Loggerhead and Kemp's Ridley Sea Turtle Habitat Models for the Chesapeake Bay

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Cover Photo Credit:

A Kemp's ridley turtle (*Lepidochelys kempii*) is released with a satellite tag from the oceanfront in Virginia Beach, VA. The turtle (VAQS20182017) was hooked by a recreational angler, recovered by the Virginia Aquarium Stranding Response Program and tagged under a U.S. Fish and Wildlife Service permit to the National Marine Fisheries Service covering sea turtle stranding response activities in the Greater Atlantic Region. Photograph taken by Virginia Aquarium staff.

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Acronyms and Abbreviations

AUC	area under the curve
Bay	Chesapeake Bay
BRTs	boosted regression trees
cm	centimeter
CV	coefficient of variation
hSSM	hierarchical state-space model
kg	kilogram
m	meter

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1 Introduction

Previous satellite-telemetry studies funded by the United States Navy found that loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempii*) turtles that are seasonally resident in the Chesapeake Bay (the Bay) spend the majority of their time foraging (Barco et al. 2015; Barco et al. 2017), reaffirming that the Bay is a seasonally important foraging ground for these animals (Lutcavage & Musick 1985; Keinath et al. 1987; Seney & Musick 2005, 2007; Mansfield 2006; Mansfield et al. 2009). The Northwest Atlantic Distinct Population Segment of loggerheads, which the loggerheads found in Chesapeake Bay fall into, are listed as threatened under the Endangered Species Act (National Marine Fisheries Service 2011). Kemp's ridleys have a single population, nesting predominantly in the Gulf of Mexico, and are listed as endangered under the Endangered Species Act. Both species face numerous threats in the region, including but not limited to ship strikes from commercial, naval, and recreational fishing vessels; dredging activities for shipping channels and beach re-nourishment; commercial and recreational fishery bycatch; climate change; and naval training and testing activities (Barco et al. 2015).

To better understand the spatial distribution of habitat usage in the Bay by these species, the Navy funded home range analyses of both species based on extant satellite-tagging data for tags deployed from 2014 to 2018 (Barco et al. 2018). Foraging habitat for Kemp's ridley turtles was identified in the southwestern corner of Chesapeake Bay, the James and York rivers, and several other nearshore locations, though there was extensive variation in home range size and location among individuals (DiMatteo et al. 2020). Loggerhead foraging habitat was found primarily in the center of the Bay, into the waters of southern Maryland, with some additional habitat closer to shore (Barco et al. 2017). Like Kemp's ridleys, there was extensive variation in the size and location of individual home ranges.

A sensitivity analysis using the same satellite telemetry dataset and tag simulation found that not enough tags had been deployed on either species to identify all additional habitat likely to be present in the Bay (DiMatteo 2019). Given the funding and logistical constraints of deploying additional tags, habitat modelling was chosen as the approach to identify additional potential habitat for both of these species in the Bay.

Habitat models, in this case habitat suitability models using presence/absence data, can: 1) describe complex relationships among species and environmental covariates, 2) be extrapolated in space and time (with caution), and 3) provide insights into species' distributions. Many frameworks for habitat suitability models exist, including but not limited to generalized additive models, maximum entropy (presence-only models), and boosted regression trees. Here we use the machine-learning technique of boosted regression trees (BRTs, Elith et al. 2008) to create habitat suitability models for both species.

BRTs allow for the fitting of complex environmental relationships, explicitly explore covariate interactions, can include factors as covariates, and are robust to outliers in the dataset as well as missing covariate values (Elith et al. 2008). BRTs are a combination of regression trees, a type of decision tree model, and boosting technique, which produces a large number of simple tree models and then combines them to maximize predictive potential (Elith et al. 2008). These features make BRTs a good option for this dataset and location. Turtles may be responding to complex environmental cues that create ephemeral features which aggregate prey or create conditions advantageous to their physiology (Schofield et al. 2009; Howell et al. 2015). Turtles are ectotherms and their metabolism is linked to their body temperature (Spotila and Standora 1985). Chesapeake Bay is a complex estuarine environment with high variability in environmental conditions (Preston 2004; Werdell et al. 2009), increasing the potential for animals to react to complex environmental cues.

Based on previous home-range research for these species, we also explored the possibility that they are partitioning their habitat (e.g., using different resources), which may complicate conservation efforts, if animals are found in different areas of the Bay. If, for example, two species are using different habitat in the Bay, time and area closures meant to protect one species may shift potentially harmful activities into the habitat of the other species.

Green and leatherback turtles also utilize the Bay, though are much less common than Kemp's ridleys and loggerheads (Keinath et al. 1987). Little tracking has been performed on green turtles in the region and none on leatherbacks, making assessing these species in the context of loggerhead and Kemp's ridley habitat use impossible.

2 Methods

2.1 Turtle-tagging and satellite-telemetry data

Data were analyzed from tags deployed on 23 Kemp's ridleys and 11 loggerheads (**Table 1**). Details on capture and tagging methods can be found in Barco et al. (2015, 2017, 2018). Some animals that were tagged were excluded from the analysis: animals whose deployments were entirely outside the Bay; animals that spent fewer than five days in the Bay; animals tagged prior to 2014, which was the earliest year the selected environmental covariates were available; and one Kemp's ridley whose entire deployment was in a small inlet not covered by the environmental covariates.

Table 1. Summary of deployments retained in the analysis for both loggerheads and Kemp's ridley turtles. SCL-NT refers to length of the turtle measured as straight carapace length, notch to tip..

