THEMED ISSUE: TELEMETRY IN THE NORTHWEST ATLANTIC AND CARIBBEAN

Identifying Important Juvenile Dusky Shark Habitat in the Northwest Atlantic Ocean Using Acoustic Telemetry and Spatial Modeling

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Abstract
    Highly mobile species can be challenging for fisheries management and conservation due to large home ranges combined with dependence on discrete habitat areas where they can be easily targeted or vulnerable to anthropogenic disturbances. Management of the Dusky Shark *Carcharhinus obscurus* in the northwest Atlantic Ocean has been particularly challenging due to the species' inherent vulnerability to overfishing and poorly understood habitat associations. To better understand habitat associations and seasonal distributions, we combined telemetry and remotely sensed environmental data to spatially model juvenile Dusky Shark presence probability in the northwest Atlantic Ocean. To accomplish this, 22 juvenile Dusky Sharks (107–220 cm TL) that were tagged with acoustic transmitters at different locations within the U.S. Middle Atlantic Bight region were tracked through networked arrays of acoustic receivers. Tag detections were summarized as daily presence records, and data describing environmental conditions, including depth, chlorophyll-*a* concentration, salinity, and sea surface temperature, were extracted at detection locations. These data were used in boosted regression tree models to predict juvenile Dusky Shark presence probability based on environmental parameters during fall 2017 and summer 2018. Telemetry observations and modeled presence probability showed consistent associations with temperatures between 16°C and 26°C and chlorophyll-*a* concentrations between 2 and 7 mg/m³, which were associated with seasonal migration timing and monthly spatial distributions.

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Dusky Shark tag detections and predicted distributions during summer and early fall overlapped areas in the Middle Atlantic Bight that were affected by fisheries and potential offshore energy development. Our methodology provides a framework for assessing climate change effects on distribution.

Highly mobile species can move across jurisdictions and even entire ocean basins, complicating fishery management and other conservation measures. However, even these species often make repeated use of discrete geographic locations or habitat conditions that may be disproportionately important to reproduction, foraging, and other activities driving population dynamics (Chapman et al. 2015). Such habitat areas fit the National Marine Fisheries Service (NMFS) definition of essential fish habitat (EFH), or habitat areas that are required for the completion of a species' life cycle (NMFS 2017). Identification of EFH is particularly important for elasmobranchs that show site fidelity, since the life history characteristics of many cartilaginous fishes, such as slow growth and late maturity, make them particularly vulnerable to overfishing in these areas (Hueter et al. 2005).

Telemetry methods have been employed in a variety of applied conservation contexts and are increasingly being used in more specialized studies (Hussey et al. 2015). When combined with environmental data and spatial modeling techniques, telemetry data can be used to predict the distribution of highly migratory species at large scales (Block et al. 2011; Curtis et al. 2014). This can be useful for applications such as identifying areas of potential fishery interactions (Haulsee et al. 2018), assessing the use of closed and protected areas (Calich et al. 2018), and predicting the effects of large-scale environmental changes (Hazen et al. 2012). Passive acoustic telemetry, which entails the deployment of ultrasonic tags that are then detected by acoustic receivers, has traditionally been used to monitor marine animals in particular habitat areas or locations along migratory routes, but the advent of collaborative acoustic telemetry networks has enabled continental-scale spatial tracking, which was previously only possible through satellite-based telemetry (Donaldson et al. 2014; Udyawer et al. 2018).

By treating telemetry detections as presence records, boosted regression tree (BRT) modeling offers a feasible approach to spatially predict the distribution of data-poor, highly migratory species. This method, which splits environmental data based on presence likelihood or abundance data, is robust to the low sample sizes and zero-inflation that are characteristic of acoustic telemetry data and is adaptable to most data distributions that are found in ecological data (Elith et al. 2008; Dedman et al. 2017). There is precedence for the use of regression tree modeling to spatially predict migratory shark habitat: it was used to

delineate habitat for juvenile Sandbar Sharks *Carcharhinus plumbeus* in their Chesapeake Bay nursery grounds based on fishery-independent survey catches and environmental data (Grubbs and Musick 2007). Recent advances in machine learning and statistical software have allowed researchers to "boost" regression tree analysis by repeating trees, with each successive tree informed by the previous one until a minimum of deviance between model runs is achieved (Elith et al. 2008). Boosting allows regression tree modeling to overcome variance between individual model runs, improving consistency and predictive performance (Elith et al. 2008). Boosted regression tree modeling based on catch rates has been used to delineate areas of high potential bycatch of skates in the Irish Sea (Dedman et al. 2015) and to identify habitat for elasmobranchs in relatively enclosed estuarine habitats (Froeschke et al. 2010; Bangley et al. 2018a).

The Dusky Shark *Carcharhinus obscurus* in the northwest Atlantic Ocean has been a data-poor species of particular conservation concern for which management and conservation may benefit from spatial modeling approaches. This species is slow growing and late maturing (Natanson et al. 1995, 2013) and has experienced considerable population declines after targeted fishing in the 1980s and 1990s (McCandless et al. 2014). Landings of Dusky Sharks have been prohibited in commercial and recreational fisheries since 2000, and the Mid-Atlantic Shark Closed Area was established in 2005, closing an area encompassing most of the continental shelf off North Carolina to bottom longline gear from January 1 through July 31 each year to protect juvenile overwintering habitat (NMFS 2003). Despite slowing population declines and increasing juvenile abundances (McCandless et al. 2014), the latest stock assessment showed the Dusky Shark to be in an overfished state with overfishing still occurring, largely due to bycatch and low fecundity (SEDAR 2016). Discard mortality is particularly problematic for juvenile Dusky Sharks, which show lower at-vessel and postrelease survival than adults (Romine et al. 2009) and other species captured in the same areas (Marshall et al. 2015). In addition, a risk assessment of climate responses in fishery management-relevant species by Hare et al. (2016) determined that the Dusky Shark is among the species that are most likely to shift their distribution in response to climate change, meaning that spatial management of this species will need to be adaptable to changes in potential Dusky Shark habitat.

TABLE 1. Identification codes (ID), demographic information (M = male; F = female), tagging date and location, and tag battery life for juvenile Dusky Sharks that were tagged with acoustic transmitters in the northwest Atlantic Ocean during 2016 and 2017. Shark 15571 (marked with an asterisk) was not detected during the focal tracking period of September 2017–October 2018.

Tag ID	TL (cm)	Sex	Tagging date	Tagging location	Tag life (d)
46065	114	M	Sep 15, 2017	Ocean City, MD	653
46066	112	F	Sep 15, 2017	Ocean City, MD	653
46067	114	M	Sep 15, 2017	Ocean City, MD	653
46068	155	F	Sep 16, 2017	Ocean City, MD	653
46078	170	F	Sep 15, 2017	Ocean City, MD	653
15416	183	F	Aug 21, 2017	Chesapeake Bay mouth	2,435
15433	109	M	Sep 14, 2017	Ocean City, MD	2,435
15434	160	M	Sep 15, 2017	Ocean City, MD	2,435
15435	163	F	Sep 15, 2017	Ocean City, MD	2,435
15436	135	F	Sep 14, 2017	Ocean City, MD	2,435
15437	150	M	Sep 14, 2017	Ocean City, MD	2,435
16950	186	F	Sep 14, 2016	Chesapeake Bay mouth	2,435
15154	186	F	Sep 14, 2016	Chesapeake Bay mouth	2,427
16085	160	F	Sep 14, 2017	Ocean City, MD	1,825
16086	112	F	Sep 15, 2017	Ocean City, MD	1,825
16087	119	F	Sep 14, 2017	Ocean City, MD	1,825
16088	155	F	Sep 14, 2017	Ocean City, MD	1,825
16089	107	F	Sep 14, 2017	Ocean City, MD	1,825
16094	218	F	Aug 21, 2017	Chesapeake Bay mouth	1,825
16095	220	F	Aug 21, 2017	Chesapeake Bay mouth	1,825
23183	132	F	Aug 15, 2016	Montauk, NY	3,650
23191	121	F	Aug 18, 2016	Montauk, NY	3,650
15571*	138	M	Aug 11, 2017	Montauk, NY	3,650

In this study, we used acoustic telemetry to obtain positional data from juvenile Dusky Sharks tagged in the U.S. Middle Atlantic Bight region to describe coastal movements and environmental associations for this species. Based on this information, we developed predictive models of Dusky Shark presence that could be used to identify key habitat areas. We paid particular attention to the fall migration period, during which juvenile Dusky Sharks travel from summer habitats in the Middle Atlantic Bight to overwintering habitats off North Carolina. Modeling of spatial distribution over the course of this migration enabled us to accomplish three objectives that are important for Dusky Shark management: demonstrating the feasibility of spatial habitat modeling at a coastal scale from acoustic telemetry data, identifying migration timing and associated environmental conditions, and identifying potential habitat areas and inferring interactions with human activities within those areas.

