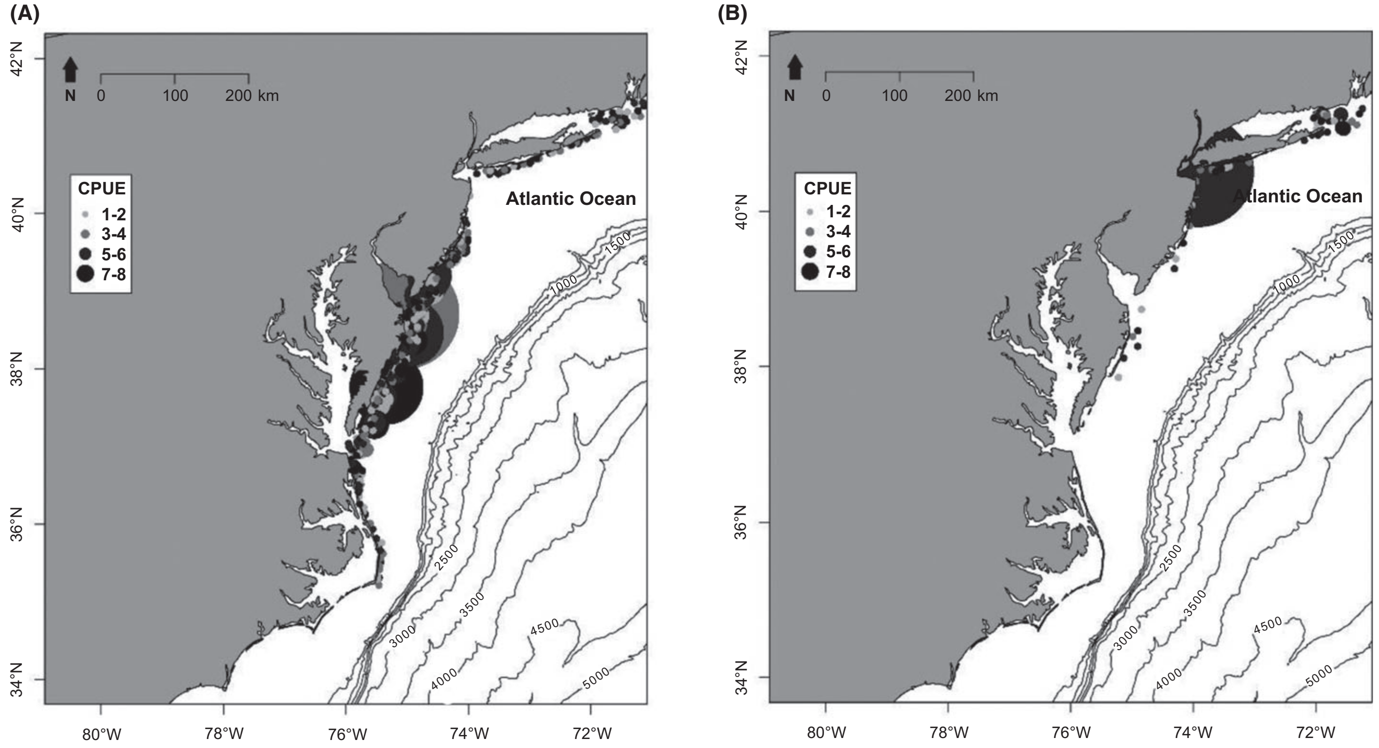

FIGURE 2. Sampling stations of the Northeast Area Monitoring and Assessment Program surveys (2007–2016), indicating male Smooth Dogfish CPUE (number of individuals/20 min of trawling; circles) in **(A)** spring and **(B)** fall seasons. Larger circle sizes indicate greater CPUEs.

Cape Hatteras, North Carolina, than for the other areas sampled, with the highest CPUE predicted in inshore waters between Delaware Bay and Nags Head, North Carolina (Figure 4A; associated map of uncertainty in model prediction: Figure S1A available separately online in the Supplement).

For the fall season, the final model retained SST and rugosity as relevant predictors (Table S2), highlighting a negative relationship of the expected CPUE with SST (posterior mean = −6.67; CrI = −5.13 to −2.24) and with the rugosity index (posterior mean = −0.43; CrI = −0.72 to −0.03). In particular, as shown in Figure 3B, the CPUE decreased continuously from 10°C and was highest for substrata that had a rugosity index of about 0.3 (i.e., moderately low terrain variation), with a decreasing trend on both sides of this value.

No relevant interannual differences were found in male CPUE variability for the fall season. Higher estimated values of adult male CPUE during the fall occurred at higher latitudes (above 40°N) and off Georges Bank relative to other sampled areas (Figure 4B; associated map of uncertainty in model prediction: Figure S1B).

Females

During 2,870 trawl hauls, adult female Smooth Dogfish were present in 524 tows, of which 348 occurred in spring and 176 occurred in fall (Figures 5, 6). Overall, 8,540 females were caught during spring, and 6,780 females were caught during fall ($W = 886{,}031.5$, $P < 0.001$).

For the spring season, the final model for adult female Smooth Dogfish retained SSS and depth as relevant predictive variables (Table S3). Both predictors showed a negative relationship with expected CPUE (SSS: posterior mean = −1.23; CrI = −1.95 to −0.23; depth: posterior mean = −0.98; CrI = −1.14 to −0.11). Figure 7A shows a continuous decreasing pattern between SSS and adult female Smooth Dogfish CPUE, with the highest estimated CPUE at salinities less than 30 psu. The bathymetry also showed a decreasing pattern, with the lowest estimated CPUEs found for water depths greater than 200 m.