PTT	Release Date	Species	Size (cm; SCL-NT)	Mass (kg)	Source	# Argos Locations in Bay
132367	7/9/2014	Kemp's ridley	36.0	7.0	stranded-cold stun	79
138114	10/20/2014	Kemp's ridley	42.4	12.8	stranded-cold stun	48
138117	9/2/2014	Kemp's ridley	35.4	6.5	recreational bycatch - hooked	92
148886	5/29/2015	Kemp's ridley	51.0	18.0	wild capture	26
148887	5/15/2015	Kemp's ridley	59.0	41.0	wild capture	156
148889	5/16/2015	Kemp's ridley	45.0	16.4	stranded-cold stun	209

PTT	Release Date	Species	Size (cm; SCL-NT)	Mass (kg)	Source	# Argos Locations in Bay
150767	6/24/2015	Kemp's ridley	35.4	6.2	recreational bycatch - hooked	25
159707	5/19/2017	Kemp's ridley	39.3	8.1	recreational bycatch - hooked	228
159708	7/2/2016	Kemp's ridley	45.2	11.9	recreational bycatch - hooked	124
159709	7/26/2016	Kemp's ridley	49.4	16.3	recreational bycatch - hooked	111
169763	6/8/2017	Kemp's ridley	29.2	3.2	recreational bycatch - hooked	74
169764	6/17/2017	Kemp's ridley	32.1	4.4	recreational bycatch - hooked	145
169765	5/19/2017	Kemp's ridley	40.0	8.1	recreational bycatch - hooked	246
169767	5/5/2017	Kemp's ridley	44.1	11.9	recreational bycatch - hooked	169
169768	5/19/2017	Kemp's ridley	45.7	12.0	recreational bycatch - hooked	155
169769	5/24/2018	Kemp's ridley	38.9	7.8	recreational bycatch - hooked	39
169770	7/10/2017	Kemp's ridley	28.9	3.4	recreational bycatch - hooked	39
169771	5/31/2017	Kemp's ridley	30.1	3.2	recreational bycatch - hooked	78
175216	5/16/2018	Kemp's ridley	48.9	16.0	recreational bycatch - hooked	141
175218	5/16/2018	Kemp's ridley	42.6	10.6	recreational bycatch - hooked	119
175219	5/24/2018	Kemp's ridley	35.9	6.1	recreational bycatch - hooked	191
175220	6/20/2018	Kemp's ridley	36.8	6.1	recreational bycatch - hooked	56
175221	5/24/2018	Kemp's ridley	46.4	13.0	recreational bycatch - hooked	250
175222	6/4/2018	Kemp's ridley	37.1	7.0	recreational bycatch - hooked	90
108053	8/27/2013	loggerhead	66.5	44.5	recreational bycatch - hooked	119
120347	6/12/2014	loggerhead	73.6	75.5	stranded-cold stun	198
120348	3/16/2015	loggerhead	70.1	58.4	stranded-cold stun	465
132363	9/28/2013	loggerhead	70.4	52.0	recreational bycatch - hooked	125
138112	6/13/2014	loggerhead	60.4	33.0	stranded-cold stun	480

PTT	Release Date	Species	Size (cm; SCL-NT)	Mass (kg)	Source	# Argos Locations in Bay
148883	7/1/2015	loggerhead	72.5	ND	wild capture	238
148884	7/1/2015	loggerhead	65.1	ND	wild capture	101
148885	8/5/2015	loggerhead	89.8	ND	wild capture	120
175708	6/29/2018	loggerhead	69.3	45.4	recreational bycatch - hooked	129
175711	6/20/2018	loggerhead	31.5	3.2	recreational bycatch - hooked	116

Argos satellite locations for the remaining turtles were run through the Douglas filter (Douglas et al. 2012) to remove unrealistic locations by using settings recommended for hardshell turtles by the Turtle Expert Working Group (2009). These Argos location errors can be up to 5 kilometers (km) depending on the quality of the satellite fix, and Argos locations are not true animal locations. The Turtle Expert Working Group Douglas filter settings included parameters for the Maximum Redundant Distance filter and the Distance Angle Rate hybrid filter algorithm which were used to account for unrealistic animal speeds and turning angles.

Locations retained by the Douglas filter were processed using a hierarchical state-space model (hSSM), segregated by species, in order to create estimated locations at regular time intervals from the irregular Argos locations reported by the tags using the R package *bsam* (Jonsen et al. 2005; Jonsen 2016; R Core Team 2020). These estimated locations reduced spatial autocorrelation from reported locations caused by animal behavior and satellite coverage. An hSSM was selected because movement parameters are estimated jointly for all individuals, along with an individual effects parameter, allowing shorter deployments to benefit from the information in longer deployments. This assumes that animals' behavior is broadly similar, which we feel is reasonable given that animals were the same species and similar reproductive class based on carapace length (immature), engaged in similar behavior (foraging), and were in the same region.

We did not include a behavioral component in the hSSM to distinguish between traveling and area restricted search (ARS) behavior. Previous state-space modeling work funded by the Navy found that both species spent the majority time of their time in the Bay engaged in ARS movements, assumed to be foraging (Barco et al. 2015; Barco et al. 2017). This is consistent with the known ecology of the species in this area (Lutcavage & Musick 1985; Keinath et al. 1987; Seney & Musick 2005; Mansfield 2006; Mansfield et al. 2009). Given that few locations in the Bay will represent travelling behavior, we assume areas identified by the habitat model will represent foraging habitat.

A 6-hr time step was chosen as the interval between locations as this was the finest-scale time step that could be fit to the Kemp's ridley data. The loggerheads had more locations reported per day than the Kemp's ridleys, which would have allowed for a finer-scaled hSSM, but we opted to keep the intervals equal so that each deployment would have the same number of locations reported per day, regardless of species.

hSSM diagnostics were examined to ensure that Monte-Carlo Markov Chains were mixing, that parameters estimates were converging, and that autocorrelation between chains was acceptably low. Models for both species performed well, converging with 80,000 posterior samples for the Kemp's ridley model and 50,000 samples for the loggerhead model. Both models used 10,000 samples as an adaptation phase, and a span parameter of 0.2.