METHODS

Acoustic telemetry.— Twenty-three juvenile Dusky Sharks ranging from 107 to 220 cm TL were tagged with acoustic transmitters during the late summer and early fall of 2016 and 2017; 22 of the 23 sharks were detected. All

acoustic transmitters were manufactured by Vemco (Vemco/InnovaSea, Bedford, Nova Scotia) and transmitted a unique identification code at a randomized interval between 60 and 180 s at a high-power, 69-kHz frequency. Three transmitter types were deployed: V13 tags with 653 d of battery life ($n = 5$), V16 tags with 2,435 d ($n = 8$) or 3,650 d ($n = 3$) of battery life, and V16T tags with 1,825 d of battery life and a built-in temperature sensor that transmitted the current ambient water temperature (°C) along with the identification code ($n = 7$; Table 1). All tags were surgically implanted into the body cavity of the sharks. We began surgical procedures by placing the shark ventral side up to induce tonic immobility while in the water or with a flowing-seawater hose inserted into the mouth to ventilate the gills. We then made a 2–3-cm incision on the ventral side of the body just lateral to the center line. The tag was inserted through the incision after sterilization with 95% ethanol, and the incision was then closed using absorbable sutures in an interrupted pattern. Sharks were released at or near the site of capture immediately after tagging. Total handling time lasted 5–10 min.

Tag transmissions were recorded on Vemco VR-series 69-kHz acoustic receivers that were deployed in the northwest Atlantic Ocean from September 2016 through December 2018. To detect sharks in their presumed

overwintering habitat within the Mid-Atlantic Shark Closed Area, we deployed four VR2W receivers on data buoys maintained by researchers at the University of North Carolina Wilmington in Onslow Bay, North Carolina. Detections from other receivers were available through the Atlantic Cooperative Telemetry Network and the FACT Network, which facilitate the sharing of tag detection data between researchers using similar equipment. Membership in these networks provided the potential to detect tagged Dusky Sharks in coastal and continental shelf waters from Nova Scotia to the Florida Keys.

Of the 23 sharks, 15 were captured by rod and reel off Ocean City, Maryland, in September 2017; 5 were captured by bottom longline during the Virginia Shark Monitoring and Assessment Program conducted by the Virginia Institute of Marine Science (VIMS) in September 2016 and August 2017 off the mouth of Chesapeake Bay and Virginia's eastern shore; and 3 were captured by rod and reel off Montauk, New York, in August 2016 and 2017 during research operations conducted by OCEARCH and its collaborators targeting White Sharks *Carcharodon carcharias* for telemetry tag deployment. Capture and tagging procedures used in Maryland and Virginia waters were approved by the Smithsonian Environmental Research Center's Animal Care and Use Committee (Protocol D16-00392 and reciprocal agreement with VIMS), and procedures used in the New York Bight were approved by NMFS and the New York Department of Environmental Conservation. Identification code, size, sex, tag battery life, and tagging location for each individual shark were recorded at the time of capture (Table 1).

To gain a general understanding of Dusky Shark seasonal movements, we visually analyzed plots of the latitude of detection and temperature sensor data by date. The time period covered by these plots began on September 1, 2017, because all sharks included in our data set had been tagged and detected at least once by the end of that month. The end point of the plotted time period was October 31, 2018, because this represented the most current tag detection data at the time our analyses were conducted.

Spatial modeling.— We used BRT modeling of Dusky Shark presence/absence at acoustic receiver locations and environmental data extracted at the receiver sites to identify environmental associations with shark presence. These models allowed us to spatially predict the probability of juvenile Dusky Shark presence in the northwest Atlantic Ocean based on environmental associations (contingent on receiver locations). To capture the seasonal change in distribution, we generated seasonal-scale models for fall 2017 (September, October, and November) and summer 2018 (June, July, and August). Fall 2017 and summer 2018 were chosen because a majority of the tagged sharks were

consistently detected during these seasons (Table S1 available in the Supplement separately online). Due to the wide latitudinal range at which sharks were detected during the annual fall migration and to gain insight into the timing of occurrence within the Mid-Atlantic Shark Closed Area, we developed models on a monthly time scale for September–November 2017.

For each season and month for which modeling was attempted, a matrix containing all receiver locations, dates, and the presence/absence of tagged Dusky Sharks at each receiver during each date within that season or month was created. Dusky Shark presence was defined as the detection of at least one tagged shark at a given receiver on a given day, and presence was counted once per receiver each day regardless of the number of individuals that were actually detected. In this way, we treated daily presence/absence as a single daily event at each receiver regardless of how many individuals were detected at a given receiver on a given day; this strategy mitigated the spatial and temporal autocorrelation issues that are common when working with telemetry data (Haulsee et al. 2018).

Environmental data were extracted at receiver locations and dates from publicly available data sets (National Oceanic and Atmospheric Administration, Environmental Research Division Data Access Program) using the package rerddapxtracto (Mendelssohn 2019) in R (R Core Team 2018). Extracted environmental variables were sea surface temperature (SST; °C) and chlorophyll-*a* concentration (Chl-*a*; mg/m^3), which were observed by the National Aeronautics and Space Administration (NASA) Moderate Resolution Imaging Spectroradiometer's Aqua sensor (Savtchenko et al. 2004); sea surface salinity (Sal; psu), which was recorded by the NASA Jet Propulsion Laboratory's Soil Moisture Active Passive satellite (Fore et al. 2016); and depth (m), which was available from the ETOPO1 Global Relief Model (Amante and Eakins 2009). These variables were chosen based on environmental associations that have been found to define habitat for highly migratory coastal species (Block et al. 2011; Curtis et al. 2014; Calich et al. 2018; Haulsee et al. 2018). Extracted data applied to each receiver location and date were mean values taken from within a radius of 0.01 decimal degrees (dd; ~0.88–1.14 km^2 between latitudes 23°N and 45°N) for SST and depth, 0.05 dd (~4.4–5.7 km^2) for Chl-*a*, and 0.25 dd (~22–28.5 km^2) for Sal, roughly matching the spatial resolution of each environmental data set.

Boosted regression tree modeling was used to determine relationships between the presence probability of tagged Dusky Sharks and environmental variables, which were then used to spatially predict potential distribution based on those relationships. Briefly, regression tree modeling divides the data at cut-points in the environmental

variables between higher and lower presence likelihood (see Grubbs and Musick [2007] for a detailed treatment of regression tree modeling in the context of shark habitat delineation). "Boosting" reduces the variability inherent in regression tree models by using machine learning to iteratively add trees in a stagewise fashion until the lowest level of deviance between trees is reached. During each iteration of this process, a proportion of the data is randomly selected to train the model and training data are cross validated against the unselected testing data. Generally, models that are fitted by using at least 1,000 trees are more likely to reach the minimum possible deviance and provide more reliable predictions (Elith et al. 2008). For a considerably more detailed description of each step of the modeling process, see Elith et al. (2008).