No relevant interannual differences were found in female CPUE variability during the spring. Similar to males, higher CPUEs for females during the spring season were found in coastal waters between Long Island Sound and north of Cape Hatteras than in other sampled areas, with the highest estimated CPUE occurring between inshore coastal waters off Ocean City, New Jersey, and the Virginia–North Carolina border (Figure 8A; associated map of uncertainty in model prediction: Figure S2A).

For the fall season, the final model for adult female Smooth Dogfish retained chl-*a*, rugosity, and year as

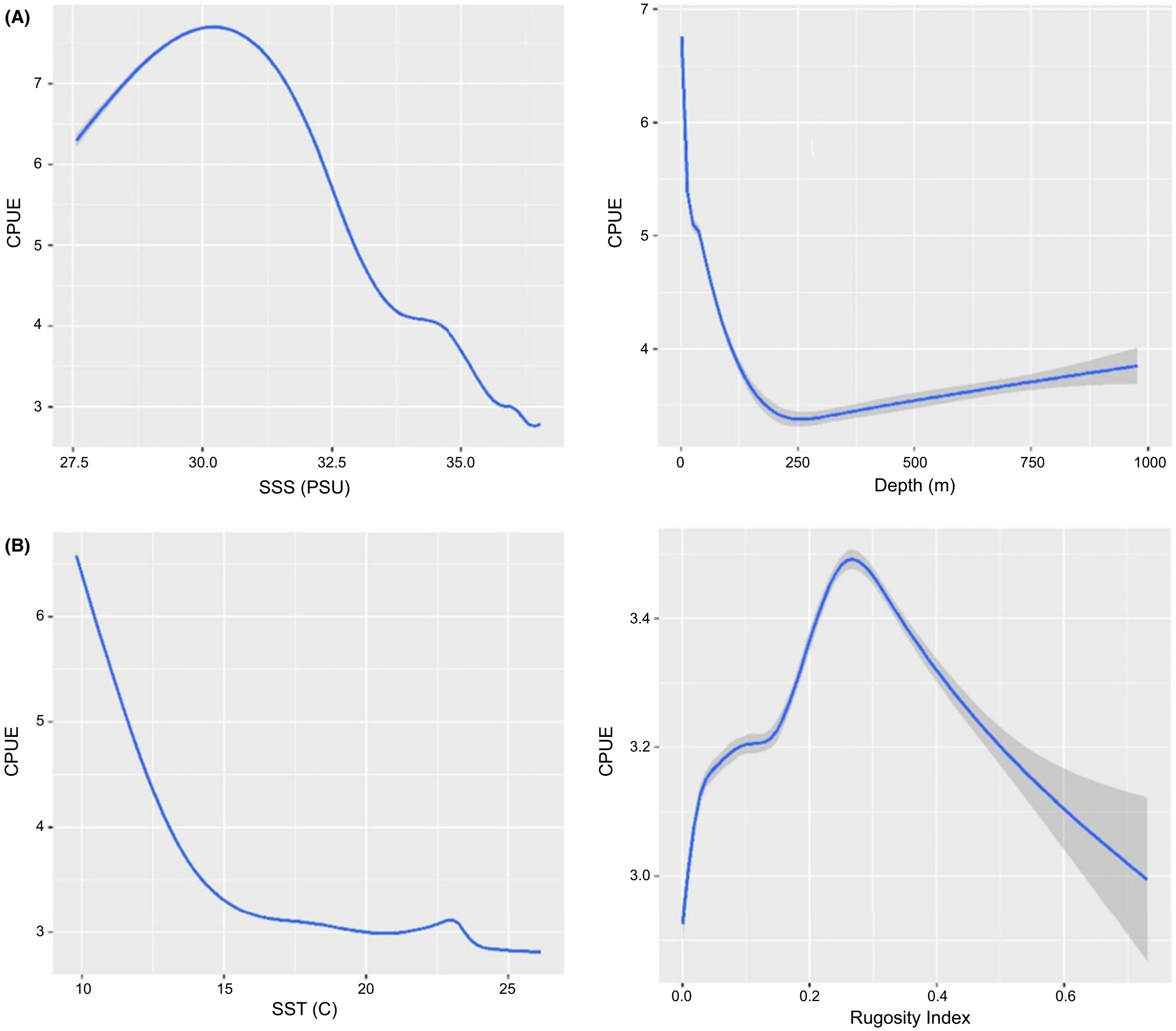

FIGURE 3. Functional response of the final Bayesian hierarchical spatial model for the CPUE (number of individuals/20 min of trawling) of male Smooth Dogfish in the **(A)** spring and **(B)** fall seasons (SST = sea surface temperature, °C; SSS = sea surface salinity, practical salinity units [psu]). The solid line represents the smooth function estimate; the shaded region represents the approximate 95% credibility interval.

relevant factors (Table S4). The expected CPUE of females showed a negative relationship with chl-*a* (posterior mean = −0.94; CrI = −2.24 to −0.29), whereas it exhibited a positive relationship with the rugosity index (posterior mean = 1.53; CrI = 0.54–2.15). The year factor showed a relevant interannual variability, highlighting that 2012 and 2013 were the years with highest CPUEs (2012 posterior mean = 0.45; CrI = 0.12–1.14; 2013 posterior mean = 0.41; CrI = 0.09–1.05), while 2016 was the year with the lowest CPUE (posterior mean: −0.23; CrI = −0.87 to −0.05) with respect to the reference level (i.e., 2007).