After state-space modeling, estimated locations from the hSSM were reviewed visually to ensure the resulting deployments were reasonable. Points on land were removed using the Global Self-consistent, Hierarchical, High-resolution Geography Database full-resolution shoreline (Wessel & Smith 1996). The remaining locations were used as presence locations for the BRT models, 2,738 for Kemp's ridleys and 2,247 for loggerheads (**Figure 1**).

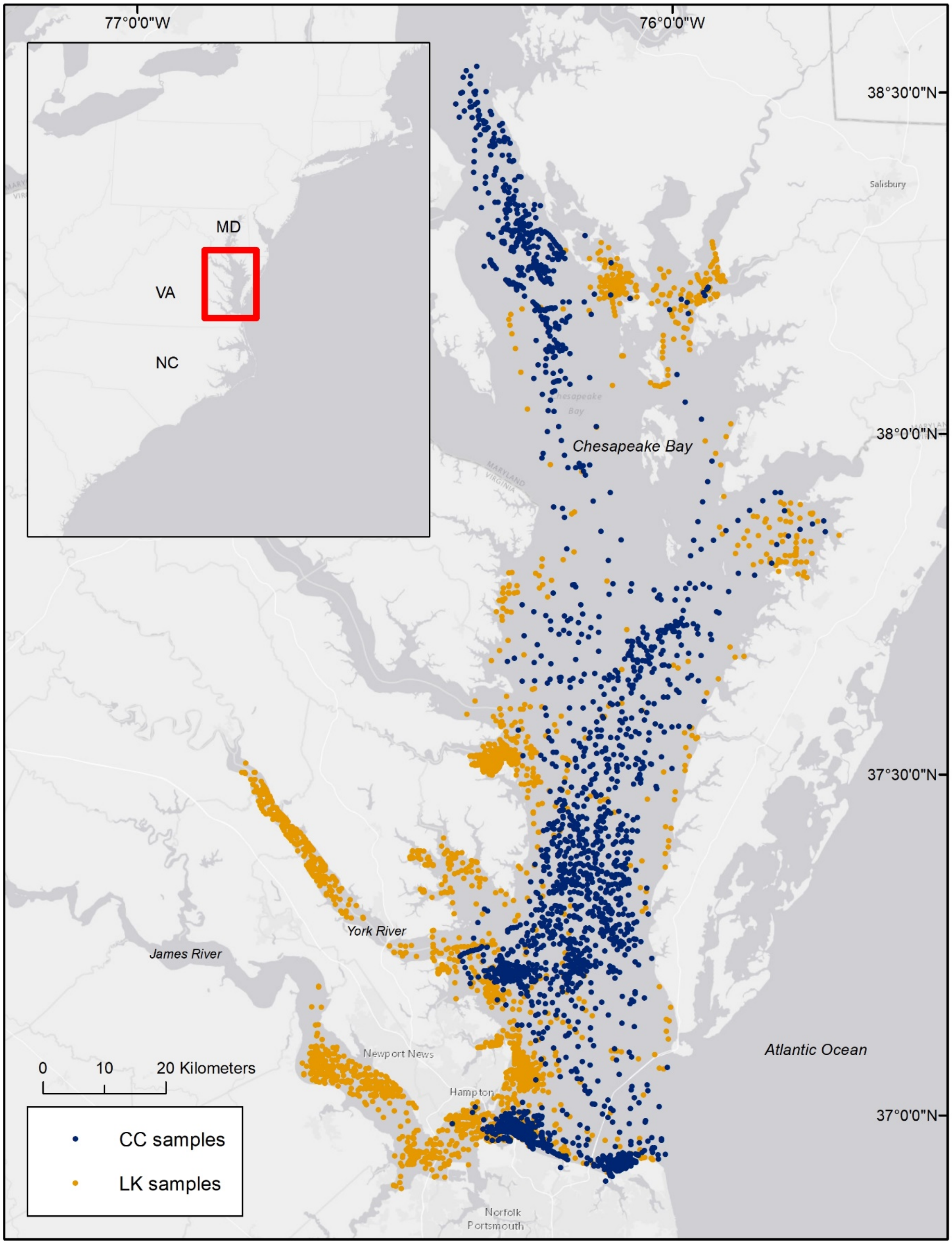

Figure 1. Loggerhead (CC) and Kemp's ridley (LK) locations used as presence points in the BRT models, as well as the high-resolution shoreline used to limit locations to being in-water.

2.2 Study area and environmental covariates

Our study area is the Chesapeake Bay, including Virginia and Maryland waters, and connected riverine systems as defined by the extent of the available bathymetry, salinity, and temperature covariates. This includes areas farther north and farther upriver than either species has been sighted. We wanted to include these areas to see if suitable habitat existed and turtles were not utilizing them, or if environmental conditions were different from where turtles frequent.

We used a mix of static and dynamic physical covariates, habitat maps, and temporal factors as candidate covariates (**Table 2**). Biological covariates such as chlorophyll a were not available at appropriate geographic and temporal scales and were not considered. We did not consider remotely sensed or ocean model covariates as the available products were at too coarse a spatial resolution, generally 5 km^2 or greater, to reflect fine-scale habitat use in the topographically complex Bay.