Binary BRT presence/absence models were fitted using the R package gbm.auto, which automates the regression tree modeling, boosting, and mapping processes as well as calculating the percentage of tree splits based on each variable, generating marginal effect plots of presence probability against each variable, and determining the interaction strength between pairs of variables based on residual variance (Dedman et al. 2017). The initial parameters of the models were tree complexity, which indicates the number of nodes in each tree split; learning rate, which indicates the contribution of each individual tree to reducing deviance; and bag fraction, which is the proportion of data that are randomly chosen at each tree step and used as training data to be cross validated with the remaining, unselected data. Combinations of these parameters were tested, and the model that generated at least 1,000 trees and had the lowest mean deviance and greatest cross validation scores and area-under-the-curve values was chosen for use in predicting presence probability. For our models, we tested tree complexity values of 2 or 4 to represent binary interactions or interactions incorporating all four environmental variables, learning rate values between 0.01 and 0.0005 to balance model repeatability and processing time (Elith et al. 2008), and bag fraction values between 0.5 and 0.7, which are near to or slightly greater than typical starting values for BRT analysis (Elith et al. 2008; Dedman et al. 2017). The relative influence of each variable in each BRT model was measured using the percentage of tree splits attributed to that variable, and marginal effect plots were generated to identify particular variable values or ranges associated with increased presence probability. To identify potential interactions between variables, we also report the two strongest pairwise interactions.

Once the best-performing models for each season and month were identified, spatial grids containing SST, Chl-a, Sal, and depth data were created to map modeled Dusky Shark presence probabilities. To accomplish this, we downloaded monthly mosaics of the same environmental data sets used for extraction, corresponding to the months covered by BRT modeling. The SST and Chl-a mosaics were downloaded from the NASA Ocean Color Web site (http://oceancolor.gsfc.nasa.gov); Sal data were downloaded from the NASA Jet Propulsion Laboratory's Physical Oceanography Distributed Active Archive Center (https://podaac.jpl.nasa.gov). These data were imported into SeaDAS version 7.5.3 (NASA) and cropped at the following latitude and longitude (dd) bounds: 45.83°N, −85.00°W, 23.67°N, and −65.08°W. These bounds roughly correspond with the Dusky Shark's range along the continental shelf and oceanic waters off the U.S. East Coast (Ebert et al. 2013). Depth data were accessed through the ETOPO1 layer built into SeaDAS. Cropped data were exported as NetCDF-4 (Network Common Data Form) rasters and imported into ArcGIS version 10.5.1 (ESRI, Redlands, California), where environmental data were extracted at points positioned every 0.05 dd within a grid covering the same latitude and longitude bounds as the cropped data sets. This allowed us to create one gridded point data set with all environmental data for each month, which we then exported as a .csv file. Gridded environmental data sets were then imported into R, and the "gbm.map" function from the gbm.auto package (Dedman et al. 2017) was used to apply BRT model results to the grids and generate maps and gridded data sets of presence probability. To determine how well the environmental data in the models reflected the monthly environmental data used for mapping, the function "gbm.rsb" was used to generate maps of unrepresentativeness, which indicate how well environmental ranges within a given cell in the grid data are represented by the samples data used in the original BRT model (Dedman et al. 2017).

RESULTS

General Acoustic Telemetry Observations

All but one of the tagged Dusky Sharks were detected at least once, with a total of 4,591 detections and 446 daily presence records since the beginning of the focal period in September 2017. Four sharks were tagged in fall 2016 and detections of these individuals prior to September 2017 were not used in statistical analyses, but the timing and location of telemetry detections from these sharks during the previous year were similar to those of tag detections from 2017–2018. As of October 2018, 16 (72.7%) of the 22 tagged sharks were still being detected. Tagged sharks were detected along the coast between the New York Bight and Onslow Bay, North Carolina (Figure 1). Detections occurred on arrays deployed in areas being leased by the Bureau of Ocean Energy Management (BOEM) for wind energy development off Delaware Bay and the Maryland eastern shore (69.5% of detections) and
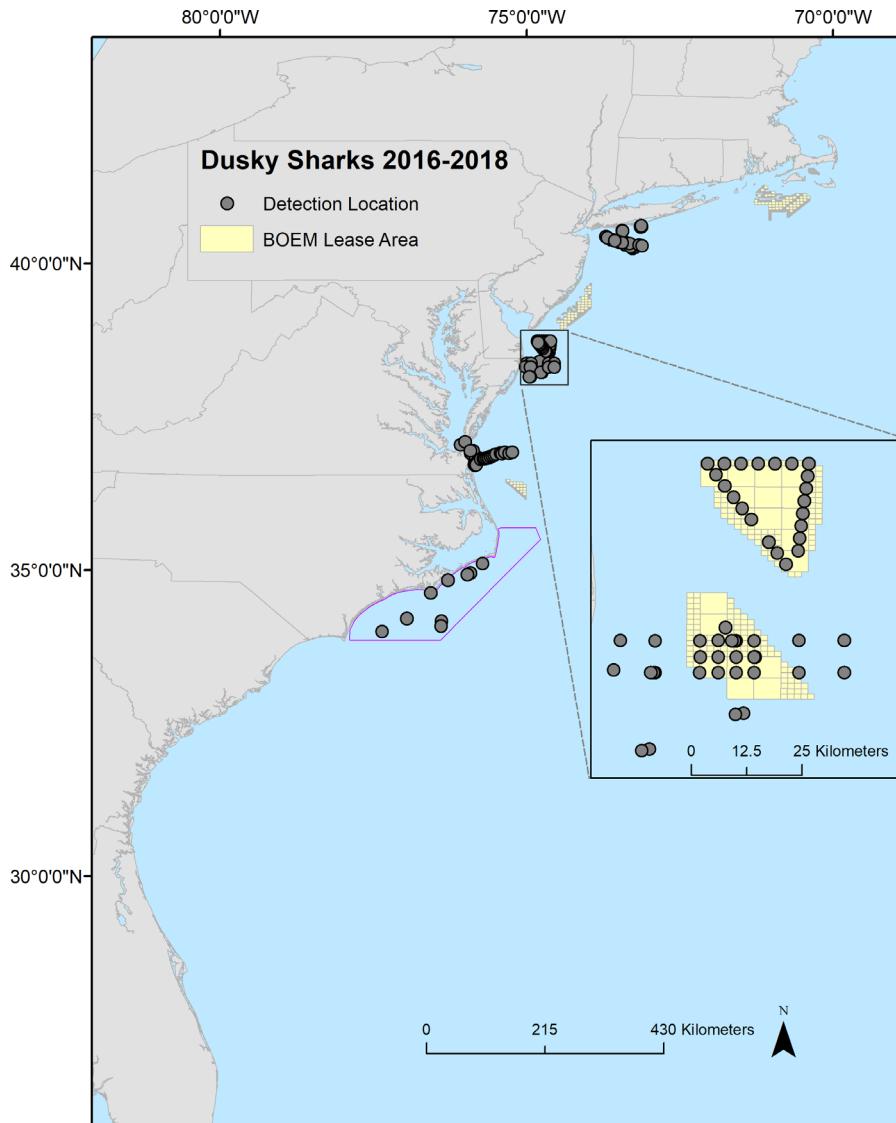
FIGURE 1. Locations of acoustic transmitter detections of tagged juvenile Dusky Sharks between September 2017 and October 2018. The Mid-Atlantic Shark Closed Area is outlined in purple. Inset map shows the area off Maryland and Delaware with Bureau of Ocean Energy Management (BOEM) wind farm lease areas.

within the Mid-Atlantic Shark Closed Area off North Carolina (6.4% of detections; Figure 1). Sharks were consistently detected from September through November, with some detections occurring up to mid-December; sharks were not detected on any acoustic receivers from mid-December through mid-April (Figure 2). Four sharks were detected on receivers within the Mid-Atlantic Shark Closed Area immediately prior to or after the period during which no transmitters were detected, and one of these sharks showed a similar pattern during the previous year. Detections were consistent through June, but relatively few detections were recorded during July and August, with frequent detection of tagged sharks resuming during the fall (Figure 2).