As shown by Figure 7B, the highest values of estimated CPUE for adult female Smooth Dogfish were found in waters with chl-*a* of approximately 27 mg/m^3 and in rocky seabed (rugosity index > 0.6). Additionally, during the fall season, the highest estimated CPUEs were observed between coastal waters of Delaware and North Carolina and mainly in inshore waters surrounding Chincoteague

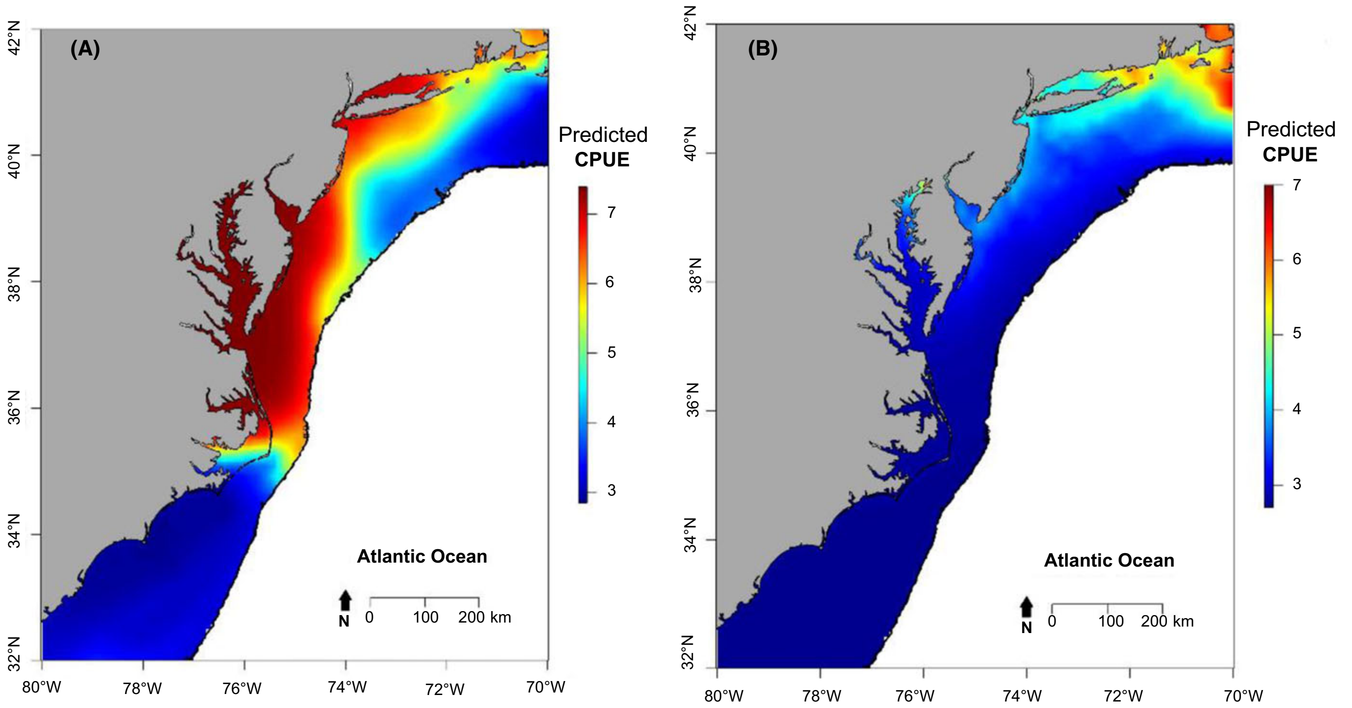

FIGURE 4. Predicted CPUE (number of individuals/20 min of trawling) for male Smooth Dogfish in **(A)** spring and **(B)** fall seasons for waters with bathymetry less than 1,000 m.