Sea turtles have been shown to be associated with ephemeral habitat features (Howell et al. 2015) that may have higher quality or quantity of prey. Hardshell turtles are also physiologically limited by temperature and will seek to maintain their body temperature or else risk becoming cold stunned (Spotila and Standora 1985). Because the Bay is a highly dynamic environment, we wanted to make predictions on the finest temporal and spatial resolution possible to reflect potential fine-scale features.

The Chesapeake Bay Operational Forecast System (CBOFS) provides daily readings of temperature (°C) and salinity (parts per thousand [ppt]) from sampling stations within the Bay and some of the major adjoining river systems. Both temperature and salinity are potentially important environmental condition for turtles and their prey, which in the Bay are mainly benthic invertebrates (Byles 1988; Seney & Musick 2005; Barco et al. 2015) for both species being modeled here.

We derived temperature and salinity rasters from CBOFS in situ sensors (n=157). We took the noon reading from each sensor and used the diffusion interpolation tool in ArcGIS 10.7 (Esri 2019) to interpolate values to match the extent of high-resolution bathymetry data for the region. The resulting daily rasters had a resolution of 500 meters (m). Though turtles may be reacting to changes in the environment on temporal scales finer than a day, we were not confident in our ability to model suitable habitat at that temporal resolution.

CBOFS data were not available prior to July 2014 so all locations prior to 2014 were removed from the analysis. Rasters were processed for the months of May–November (with the exception of May and June 2014), the months with turtle locations present in the Bay. Turtles can enter the Bay as early as mid-April (Mansfield et al. 2009) but none of these animals were in our tag record so we opted not to model this month. Turtles usually attempt to depart the Bay by the end of November to avoid being cold-stunned as water temperatures drop.

Temporal covariates, day of year and year, were derived from the timestamp of estimated locations. We included these covariates to account for intra- and inter-annual variability in habitat not accounted for by other covariates. Latitude was also included as a covariate to account for north-south variability not captured by other covariates.

We also assessed static maps of benthic habitat (National Marine Fisheries Service 2020) and submerged aquatic vegetation (Lefcheck et al. 2018) on the assumption that these may reflect important habitat for prey species. Ultimately, we dropped these covariates from consideration as there were many missing values compared to the extent of other available covariates and the submerged aquatic vegetation data had missing years (the benthic habitat map did not vary temporally). Even though BRTs are generally robust to missing covariate values, here the missing data were extensive both spatially and temporally.

Table 2. Summary of available covariates for the boosted regression tree models.

Covariate	Type	Resolution	Source
bathymetry	physical	1/3 arc second (500 m)	NOAA/NOS Chesapeake Bay Bathymetric Digital Elevation Model (mean lower low water, NCEI 2017)
surface temperature	physical	daily, 500 m	Chesapeake Bay Operational Forecast System
salinity	physical	daily, 500 m	Chesapeake Bay Operational Forecast System
year	temporal	NA	NA
day of year	temporal	NA	NA
latitude	spatial	meter	NA

2.3 Boosted Regression Trees

Interpolated animal locations from the hSSMs for loggerheads (*n*=2,247) and Kemp's ridleys (*n*=2,738) were used as presence data for their respective boosted regression tree models.

The BRTs require absence data to fit the model. Because we were using satellite-tag-derived locations for presence data, confirmed absences did not exist for our study. Pseudo-absences were generated in one of two ways:

1) Random absences equal to the number of presence samples were created by selecting a random location on a random day from within the study area and time period. Using the same number of presence and pseudo-absence locations has been shown to have the best predictive performance in machine-learning techniques such as BRTs (Barbet-Massin et al. 2012). Random locations were drawn from the centroids of raster cells of the bathymetry covariate. Using randomly generated pseudo-absences assumes that animals are not distributed randomly in the study area and that the selected covariates will be able to distinguish between the random absences and the true habitat of the target species (Hirzel et al. 2001). A separate set of random absences was generated for the Kemp's ridley and loggerhead datasets.

2) Target-group absences, where confirmed presences of a related but distinct species are used as absences (Phillips et al. 2009). Target-group absences have been shown to outperform

randomly generated pseudo-absences in some cases (Cerasoli et al. 2017). Here we used loggerheads for absences in the Kemp's ridley model, and vice-versa. Target-group absences were unweighted, as the number of locations of Kemp's ridley and loggerhead turtles were similar. The target group absence group method assumes that the species are utilizing distinct habitats within the study area. Previous home range analyses indicated that this may be the case (Barco et al. 2018).

We started the modeling process by fitting exploratory models with random absences that included all possible covariates and examining covariate interactions and contributions to the model. For covariate pairs that were highly correlated, the covariate with a lower contribution to the model was removed to simplify the models. In this exploratory phase, tree complexity, learning rate, and bag fraction, the primary parameters for adjusting how BRTs are fit, were adjusted manually to improve model performance.

Model performance was assessed by examining residual deviance, coefficient of variation (CV), and the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. Respectively, these assess the explanatory power of the model, the associated uncertainty, and true positive rate compared to the false positive rate at various thresholds.

Sample predictions for random days, the finest temporal scale of the available covariates, were made throughout the exploratory modeling phase to assess whether predictions contained obviously spurious artifacts. If a covariate was causing clearly unrealistic predictions, it was dropped from subsequent models.

After the exploratory phase, the retained covariates were used to create four final models for each combination of species and absence generation method—Kemp's ridley with random absences, Kemp's ridley with target-group absences, loggerhead with random absences, and loggerhead with target-group absences—in a more systematic fashion. A set of models was generated for each final model, with tree complexity, learning rate, and bag fraction being systematically changed between commonly used values for each (Elith et al. 2008): 1, 2, and 3 for tree complexity; 0.1, 0.05, 0.01, 0.005, 0.001, and 0.0005 for learning rate; and bag fraction values of 0.1-0.9 in increments of 0.1. This resulted in a total of 162 candidate models, based on all possible combinations of the parameter values.