Latitude of detection showed evidence for migration along the coast between warm-season habitats from Maryland to New York and potential overwintering areas off North Carolina (Figure 3A). Sharks were detected at North Carolina latitudes immediately before and after the period of no tag detections between mid-December and mid-April (Figure 3A). Transmissions from temperature sensors showed Dusky Sharks occurring at water temperatures between approximately 16°C and 25°C; sharks occurred at higher temperatures during the late summer and early fall and at lower temperatures during late fall and late spring (Figure 3B). Temperatures at detections during early summer between May and June were among the lowest recorded, and these detections occurred within
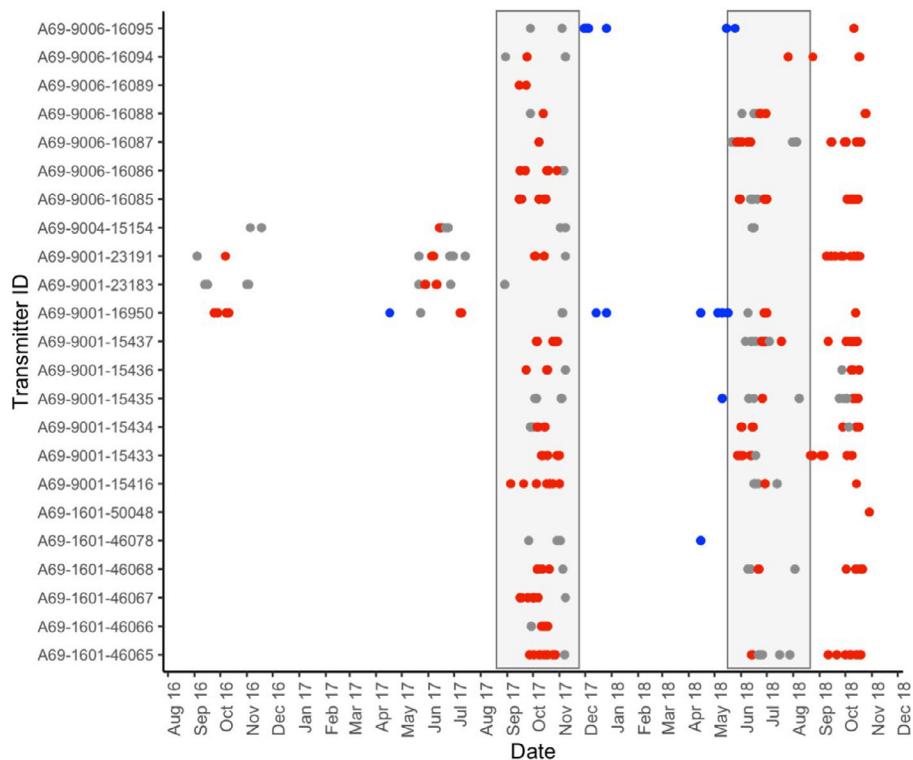
FIGURE 2. Abacus plot of acoustic detections by date for each tagged juvenile Dusky Shark. The areas highlighted in gray denote seasons for which habitat modeling based on tag detections and environmental data was attempted. Red points represent detections within arrays in potential wind farm sites off Delaware and Maryland, blue points represent detections within the Mid-Atlantic Shark Closed Area, and gray points represent detections outside of either of those areas. Fall 2018 data were the most recent data at the time of analysis, and we could not verify that all tag detection data had been received.

potential wind farm lease areas off Delaware and the Maryland eastern shore (Figure 3).

Spatial Modeling

At least 19 daily presence events at acoustic receivers were recorded during each season and month chosen for BRT modeling; 100% of tagged sharks were detected during fall 2017, and at least 59% of tagged sharks were detected during summer 2018 and each individual month during fall (Table S1). All seasonal and monthly models performed relatively well, with cross validation scores approximately 0.6 or greater and area-under-the-curve values of 0.93 or greater (Table 2). Maximum presence likelihood ranged from 0.51 to 0.88 (Table 2). In seasonal models, Chl-*a* and SST accounted for nearly equal percentages (35.56% and 35.59%, respectively) of tree splits in the fall 2017 model, suggesting nearly equal influence, whereas Sal accounted for the most tree splits (36.02%), followed by SST (33.11%), in the summer 2018 model (Table 3). In the monthly models, the most influential variables were Chl-*a* during September, depth during October, and SST during November, with each variable accounting

for at least approximately 40% of tree splits. Chlorophyll-*a* concentration accounted for the second-highest percentage of tree splits during October and November, and depth was the second most important variable during September. The strongest interactions included SST and the second strongest included Chl-*a* in all models except fall 2017, for which SST and depth showed the second-strongest interaction (Table 3).

Marginal effect plots from both seasonal and monthly models showed that SST measurements between approximately 17°C and 26°C and Chl-*a* between approximately 2 and 7 mg/m^3 were consistently associated with elevated Dusky Shark presence probability, although the full range of SSTs was not encountered during all months (Figures 4, 5). Salinity and depth associations differed between fall and summer and varied by month. Dusky Shark presence during fall was positively associated with greater Sal and shallower depth than presence during summer (Figure 4). In monthly models, Sal had no effect during September, whereas measurements less than 32 psu during October and greater than 35 psu during November were positively associated with presence
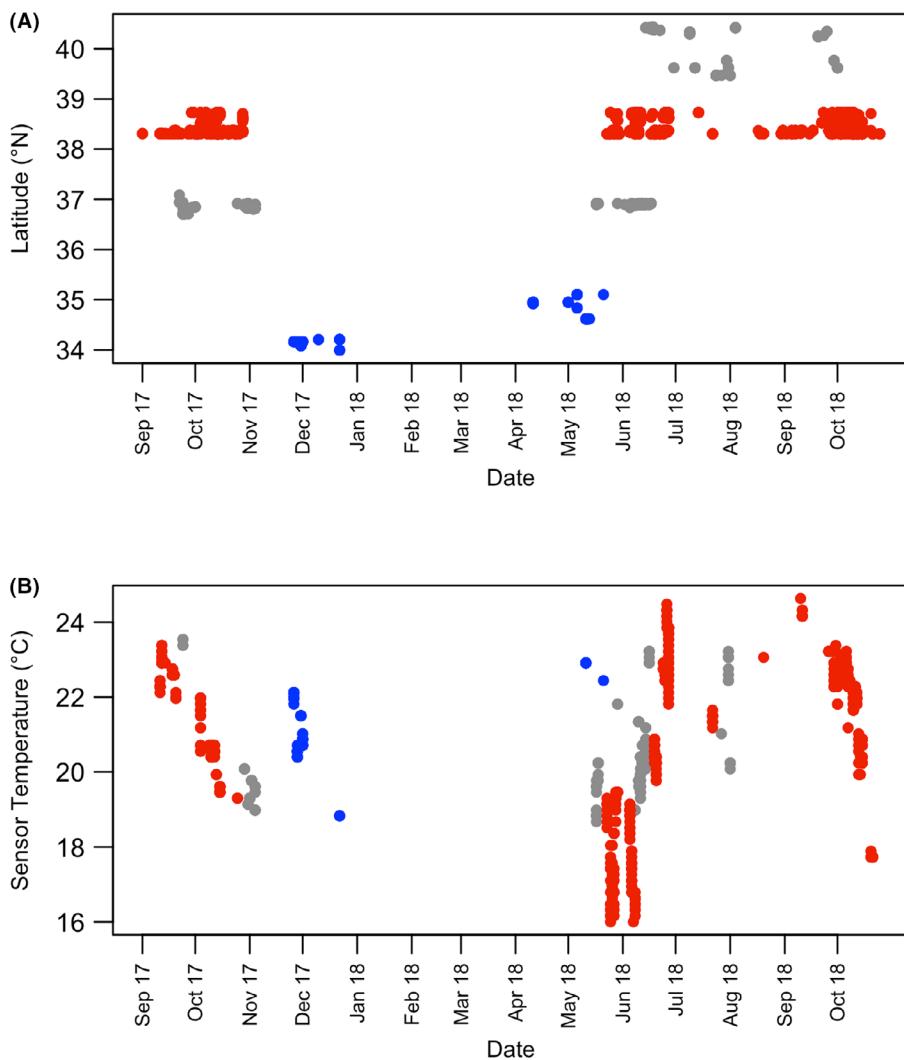
FIGURE 3. Detections over date for tagged juvenile Dusky Sharks by **(A)** latitude of detection (°N) and **(B)** water temperature (°C) transmitted by onboard temperature sensors. Red points represent detections within arrays in potential wind farm sites off Delaware and Maryland; blue points represent detections within the Mid-Atlantic Shark Closed Area.