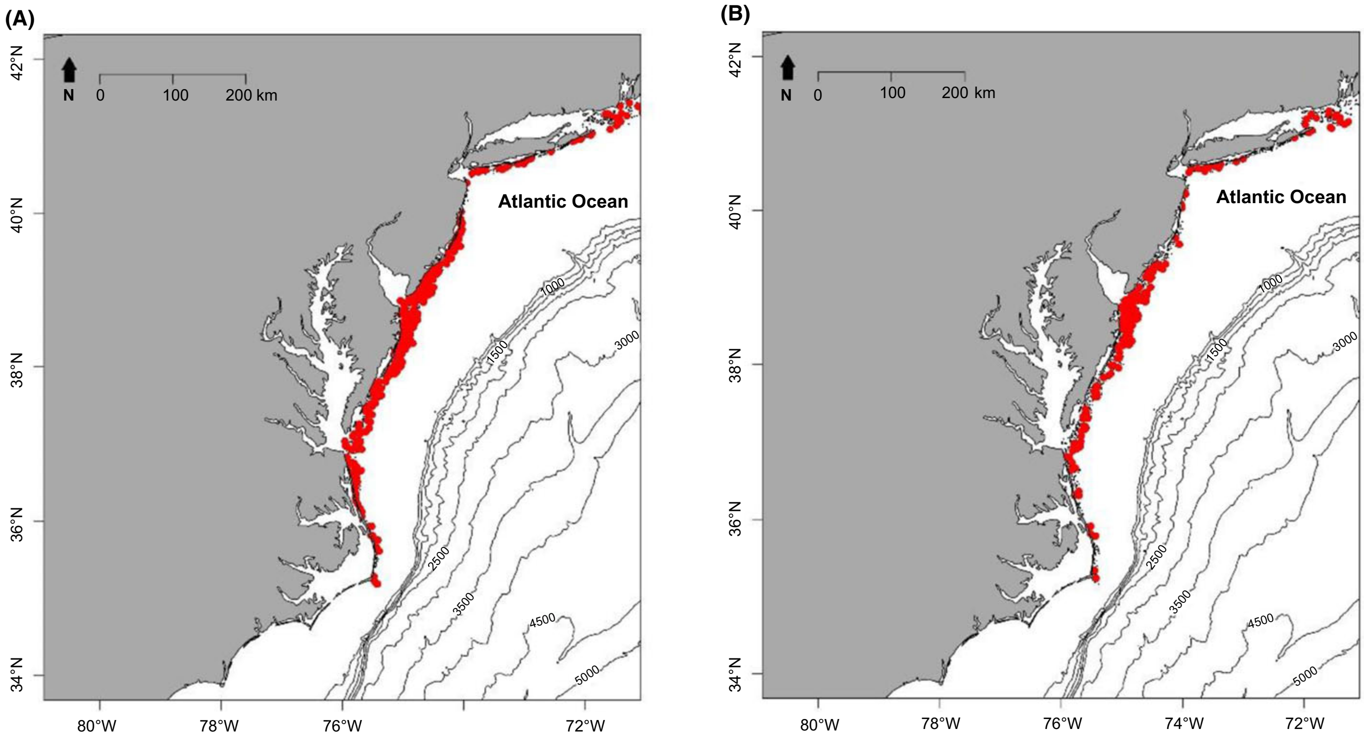

FIGURE 5. Sampling stations of the Northeast Area Monitoring and Assessment Program surveys (2007–2016) for female Smooth Dogfish in **(A)** spring and **(B)** fall seasons, indicating female presence (red dots) or absence (black dots).

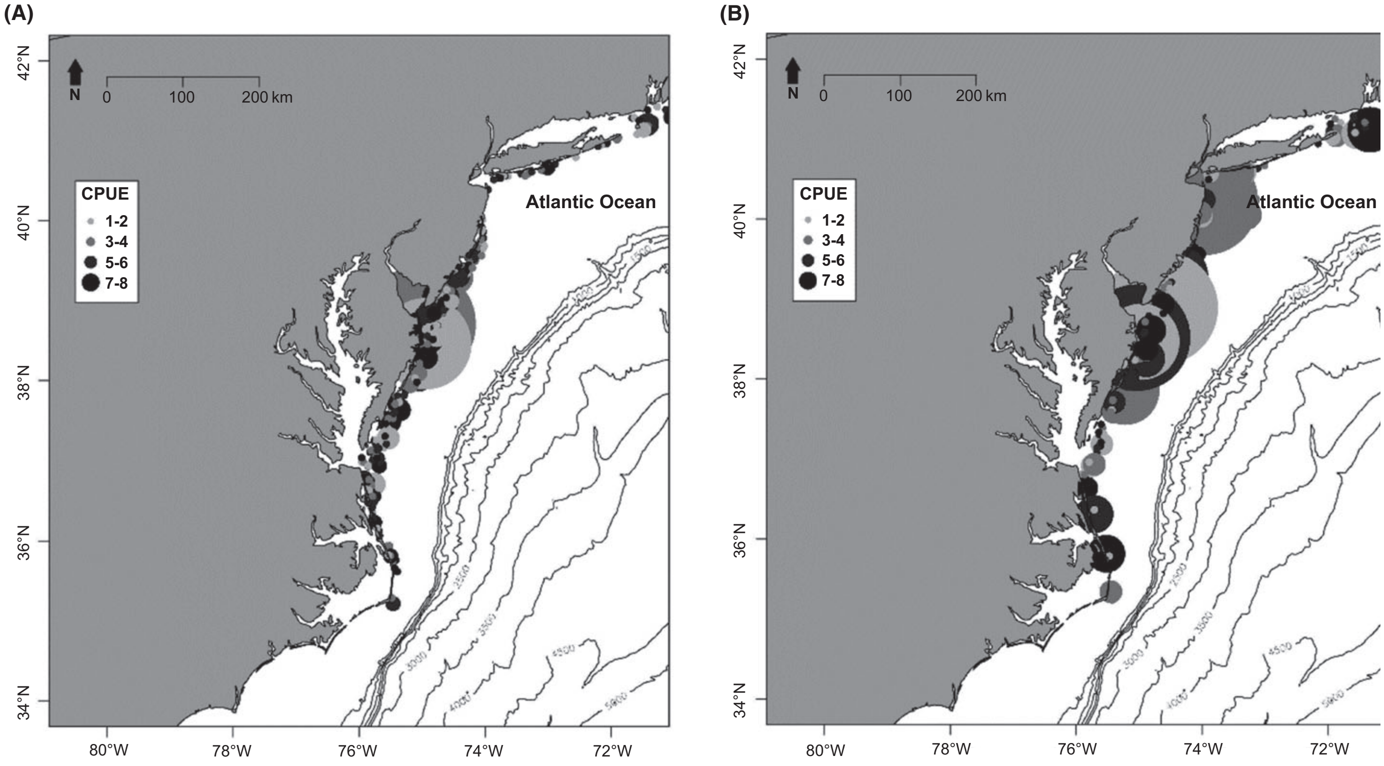

FIGURE 6. Sampling stations of the Northeast Area Monitoring and Assessment Program surveys (2007–2016), indicating female Smooth Dogfish CPUE (number of individuals/20 min of trawling; circles) in **(A)** spring and **(B)** fall seasons. The size of the circles is relative to the CPUE.

Island, Virginia (Figure 8B; associated map of uncertainty in model prediction: Figure S2B).

Model Performance

For the final selected models, high values for Pearson's *r* were obtained for both sexes and seasons. For adult males, Pearson's *r*-values of about 0.64 for the spring and 0.68 for the fall were obtained in cross-validation with the original data set. In cross-validation with half of the data set, Pearson's *r*-values were approximately 0.76 for spring and about 0.73 for fall (Table 2).

For adult females, Pearson's *r*-values of about 0.63 for the spring and about 0.68 for the fall were observed in the cross-validation with the original data set. During cross-validation with half of the data set, Pearson's *r*-values were approximately 0.72 for spring and approximately 0.76 for fall.