The final models were selected from the candidate models by assessing residual deviance, coefficient of variation (CV), and the area under the curve (AUC) of the receiver operating characteristic (ROC) curve, which is an indication of the models' ability to make correct predictions. If one candidate model did not score the best on all three metrics, professional judgement was used to assess the relative quality of top-scoring models and make the final selection. The selected final models all had at least 1000 trees (Elith et al. 2008). Afterwards, we compared final models between the two absence-generation methods and selected the better of the two to carry forward into the analyses described subsequently. This selection was made by examining both model diagnostics and a qualitative assessment of the resulting predictions.

2.4 Important habitat and habitat partitioning

Often, habitat suitability models are predicted for a single time period, with habitat suitability values ranging from zero (poor habitat) to one (excellent habitat). These habitat suitability scores can be subsequently classified into habitat versus non-habitat by selecting a cutoff value that maximizes the ratio of true positives to true negatives predicted by the model (Bradley 1997).

In our case, we were interested in assessing habitat quality over the entire period of the study, which covered five seasons from 2014 to 2018. Given the fine temporal scale of available covariates relative to the length of the study and our assumption that turtles utilized ephemeral habitat based on prey distribution and physiological requirements, averaging habitat suitability scores over many days did not seem reasonable. This would have the effect of 'washing out' suitable habitat as conditions changed day to day.

Instead, we assessed the number of 'habitat days' present in locations in the Bay at various temporal scales. We defined habitat days as the number of days suitable habitat was found in each predicted location within the Bay. For each final model, habitat suitability was predicted for each day within the study period. They daily habitat suitability surfaces were reclassified into habitat and non-habitat using a cutoff value to maximize the ratio of true positives to true negatives predicted by the model.

The cutoff value was determined by randomly splitting the modeling data sets (presences and random absences) into training (70%) and testing (30%) datasets. The model was then fit with the training data and used to predict the testing data, which allowed the cutoff value (Bradley 1997) to be determined. This process was repeated ten times and the cutoff value from the ten replicates was averaged and subsequently used to reclassify the daily prediction rasters. This process was performed independently for each of the four final models.

This process yielded a set of rasters representing daily habitat within the Bay, classified as 1 – habitat, or 0 – non-habitat. We summed these rasters by month, year, and across all days to assess the number of days suitable habitat could be found in a location. Higher numbers of 'habitat days' were an indicator of better habitat, with suitable conditions found there more often than elsewhere.

Lastly, the overall habitat-days analysis for each model was reclassified into important habitat. Important habitat was defined as the quartile of locations (raster cells) with the highest number of habitat days. This provided a map of the most suitable habitat areas within the Bay, for each species, over the entire study period. These maps were then used to assess habitat partitioning between the two species.

Habitat partitioning was examined using three different metrics: Schoener's D (Schoener 1968), Hellinger's-based I (van der Vaart 1998; Warren et al. 2010), and Syrjala's test (Syrjala 1996). Schoener's D calculates the range of a species based on probability distributions of abundance over a set of locations and calculates niche overlap based upon species abundance in those locations. Hellinger's I is based on probability distributions without the assumptions of

Schoener's D (Warren et al. 2010; Hosseinian Yousefkhani et al. 2016). Syrjala's test assesses whether two distributions are equivalent, invariant of abundance. For our purposes we assumed habitat days corresponded proportionally to species occupancy and converted the overall habitat-days rasters to proportional occupancy by summing all cells and then dividing all cells by that sum. It is unlikely that habitat days corresponded directly to occupancy, but we could not test this assumption without extensively surveying the Bay.

2.5 RESULTS

2.5.1 Boosted Regression Trees

Our exploratory models indicated that day of year was highly correlated with temperature and that latitude was highly correlated with salinity. Additionally, models that included latitude only predicted suitable habitat at latitudes where animals were located. Because of these factors we opted to drop these two covariates, day of year and latitude, from consideration in the final models. While BRTs can include correlated covariates, we preferred to limit the complexity of models as well as to preferentially include covariates related to habitat conditions where possible.

Upon examination of exploratory models that included year as a covariate, it appeared that predictions were more closely related to the number of animal locations in that year than underlying changes in environmental conditions. Because we did not have similar numbers of animals tracked or locations in each year, or a way to reasonably standardize effort between years, we opted to drop year as a candidate covariate.

This left temperature, salinity, and bathymetry as available covariates. For each combination of species and absence-generation method, BRT parameters were systematically varied, and the best model was selected based on assessing residual deviance, CV, and AUC (**Table 3**). The best model for all four combinations included all three remaining covariates.

Table 3. Best models for each combination of species and absence generation method, including BRT parameters, residual deviance, CV, and AUC. Values with an asterisk indicate that they were the best from all evaluated models.

Species	Pseudo-absence generation method	BRT Parameters			Model Assessment Values			
		tree complexity	learning rate	bag fraction	residual deviance	CV	AUC	best number of trees
Kemp's ridley	random	3	0.05	0.8	0.46	0.62*	0.94*	1,250
	target group	3	0.05	0.4	0.13	0.30	0.98*	2,750
Loggerhead	random	3	0.05	0.4	0.36	0.64*	0.93*	2,900
	target group	3	0.05	0.2	0.14	0.30	0.98*	3,100

For Kemp's ridleys, the model with randomly generated pseudo-absences was selected. Even though the target-group absence model performed better when examining the model assessment values, on qualitative review of the predictions, the target-group absence model predicted most of the suitable habitat north of the Choptank River in Maryland, much farther north than Kemp's ridley turtles have been detected previously. Little suitable habitat was detected in the southern Bay. We felt this did not accurately reflect either the known ecology of the species or the distribution based on stranding data.