TABLE 2. Starting parameters (tc = tree complexity; lr = learning rate; bf = bag fraction) and performance metrics (cross validation score, with SE in parentheses; AUC = area under the curve; Max P = maximum presence likelihood) for the best-performing boosted regression tree models of juvenile Dusky Shark presence for fall 2017 (September–November 2017 aggregated data), summer 2018 (June–August 2018 aggregated data), and each month during fall 2017.

Model	tc	lr	bf	n trees	Cross validation score (SE)	AUC	Max P
Fall 2017	4	0.0075	0.5	2,300	0.56 (0.03)	0.93	0.95
Summer 2018	4	0.0075	0.5	2,100	0.60 (0.03)	0.94	0.55
Sep 2017	4	0.0015	0.6	1,300	0.60 (0.06)	0.96	0.66
Oct 2017	4	0.005	0.6	3,350	0.57 (0.04)	0.94	0.51
Nov 2017	4	0.005	0.6	1,300	0.72 (0.08)	0.97	0.88

likelihood. Dusky Shark presence probability was positively associated with depths less than 20 m during September and November and depths between 10 and 30 m during October (Figure 5).

Predictive maps showed discrete hot spots of Dusky Shark presence probability and inshore–offshore movements between fall and summer and over the course of the 3 months during fall 2017 (Figures 6, 7). During fall 2017,

TABLE 3. Relative importance (percentage of tree splits) of depth, chlorophyll-*a* concentration (Chl-*a*), salinity (Sal), and sea surface temperature (SST) in boosted regression tree models for each month, with interaction strength (str) and variables included in the strongest pairwise interaction (Int 1) and second-strongest pairwise interaction (Int 2).

Model	Variable (% of tree splits)				Int 1	Int 1 str	Int 2	Int 2 str
	Depth	Chl-*a*	Sal	SST				
Fall 2017	22.87	35.56	5.98	35.59	SST, Sal	147.01	SST, Depth	101.53
Summer 2018	11.81	19.05	36.02	33.11	SST, Chl-*a*	141.73	Sal, Chl-*a*	140.12
Sep 2017	26.65	48.16	0.00	25.18	SST, Depth	54.19	Chl-*a*, Depth	5.62
Oct 2017	39.66	26.77	7.89	25.68	SST, Chl-*a*	135.10	Chl-*a*, Depth	121.43
Nov 2017	10.59	36.13	5.45	47.83	SST, Sal	55.28	SST, Chl-*a*	12.73
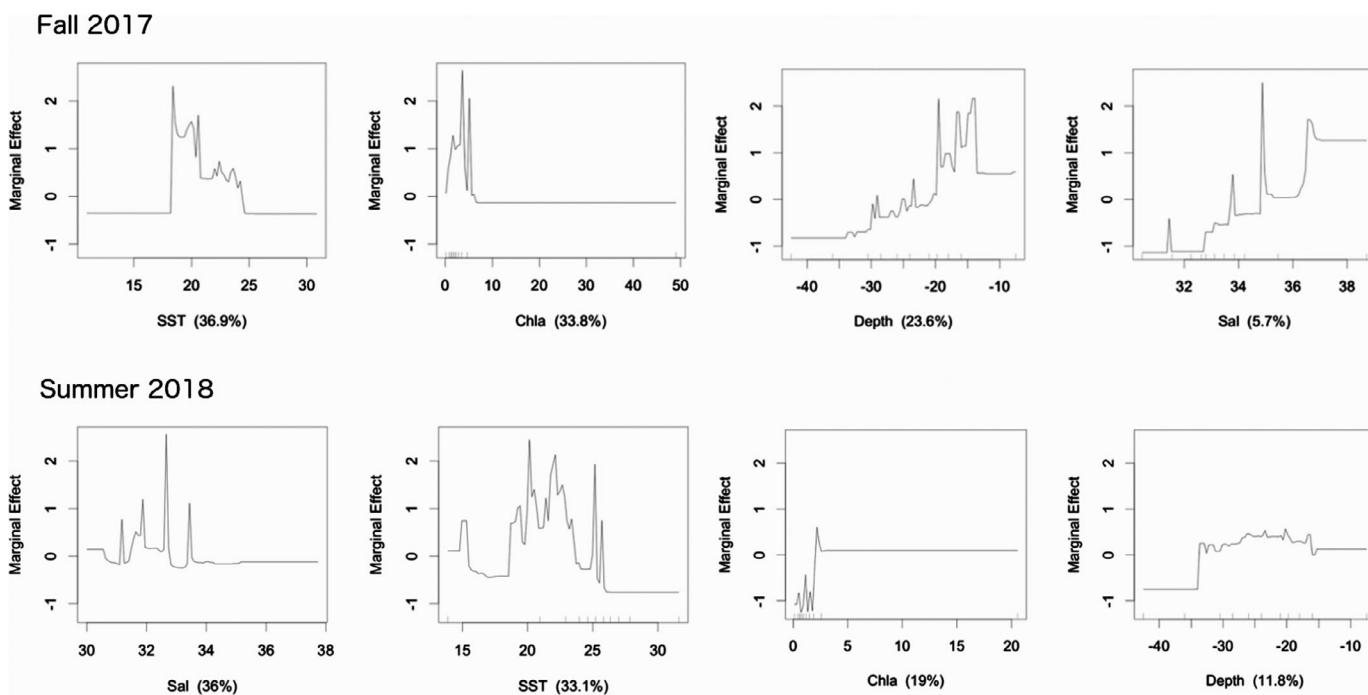
FIGURE 4. Marginal effect plots of the influence of environmental variables on the likelihood of juvenile Dusky Shark presence from boosted regression tree models for fall 2017 (aggregated data from September to November 2017) and summer 2018 (aggregated data from June to August 2018). Percentages of tree splits attributed to each variable in the given model are shown in parentheses (Chla = chlorophyll-*a* concentration, mg/m^3; Sal = salinity, psu; SST = sea surface temperature, °C; Depth = depth, m).