Low values of RMSE and average error were achieved in the cross-validation with the original data set for adult males, with an RMSE of 0.88 and an average error of 0.05 for spring and an RMSE of 0.86 and an average error of 0.04 for fall (Table 2). In the cross-validation with half of the data set for adult males, an RMSE of 0.92 and an average error of 0.05 were observed for spring, and an RMSE of 0.91 and an average error of 0.05 were obtained for fall.

Like the results for adult males, the models for adult females obtained low values of RMSE and average error in the cross-validation with the original data for both seasons (spring: RMSE = 0.99, average error = 0.06; fall: RMSE = 0.97, average error = 0.03). Similarly, in cross-validation with half of the data set, an RMSE of 0.99 and an average error of 0.07 were achieved for adult females in spring, and an RMSE of 0.98 and an average error of 0.06 were observed for females in fall (Table 2). The validation results for both males and females indicated good performance for all models.

DISCUSSION

This study represents the first attempt to provide predictive spatiotemporal information on the habitat distribution of Smooth Dogfish by sex and season in U.S. northwest Atlantic coastal waters—and the environmental variables that influence this distribution—by modeling the CPUE obtained from a large, fishery-independent trawl survey (i.e., NEAMAP) as a proxy for the species' abundance and distribution. Based on the results of our hierarchical Bayesian spatial model, the abundance of adult Smooth Dogfish in the U.S. northwest Atlantic coastal region changes seasonally, with adult males showing a

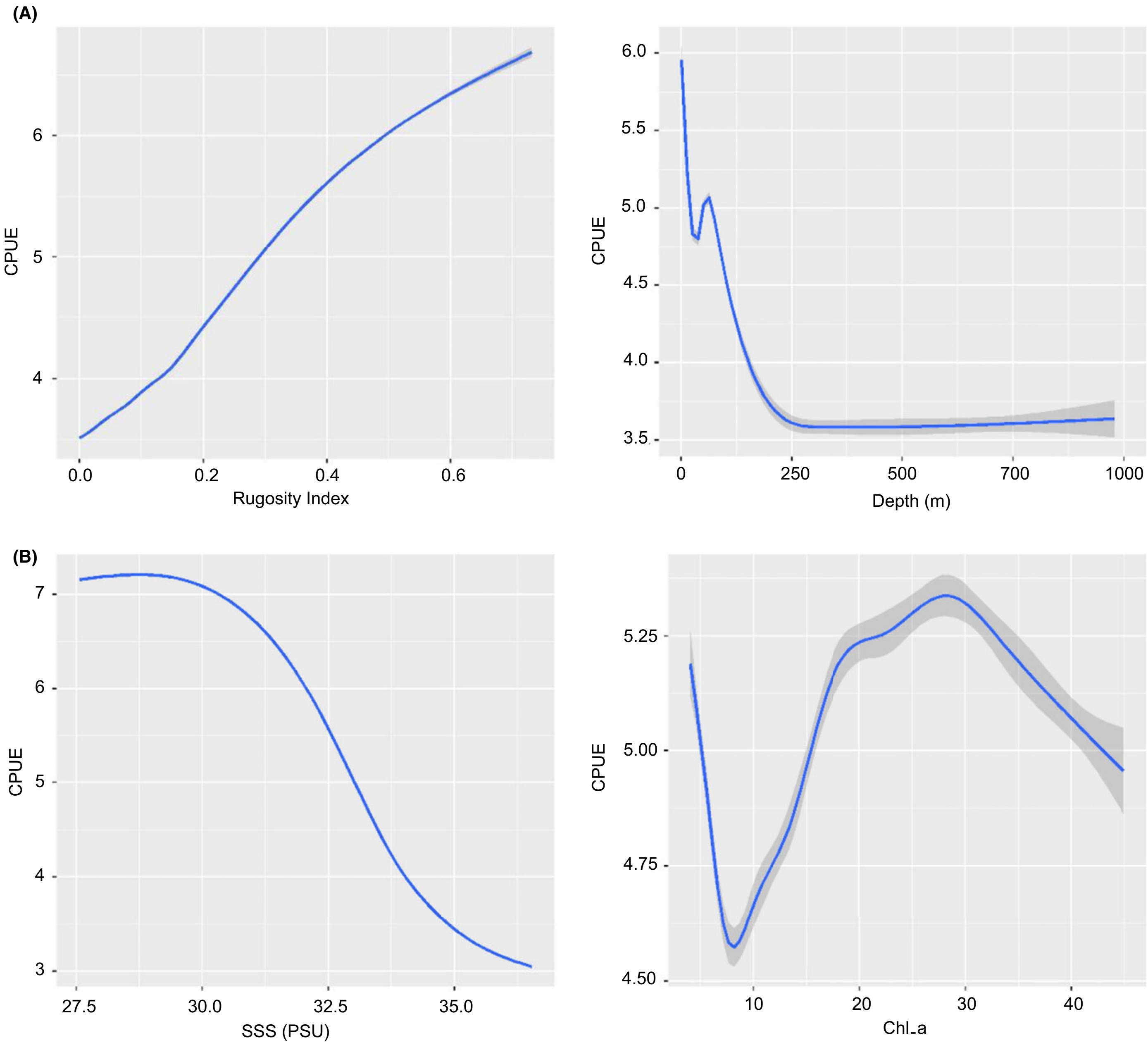

FIGURE 7. Functional response of the final B-HSM CPUE (number of individuals/20 min of trawling) female Smooth Dogfish model for (A) spring and (B) fall seasons. SST = sea surface temperature, SSS = sea surface salinity. The solid line is the smooth function estimate, and the shaded regions represent the approximate 95% credibility interval (CrI).

more pronounced pattern of seasonal migration than adult females in the study area.