Based on the functional plots of covariates, Kemp's ridley turtles showed a preference for depths shallower than 15 m, temperatures ranging from 17 to 28°C, and salinities of 15–28 ppt (**Figure 2**), consistent with known ecology and previous studies of Kemp's ridleys within the Bay. Each of the three covariates had relatively equal importance in the model: bathymetry – 37.3%, temperature – 31.7%, and salinity – 31%.

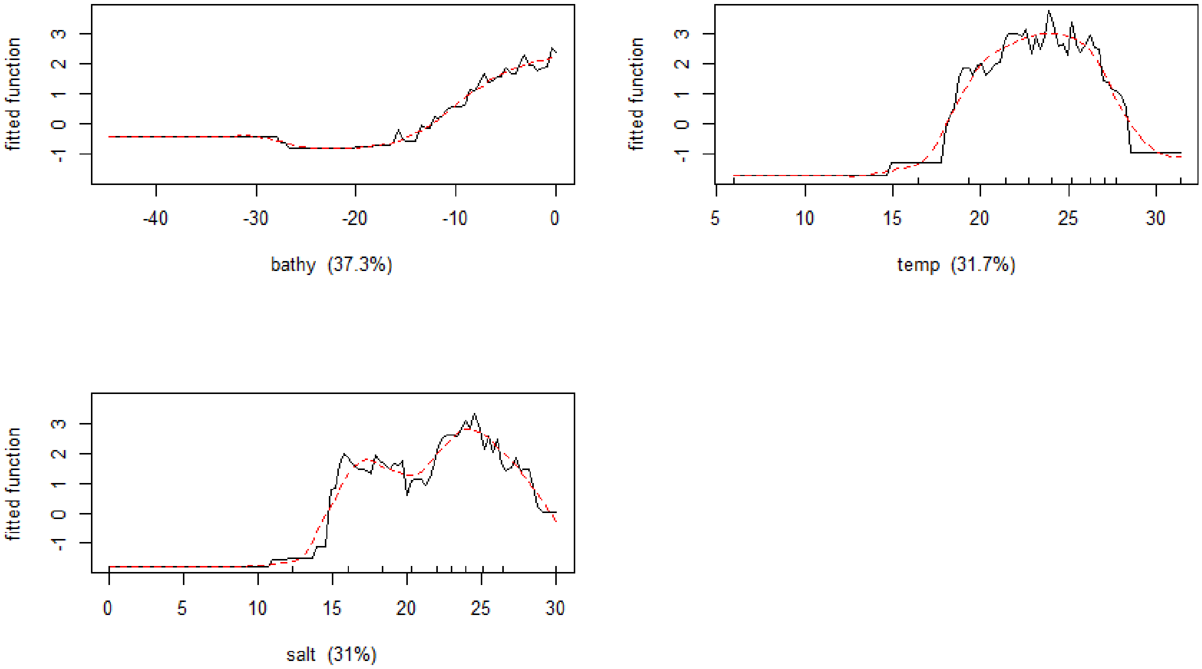

Figure 2. Functional plots and relative importance to the model of covariates for the Kemp's ridley BRT model using randomly generated pseudo-absences. Red dashed lines are fitted smooths of the functional relationships. Bathy = bathymetry (m), temp = temperature (°C), and salt = salinity (ppt).

For loggerheads, the model with target-group pseudo-absences was selected. The target-group model performed better than the random model when looking at model assessment values (**Table 2**). In the qualitative assessment, both models predicted similar extents of suitable habitat, but the target group model predictions were more compact and consistent across time periods.

Based on the functional plots of covariates, loggerheads showed a preference for depths deeper than 10 m, temperatures warmer than 25°C, and salinities greater than 15 ppt (**Figure 3**). This contrasts with Kemp's ridleys which preferred shallower waters and a more defined temperature range. For loggerheads, bathymetry was the most important covariate (43.6%), followed by salinity (29.5%), and temperature (26.9%).