areas of presence probability greater than 0.25 were distributed across a broad portion of the U.S. East Coast from the mouth of Chesapeake Bay to Cape Canaveral, Florida (Figure 6A). During summer 2018, areas of elevated presence probability were distributed in the vicinity of the mouth of Delaware Bay, along the northern New Jersey shoreline, and in New England waters from Long Island to just north of Cape Cod (Figure 6B). Maps based on monthly models showed changes in presence probability by latitude and distance to shore over the course of the fall 2017 southward migration (Figure 7). During September 2017, areas with the greatest presence probability were

in the U.S. mid-Atlantic region between Cape May, New Jersey, and the mouth of Chesapeake Bay, with another predicted southeast of Nantucket off Massachusetts (Figure 7A). High presence probability during October 2017 was distributed near the mouth of Delaware Bay and nearshore in Onslow Bay, North Carolina (Figure 7B). During November 2017, areas of presence probability greater than 0.25 were nonexistent north of the mouth of Chesapeake Bay, distributed relatively close to shore south of Chesapeake Bay and along the North Carolina Outer Banks, and distributed farther offshore over the continental shelf south of Onslow Bay (Figure 7C).
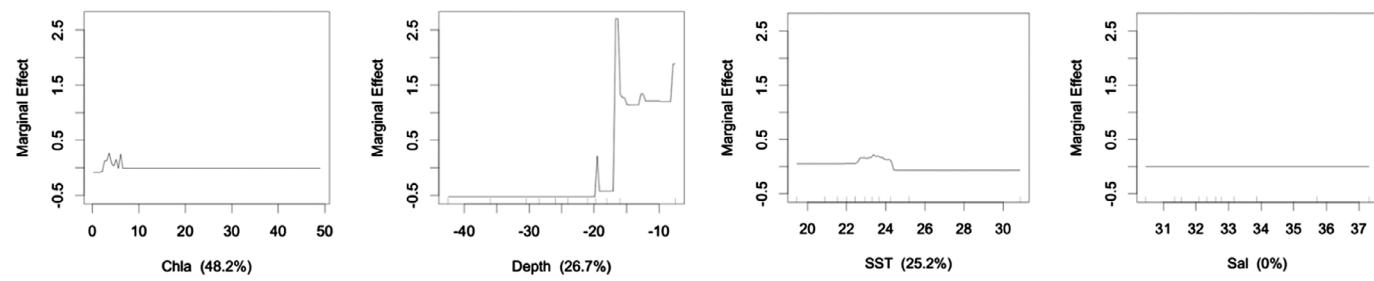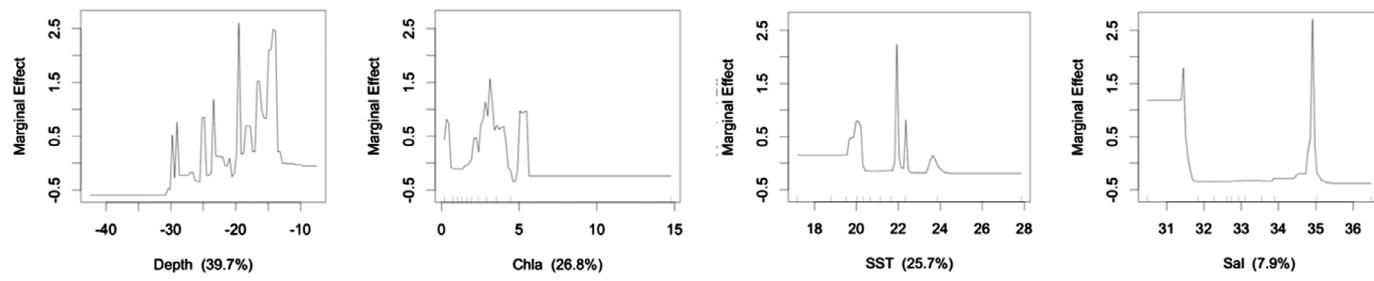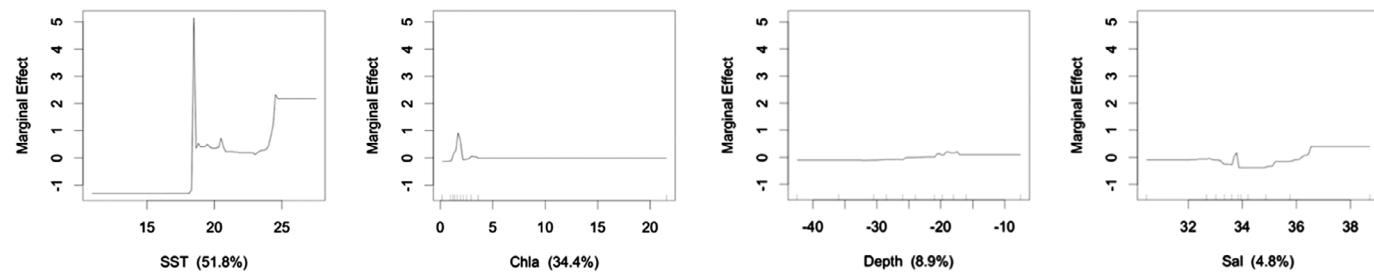
FIGURE 5. Marginal effect plots of the influence of environmental variables on the likelihood of juvenile Dusky Shark presence from boosted regression tree models of each month during fall 2017. Percentages of tree splits attributed to each variable in the given model are shown in parentheses (Chla = chlorophyll-*a* concentration, mg/m³; Sal = salinity, psu; SST = sea surface temperature, °C; Depth = depth, m).

Unrepresentativeness maps showed that environmental data extracted at acoustic receivers were representative (<0.25 unrepresentativeness) of gridded environmental data along most of the continental shelf in both seasonal models (Figure S1 available in the Supplement separately online) and monthly models (Figure S2).

DISCUSSION

The results of our telemetry study and spatial models provide updated information on the seasonal movement patterns and environmental associations of juvenile Dusky Sharks in their range along the U.S. Atlantic coast. We further demonstrate that BRT modeling of acoustic tag detections can improve our understanding of the environmental drivers of seasonal distribution for this overfished species. In particular, our results provide a mechanism for improving the characterization of EFH, assessing the use of spatial management measures like the Mid-Atlantic Shark Closed Area, and quantifying the potential overlap of offshore energy development with seasonal movements and distribution. This information may allow for more precise spatial management and bycatch avoidance measures, which could help continue the recovery of the northwest Atlantic Dusky Shark population.