For adult males, the highest estimated CPUE values were found during the spring, when males were predicted to inhabit primarily inshore coastal waters between New Jersey and Cape Hatteras. During the fall, adult males were found only in the northern portion of the sampled area, with predicted CPUEs found almost exclusively in Georges Bank's coastal waters. Conversely, adult females were sampled throughout the study area during both seasons, although at the highest abundance during the spring in coastal waters between North Carolina and Delaware. A higher abundance of adult females was predicted to occur in the spring within Chesapeake Bay and adjacent inshore, shallow coastal waters as well as within Delaware Bay and associated inshore coastal areas.

The results of our analysis suggest that Smooth Dogfish, particularly adult males, undergo seasonal migration,

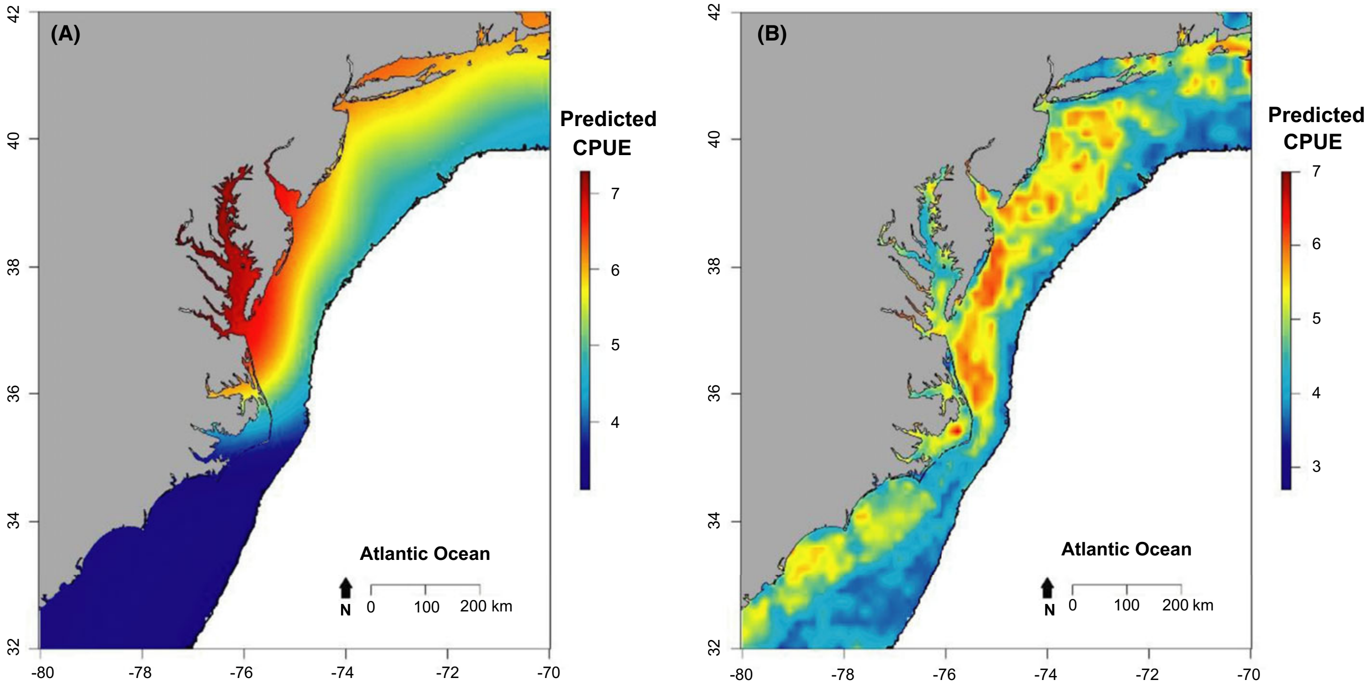

FIGURE 8. Predicted CPUE (number of individuals/20 min of trawling) for female Smooth Dogfish in **(A)** spring and **(B)** fall seasons for waters with bathymetry less than 1,000 m.

although the data used for this study do not help to elucidate whether this migration is north–south, inshore–offshore, or a combination of these two scenarios, as NEAMAP surveys are conducted only in inshore coastal waters. However, given the available information on the species' biology and habitat use, it is less likely that males would move toward the continental shelf in waters deeper than 200 m, thus supporting the most accepted notion of a north–south, coastal seasonal migration in this species (Bigelow and Schroeder 1948; Castro 2011). More studies are needed to describe in greater detail the Smooth Dogfish's migratory behavior by sex and the specifics (e.g., directionality and timeline) of the population's seasonal migration—for example, by using conventional mark–recapture tags or other telemetry (e.g., acoustic and satellite) tags, which were successful in studies of the movement and migratory behavior of Spiny Dogfish populations in the northwest Atlantic (Campana et al. 2007; Campana 2010; Rulifson et al. 2012; Carlson et al. 2014).

In regard to key environmental variables affecting the abundance and distribution of Smooth Dogfish in the study area, our results suggest that they differ based on season and sex. The estimated abundance of male Smooth Dogfish is affected by SSS and depth (negative relationships with CPUE) in the spring and by SST and rugosity (negative relationships with CPUE) in the fall. These results indicate that in the spring, a higher occurrence of males is predicted for inshore, shallow, and less-saline waters. Conversely, in the fall, males inhabit colder waters, with higher estimated CPUEs for SST less than 15°C and for seafloor habitats characterized by a rugosity index typically associated with moderately scattered low-relief seabed.

The main environmental factors affecting the abundance of adult females are SSS and depth (negative relationships with CPUE) in the spring and rugosity (positive relationship with CPUE) and chl-*a* (negative relationship with CPUE) in the fall. These results suggest that in the spring, a higher abundance of adult females should be found in inshore, shallower, and less-saline coastal waters, while in the fall their abundance should be higher in waters characterized by rocky seabeds and in less-productive waters (i.e., low chl-*a*), although a peak of abundance is estimated in more productive waters with chl-*a* of about 27 mg/m^3.