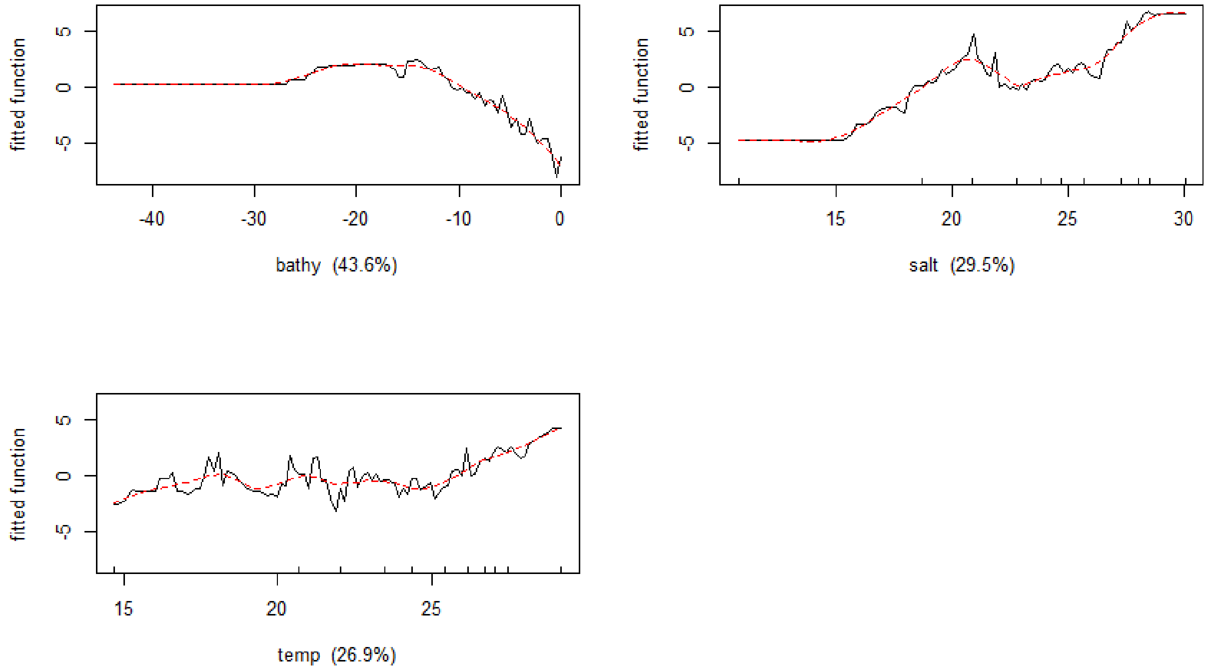

Figure 3. Functional plots and relative important to the model of covariates for the loggerhead BRT model using randomly target group absences. Red dashed lines are fitted smooths of the functional relationships. Bathy = bathymetry (m), temp = temperature (°C), and salt = salinity (ppt).

2.6 Important habitat and habitat partitioning

For the Kemp's ridley model, a cutoff value 0.48 was used to partition daily habitat suitability predictions into habitat versus non-habitat. Values less than or equal to 0.48 were classified as non-habitat, and values greater than 0.48 were classified as habitat, which maximized the ratio of true positive to true negative predictions in ten tests where Kemp's ridley locations and randomly generated absences were randomly split into training and testing data sets.

Aggregating the daily habitat predictions by year, we saw the year with more suitable habitat days, both total number of days and total area, was 2017 and the year with the least suitable habitat was 2014 (**Figure 4**). In all years, habitat was largely found in coastal areas of the Bay characterized by shallow depths. Some habitat did occur in Maryland Chesapeake Bay waters, although the number of suitable habitat days generally decreased with increasing latitude, as salinity decreased.

Aggregating the daily habitat predictions by month, we saw the most suitable habitat, both total number of days and total area, in June and October and the least in November (**Figure 5**). In general, suitable habitat was first found in the southern Bay, extending northward into Maryland as the summer progressed, and retreating into the southern Bay in November. These latitudinal shifts in prediction were driven largely by temperature, which peaks in mid- to late summer. The dip in predicted habitat suitability in July and August was likely caused by the model predicting

Kemp's ridleys do not prefer habitat warmer than 28°C. Again, we saw most suitable habitat predicted in shallow, coastal regions of the southern Bay, extending north into Maryland in peak months.

Aggregating all the daily habitat predictions into a single surface, we found the areas with the highest suitability had over 700 days where suitable habitat was found over the course of the study period, or over 120 per year. The areas with the highest number of habitat days were in coastal Virginia waters characterized by shallow depths, moderately high temperature, and higher salinity than the northern reaches of the Bay. Some suitable habitat was identified in Maryland waters, but it was, in general, predicted to be less suitable than the lower and middle portions of the Bay in Virginia. Almost no important habitat (top quartile of habitat days by grid cell), was identified in Maryland waters. The total predicted important habitat covered 2,808 km^2 (**Figure 6**) and was primarily located in nearshore areas of the southern Bay and the James and York Rivers.