Telemetry detections showed a seasonal migration mostly within the U.S. Middle Atlantic Bight that crossed into subtropical waters south of Cape Hatteras during the winter. Although our interpretation of telemetry results is mostly based on tag detections recorded since September 2017, the four sharks that were tagged in fall 2016 showed similar patterns over the course of the previous year. Most of the tagged sharks were detected off Delaware and Maryland during the fall and moved south past the mouth
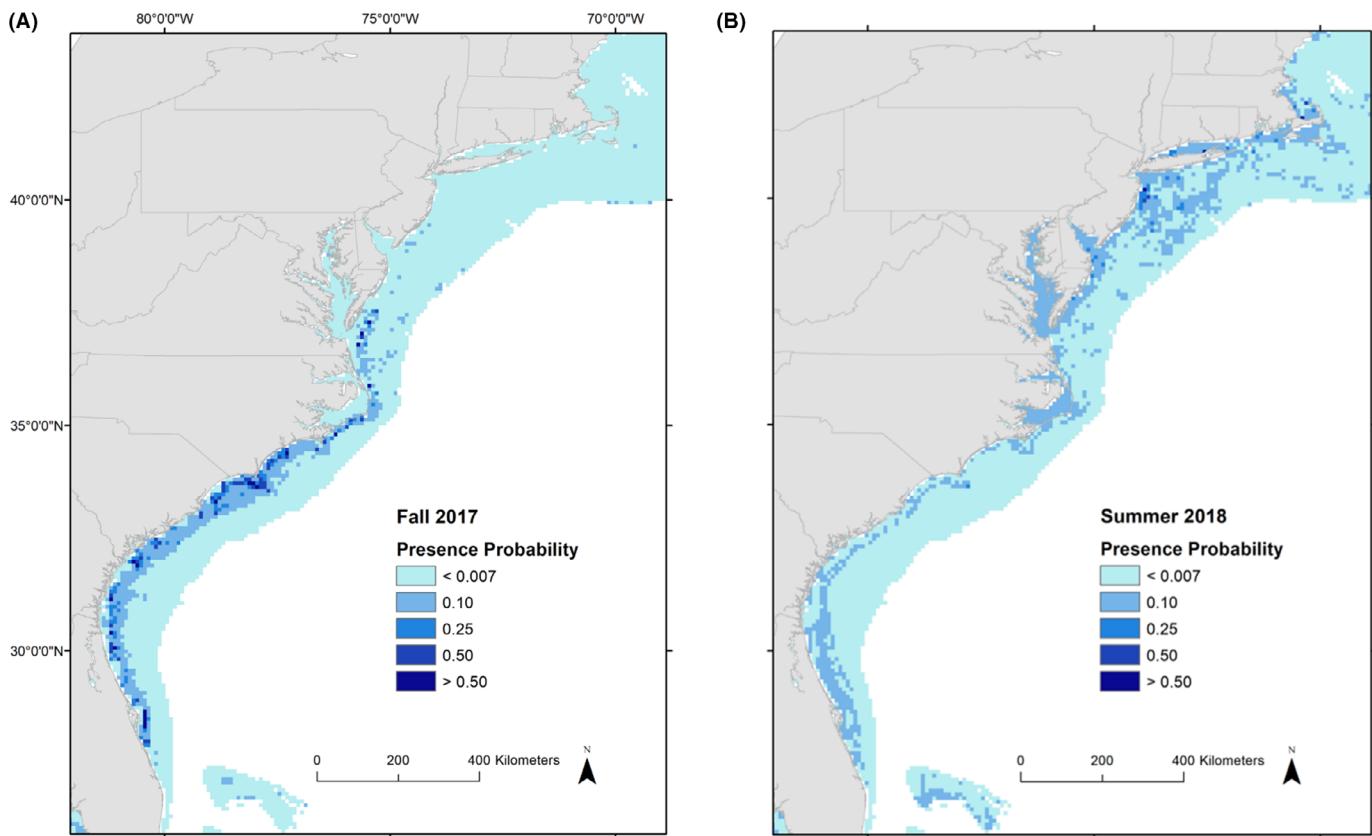
FIGURE 6. Mapped presence probability based on boosted regression tree modeling of juvenile Dusky Shark tag detections and satellite-recorded environmental data during **(A)** fall 2017 (aggregated data from September to November 2017) and **(B)** summer 2018 (aggregated data from June to August 2018).
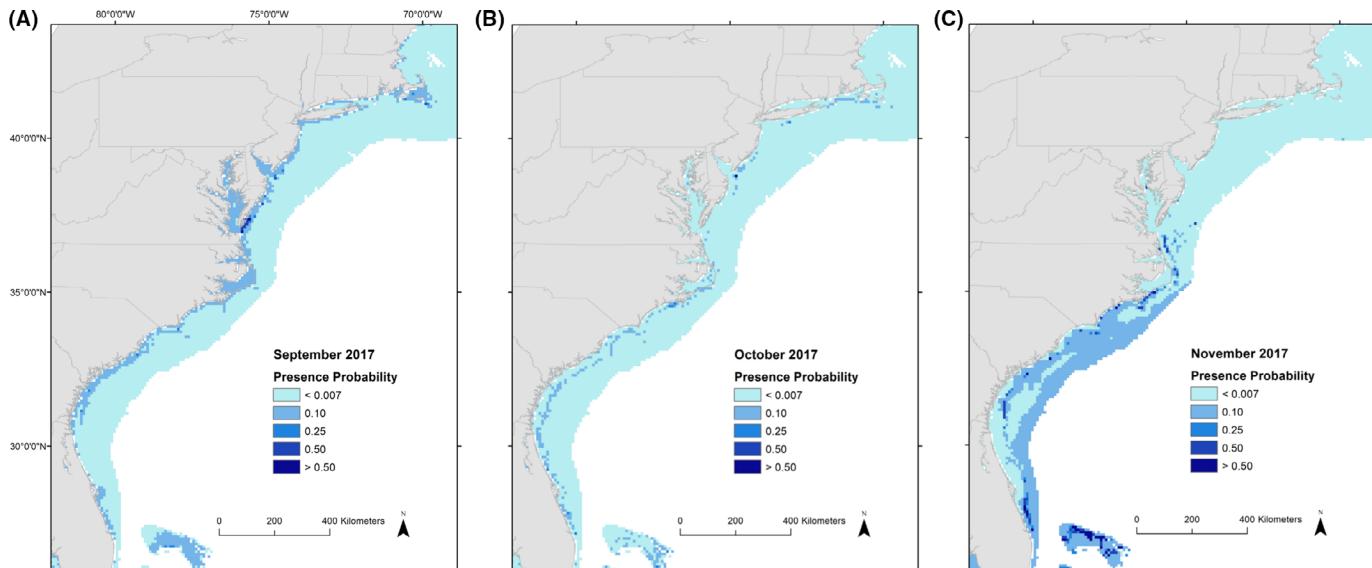
FIGURE 7. Mapped presence probability based on boosted regression tree modeling of juvenile Dusky Shark tag detections and satellite-recorded environmental data during **(A)** September 2017, **(B)** October 2017, and **(C)** November 2017.

of Chesapeake Bay and into North Carolina waters during the late fall and early winter. No tag detections were recorded from mid-December through mid-April during both 2016–2017 and 2017–2018, although detections of other tagged elasmobranchs at receivers south of North Carolina during this time period confirmed that receivers were available to detect the tagged Dusky Sharks (C.W.B. and T.H.C., unpublished data). The most likely explanation is that the tagged Dusky Sharks were distributed somewhere outside of acoustic receiver coverage, which is supported by predicted habitat distributions farther offshore during November. Larger juvenile and adult Dusky Sharks that were tracked using pop-off satellite tags in the Gulf of Mexico showed movements along the continental shelf edge and into pelagic waters (Hoffmayer et al. 2014), so offshore movements are possible for smaller juveniles. Tagged sharks appeared to return to North Carolina waters in mid-April and were detected in arrays off Maryland and Delaware by May. During the summer, some individuals remained in that area, while others were detected as far north as the south shore of Long Island, New York. By October 2018, the southern migration appeared to have begun. These findings are consistent with migratory patterns for juvenile Dusky Sharks as inferred from the timing and location of observed fishery captures and conventional tag and recapture locations from the NMFS Cooperative Shark Tagging Program, which showed a wide distribution along the continental shelf during fall and summer and a more restricted distribution south of Cape Hatteras during winter (NMFS 2017; Kohler and Turner 2019). The results are also consistent with telemetry studies of Dusky Sharks off western Australia, which showed seasonal migrations between biogeographic regions (Braccini et al. 2018).

Temperature and primary productivity (measured as Chl-*a*) consistently accounted for the strongest interactions in BRT model results, suggesting that these variables may influence Dusky Shark habitat selection. Areas of high primary productivity tend to aggregate prey species, increasing foraging opportunities for higher-trophic-level species (Benoit-Bird and McManus 2012). The ranges of temperature and primary productivity associated with an increased likelihood of Dusky Shark presence were also consistent across all seasonal and monthly models. Although the Chl-*a* range that was positively associated with Dusky Shark presence was low compared to all values measured in environmental data sets, Chl-*a* levels were among the highest available in coastal areas outside of estuaries where the tagged sharks were detected. Comparisons of model results between fall and summer and between months encompassing the southern migration from summer to winter habitats captured an apparent seasonal shift in the relative influence of temperature and productivity. Temperature was the most influential variable during fall

but decreased in relative influence during summer. During September, Chl-*a* accounted for nearly half of all tree splits; during October, depth was the most influential variable, while SST and Chl-*a* accounted for nearly equal percentages of splits. In November, SST was the most influential variable, accounting for nearly half of all tree splits. This may indicate a switch in which environmental conditions are prioritized by juvenile Dusky Sharks for habitat selection: during the late summer and early fall, when water temperatures within the range of the sharks' temperature preference are broadly distributed, they may be free to select areas of greatest foraging opportunity, whereas decreasing water temperatures during the late fall and early winter force the sharks to seek out optimal temperature ranges for transit or foraging. Habitat selection by highly migratory pelagic predators is largely driven by trade-offs between temperature and productivity (Block et al. 2011), and this is likely also the case for highly migratory coastal species. Areas where Dusky Sharks can optimize both temperature preference and foraging success are likely to be the most important habitats.