Overall, we interpret these results as a reflection of the different habitats—and their associated key environmental characteristics—that are inhabited by each of the sexes in spring and fall, respectively. Specifically, in the spring, both adult males and females are predicted in higher abundances inside major estuaries and bays and inshore coastal waters across the study area. These inshore, coastal habitats are usually characterized by lower salinity and bathymetry compared to more offshore habitats. Conversely, during the fall, the two sexes are segregated and live in different areas along the U.S. mid-Atlantic coastal region. Adult males are estimated to occupy primarily

TABLE 2. Model prediction performance statistics for the final models (based on the lower deviance information criterion and containing only relevant predictors) for Smooth Dogfish by sex and season (r = Pearson's product-moment correlation coefficient with the original data set; RMSE = root mean square error with the original data set; avg. error = average error with the original data set; r–cross = Pearson's r with the half of the data set used for cross-validation; RMSE–cross = RMSE with the half of the data set used for cross-validation; avg. error–cross = average error with the half of the data set used for cross-validation).

Sex (season)	r	RMSE	Avg. error	r–cross	RMSE–cross	Avg. error–cross
Males (spring)	0.64	0.88	0.05	0.76	0.92	0.05
Males (fall)	0.68	0.86	0.04	0.73	0.91	0.05
Females (spring)	0.63	0.99	0.06	0.72	0.99	0.07
Females (fall)	0.68	0.97	0.03	0.76	0.98	0.06

coastal waters off Georges Bank that are more directly influenced by the cold, inshore Labrador Current coming from the Arctic Ocean and the Newfoundland shelf, which has its highest flow and strength in the fall/winter (Wang et al. 2015), compared to the warmer, more southerly coastal waters occupied by females.

Overall, our results indicate that the Smooth Dogfish's distribution is characterized by sexual segregation, mainly in the fall compared to the spring. This is common in many shark species (Pratt and Carrier 2001; Sims 2005; Mucientes et al. 2009; Dell'Apa et al. 2014). However, the data used for our analysis did not help to fully clarify whether sexual segregation in Smooth Dogfish is spatial or temporal (Conradt 2005; Wearmouth and Sims 2008), as observed and investigated for the Spiny Dogfish population in the U.S. North Atlantic (Nammack et al. 1985; Dell'Apa et al. 2014, 2017; Sagarese et al. 2014; Haugen et al. 2017). Nevertheless, the preliminary results from the surveys indicate that the habitat distributions of the two sexes overlap during the spring in inshore coastal waters of the U.S. mid-Atlantic region. Smooth Dogfish have a gestation period of approximately 10 months, and adult females off the southeastern USA are reported to give birth in the spring (April–May; Castro 1993), with estuaries having a key role as potential nurseries for Smooth Dogfish (Bangley et al. 2018). Hence, our results suggest that Chesapeake Bay and Delaware Bay may be two important pupping grounds and nursery areas for Smooth Dogfish in the spring. The lack of spatial overlap between the two sexes is found during the fall, with adult males inhabiting primarily the northern portion of the study area and adult females found mainly in inshore coastal waters between New Jersey and North Carolina. These results suggest that sexual segregation in Smooth Dogfish may be spatial and driven by social avoidance (Sims 2005) in adult females during the fall, with mature females actively selecting coastal habitats in the southern portion of the study area as an attempt to avoid adult males and their aggressive courtship and mating behavior. This avoidance behavior in mature females has been observed in other sharks, such as the Spotted Dogfish *Scyliorhinus canicula* (Sims et al. 2001) and the Nurse Shark *Ginglymostoma cirratum* (Carrier et al. 1994), and has been theorized to occur in Spiny Dogfish (Dell'Apa et al. 2014). However, these results may also support the hypothesis of habitat segregation (Wearmouth and Sims 2008) in Smooth Dogfish during the fall, with the two sexes inhabiting different geographic areas and habitats characterized by differences in physical and environmental characteristics or prey species.

A second hypothesis proposed for sexual segregation in elasmobranchs is the thermal condition hypothesis (Sims 2005), which states that pregnant females occupy warmer waters as a strategy to increase their growth rate, embryo growth rate, and fecundity. Adult females showed similar geographic distributions in the spring and fall, which may be indicative of a reduced migratory range compared to adult males, allowing the females to remain in warmer, more southerly waters for longer periods of time. The thermal condition hypothesis was suggested for the Gray Reef Shark *Carcharhinus amblyrhynchos* (Economakis and Lobel 1998), Leopard Shark *Triakis semifasciata* (Hight and Lowe 2007), and Atlantic Stingray *Dasyatis sabina* (Wallman and Bennett 2006); however, based on our results, this strategy may not hold true for Smooth Dogfish, as was also theorized for the Spiny Dogfish (Dell'Apa et al. 2014). In fact, SST was not identified as a key environmental factor affecting the distribution of mature females in both seasons, which further supports the hypothesis that sexual segregation in Smooth Dogfish may be driven by social avoidance in adult females. However, NEAMAP data were only available during the spring and fall—the two seasons in which Smooth Dogfish would likely be migrating between summer and winter habitats and distributed over the widest area of the coast. Temperature may be more important in defining summer and winter distributions for both sexes, and the thermal condition hypothesis cannot be definitively rejected without distribution data during these seasons. More studies are needed to clarify the specific type of sexual segregation in Smooth Dogfish and the specific drivers (i.e., ultimate factors).