Tag detection locations, temperature sensor data, and spatial modeling suggested the importance of two distinct oceanographic features as juvenile Dusky Shark habitat: the Hatteras Bight and the Middle Atlantic Bight Cold Pool. The Hatteras Bight marks the transition area between temperate and subtropical marine biogeographic regions along the U.S. East Coast (Hayden et al. 1984; Fautin et al. 2010). In this area, the cold Labrador Current from the north and the warm Gulf Stream to the south meet in a location where the continental shelf is narrow, leading to high primary productivity during the winter (Lohrenz et al. 2002). This productivity may provide access to high prey densities for juvenile Dusky Sharks migrating south for the winter while still allowing the sharks to avoid temperatures below their thermal tolerances and may explain the tendency of juveniles to aggregate within Raleigh and Onslow bays. The Middle Atlantic Bight Cold Pool, stretching from southern Georges Bank to the northern Outer Banks, shows extreme temperature stratification vertically in the water column, particularly off the coast between Delaware and Chesapeake bays (Houghton et al. 1982; Lentz 2017). In this area, which covers a variable portion of the mid-continental shelf, cold water remaining from winter becomes trapped by the seasonal thermocline in the lower 20–60 m of the water column during the spring and summer (Houghton et al. 1982; Lentz 2017). During May and June, colder bottom waters associated with this feature are at their nearest point to shore in the vicinity of coastal Maryland and Delaware (Lentz 2017), an area that includes the acoustic arrays in the Delaware and Maryland wind farm areas. The lowest temperatures measured by V16T tags for the entire year were encountered by

Dusky Sharks detected in this area during May and June, but they did not match the lowest temperatures available during this time, which range between 8°C and 15°C in the Maryland array area (D.H.S., unpublished data). This may be evidence that juvenile Dusky Sharks are spending time just above the thermocline at the upper vertical edge of the Middle Atlantic Bight Cold Pool, which may provide access to both warmwater and coolwater prey species available in the area while avoiding the coldest temperatures. Cooling temperatures and late-summer storms cause destruction of the Middle Atlantic Bight Cold Pool through permanent destratification (Secor et al. 2019). September storms in 2017 and 2018 resulted in destratification and permanent declines of temperature throughout the water column in the Maryland array area (D.H.S., unpublished data), aligning with temperatures less than 20°C encountered by tagged sharks during October in each year. Spatiotemporal associations of sharks with the Middle Atlantic Bight Cold Pool warrant further investigation.

Dusky Shark habitats that were identified by our analyses overlap with human uses of the marine environment, including fisheries and offshore wind development. Coastal North Carolina has long been recognized as an important aggregation area and secondary nursery for Dusky Sharks, which are among the most common bycatch species in fisheries operating there (Jensen and Hopkins 2001; McCandless et al. 2014). This was a major reason for the establishment of the Mid-Atlantic Shark Closed Area (NMFS 2003). However, our results suggest that the timing of juvenile Dusky Shark arrival within this area may not precisely match the dates during which the closure occurs (January 1–July 31 of each year). Tagged Dusky Sharks were detected on receivers within the closed area beginning in November and were mostly detected outside of the area by May, 2 months prior to the start and end dates, respectively, of the seasonal closure (NMFS 2003). The Dusky Shark is not the only species that is protected by the Mid-Atlantic Shark Closed Area, but populations of Sandbar Sharks and other coastal sharks appear to be recovering (Peterson et al. 2017), so assessing potential changes in the closure's timing to more precisely match the presence of juvenile Dusky Sharks could be considered. Another potential area of concern is the location of potential wind farm sites in the portion of the Middle Atlantic Bight Cold Pool with which the tagged sharks were associated during the summer. Electromagnetic fields produced by undersea power cables connecting wind turbines to the shore have been found to affect fine-scale movements in skates within the immediate area around the cables, but they did not create barriers to movement (Hutchison et al. 2018). Construction noise created by pile-driving, turbine assembly, and associated vessel traffic may also affect habitat use by sharks and other species in the area. Conversely, structure created by wind turbines may provide long-term increased foraging opportunities for Dusky Sharks by attracting reef-associated fishes (Rooker et al. 1997). The effects of electromagnetic fields and wind farm construction and operation on large-bodied, highly migratory elasmobranchs have received little study and are still largely unknown.

Dusky Sharks and other coastal migratory elasmobranchs are among the most likely species to shift distribution in response to climate change (Hare et al. 2016). Summer and winter habitat areas where tagged Dusky Sharks were located are defined by local temperature and primary productivity ranges, which can be strongly influenced by long- and short-term climate effects, such as warming, increased storm events, increased thermal stratification of the water column, and changes in seasonal atmospheric pressure patterns. In the northwest Atlantic Ocean, temperature effects have been shown to more strongly impact species at higher trophic levels (Friedland et al. 2019) and have the ability to dramatically influence features like the Middle Atlantic Bight Cold Pool (Lentz 2017) as well as influence distributions of coastal fishes (Secor et al. 2019). There is already evidence that some elasmobranch species are expanding or shifting their distributions in response to changing ocean conditions (e.g., Bangley et al. 2018b), and such shifts are likely in other migratory elasmobranchs in the U.S. mid-Atlantic region (Haulsee et al. 2018; Ogburn et al. 2018). If thermal and productivity patterns are altered by climate change, Dusky Sharks are likely to shift their distributions poleward in response, as has been observed for other temperate mid-Atlantic species (Nye et al. 2009; Pinsky et al. 2013).

The distribution of tag detections and predicted presence likelihood fell within the known Dusky Shark distribution in the northwest Atlantic, and the migratory extent covered most of the area designated as EFH for juveniles (NMFS 2017). Temperature associations from both sensor tag data and BRT modeling results also fell within ranges that were previously identified in assessments of Dusky Shark habitat (McCandless et al. 2014; NMFS 2017). The consistency of our results with previously published data supports spatial modeling of acoustic telemetry detections paired with remotely sensed environmental data as a tool for making ecologically realistic predictions of potential habitat for migratory species at regional scales. However, there are a number of limitations to our analysis. The foremost is that acoustic telemetry relies on receivers to document the presence of tagged animals, which means that no data are available from locations without receivers and modeling results based on acoustic telemetry data may be biased by receiver deployment locations (e.g., mostly close to shore). This has been mitigated somewhat by leveraging acoustic receiver networks, which allow acoustic telemetry data to be recorded at a coastwide scale

in areas like the U.S. East Coast (L. M. Brown, paper presented at the Annual Meeting of the American Fisheries Society, 2012) and Australia (Udyawer et al. 2018). However, outer shelf and deepwater habitats may be challenging to cover with acoustic receiver arrays. For this reason, we spatially constrained our modeling results to the continental shelf, where environmental conditions and interactions are more likely to be similar to the nearshore areas where receivers were deployed. Future studies should also incorporate satellite-based telemetry methods to track Dusky Sharks beyond the detection range of acoustic receivers.

Inclusion of new data may also help to improve the performance of BRT modeling. Despite being robust to low sample sizes and zero-inflation (Elith et al. 2008), this modeling approach still required more presence records to resolve the models than were available during some months. In addition, low sample size for presence data in combination with gaps in satellite data decreased the likelihood that a given presence location would occur in an area where environmental data were recorded. Although spatial resolution differed between environmental data sets, this did not appear to affect overlap with telemetry locations. These issues with sample size caused us to limit our modeling efforts to seasons and months with at least 20 daily presence records. As data beyond the first year of tracking are collected, we expect that more detection days will be available either through expanded acoustic receiver coverage or combining data over multiple years.

We have identified environmental associations, migration phenology, and potential important habitat areas at a spatiotemporal precision that has not previously been achieved for Dusky Sharks in the northwest Atlantic Ocean. Our results also further highlight the value of networked acoustic telemetry arrays for studying the spatial ecology and movement patterns of coastal migratory fishes. This will help to guide future studies and fishery management measures focused on Dusky Sharks, and our approach may be helpful for management of other data-poor, highly migratory species.

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SUPPORTING INFORMATION

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