The results for the influence of rugosity on the abundance of both sexes during the fall, when the two sexes are predicted to occupy different coastal habitats within the study area, may be a direct consequence of the association between morphological characteristics of the seafloor and the composition and distribution of important prey species for adult male and female Smooth Dogfish. Given the presence of sexual dimorphism in this species, with adult females being larger than adult males, this scenario would suggest that during the fall, the two sexes may occupy different habitats characterized by different prey compositions (Sims 2005). In fact, sexual dimorphism in elasmobranchs may be the result of the two sexes having evolved different physiological needs and associated feeding habits, which lead to specific diet and prey preferences (Ruckstuhl and Clutton-Brock 2005; Sims 2005).

In this regard, our results showed a positive relationship between rugosity and predicted CPUE for both sexes during the fall, indicating that an increase in substratum complexity may correspond to an increase in the availability of refuge and the variety of microhabitats available to marine fauna (Graham and Nash 2013), including the prey of Smooth Dogfish. In fact, rugosity, as an index for seafloor habitat complexity, has been used successfully to predict fish species richness and distribution across reef fish communities and ecosystems (Gratwicke and Speight 2005; Pittman et al. 2007). More studies are needed to clarify the potential presence of important differences in prey composition for Smooth Dogfish based on sex and season.

The presence of significant interannual variability in fall abundance of adult females between 2007 and 2016, with the highest CPUEs found in fall 2012 and 2013 and the lowest CPUEs reported in fall 2007 and 2016, could be the result of other important environmental variables and habitat quality characteristics that were not included in the analysis, such as oceanographic conditions and habitat degradation (Lindo-Atichati et al. 2012; Thiaw et al. 2017). Further investigations are needed to clarify the causes of this interannual variability based on season in adult females only.

For our modeling approach, we assumed that CPUE is a valid proxy for the species' abundance (i.e., CPUE is proportional to relative abundance) and that CPUE should be the same for each of the two sexes. However, CPUE is not always proportional to relative abundance because many factors affect catch rates (e.g., fleet efficiency, gear effects, and environment), and, mainly for sexually dimorphic species like the Smooth Dogfish, the CPUE often differs between sexes due to intrinsic variability in the catchability coefficient as fish size changes (Hilborn and Walters 1992; Walters 2003; Maunder and Punt 2004; Maunder et al. 2006). Nevertheless, CPUE has been commonly used as a proxy for fish population trends and abundance when derived from standardized fishery-independent surveys (Runcie et al. 2016; Dell'Apa et al. 2017), which was done in this study, as this can reduce the lack of linearity between CPUE and fish relative abundance (Maunder and Punt 2004).

Our results provide valuable information for fishery managers that could be used and integrated to enhance the sustainability of the Smooth Dogfish fishery in the U.S. mid-Atlantic coastal region. Management of this commercial fishery is still relatively recent, with quotas that were first introduced by NMFS in 2009. The stock is not overfished and is not experiencing overfishing. In 2018, the federal quota for the Smooth Dogfish commercial fishery was set at 1,802 metric tons in dressed weight (NOAA 2017). An important aspect of this quota allocation is that based on historical landings, North Carolina and Virginia (combined) are allocated approximately 60% of the total quota for the U.S. Atlantic region from Maine to South Carolina. Moreover, this quota does not differentiate between sexes or seasons, and there is no size limit for Smooth Dogfish in either the commercial or recreational fisheries in the U.S. Atlantic.

Collectively, the results of our study suggest that there could be potential benefits in discussing the development of a male-only targeted fishery for Smooth Dogfish in the U.S. Atlantic coastal area based on season and geographic region. Specifically, the potential development of a targeted fishery for adult males in the northern portion of the study area during the fall may help to reduce the negative effects of fishing pressure on the adult female component of the population, which contributed to reducing the sustainability of the Spiny Dogfish fishery (Dell'Apa et al. 2015). In turn, a male-targeted fishing strategy may help to enhance the sustainability of the Smooth Dogfish commercial fishery.

Additionally, the commercial fishery for Smooth Dogfish has expanded the practice of fin removal for commercial purposes, with an allowed fin-to-carcass-weight ratio of 12%, because the Smooth Dogfish is the only species for which finning is allowed in the USA. However, this management regulation has been considered particularly controversial, given the specific exception made only for Smooth Dogfish and the higher fin-to-carcass ratio than is used for other shark species (i.e., 5%). In fact, Cortés and Neer (2006) reported an average fin-to-dressed-carcass-weight ratio of approximately 3.7–3.8% for various shark species and a ratio of 3.51%—much lower than the current 12% ratio—for Smooth Dogfish in the U.S. Atlantic.

Assuming no future changes in the 12% ratio, it may be argued that over the long term, this ratio may contribute to undermining the sustainability of the Smooth Dogfish commercial fishery. Similarly, excessive fishing pressure in the southern portion of the U.S. mid-Atlantic coastal area during fall, particularly off Virginia and North Carolina, may eventually reduce, over time, the spawning stock biomass (i.e., adult female) of the Smooth

Dogfish population to unsustainable levels, as occurred with Spiny Dogfish in the past (Dell'Apa et al. 2015). Therefore, a seasonal, area-based, male-directed fishery could potentially help to maintain the stock at sustainable levels.

The present results provide new information on the spatial distribution of Smooth Dogfish that can be of interest to fishery managers and can help to maintain the fishery sustainability for this stock. Collectively, these results enhance our understanding of the environmental factors that affect the distribution of Smooth Dogfish by sex and season, which may contribute to shedding light on the population dynamics of the U.S. Atlantic population.

ACKNOWLEDGMENTS

We are grateful to the Ruhle family members, who own, operate, and crew the F/V *Darana R*, and to the members of the VIMS Multispecies Research Group. We also thank the two anonymous reviewers whose comments greatly helped to increase the quality of the manuscript. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.