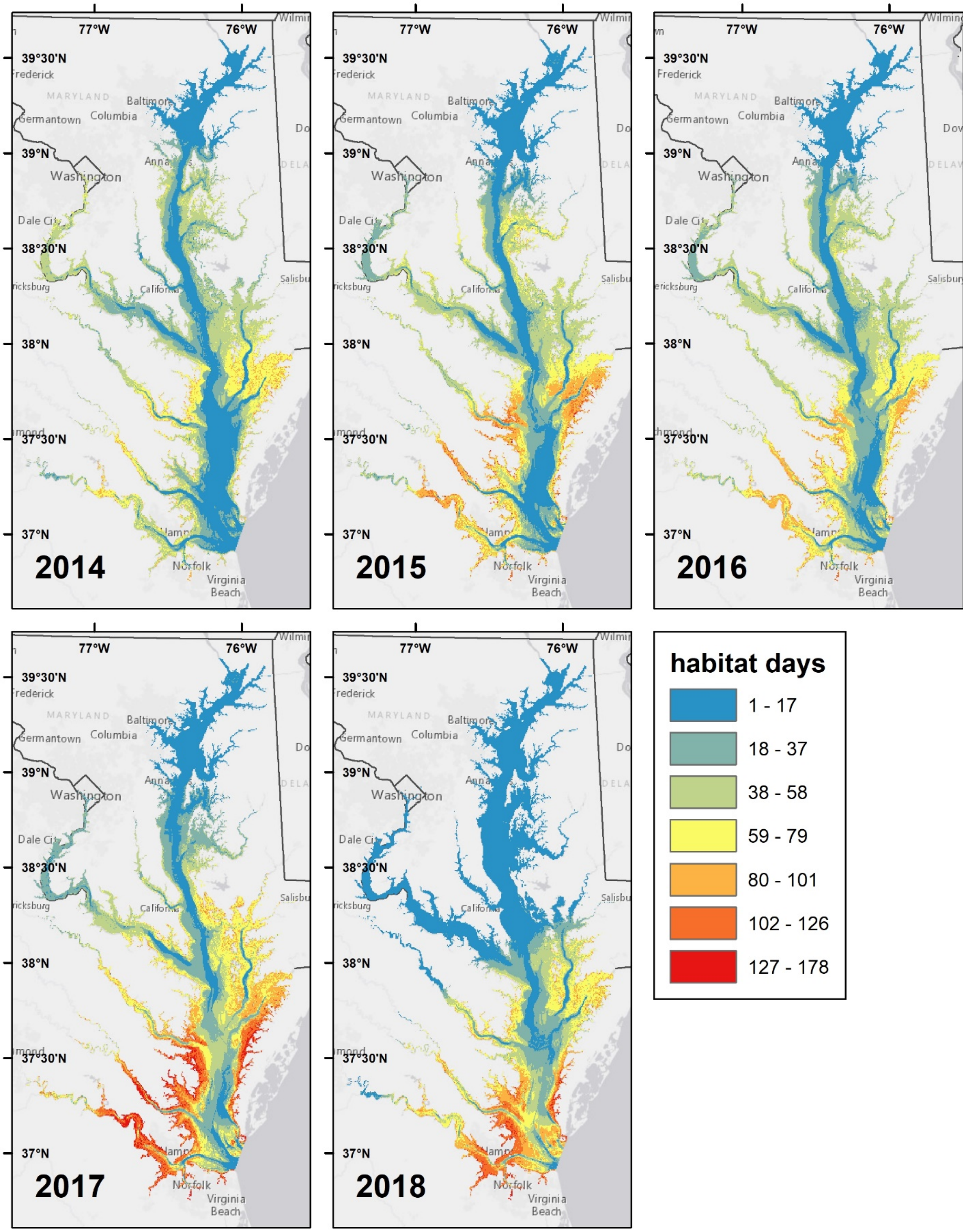

Figure 4. Number of suitable habitat days by year for the Kemp's ridley using the random pseudo-absence model.

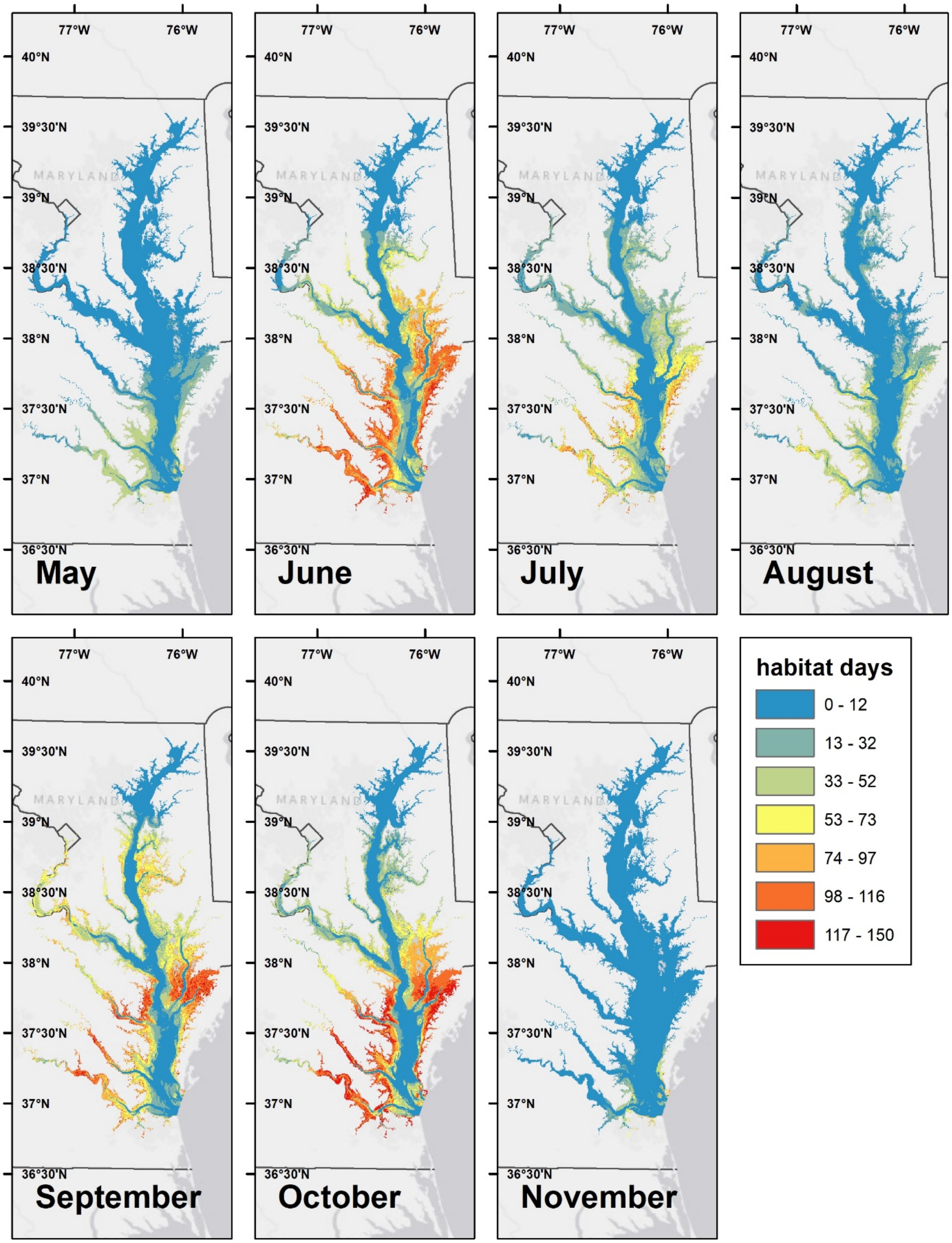

Figure 5. Number of suitable habitat days by month for the Kemp's ridley turtle using the random pseudo-absence model.

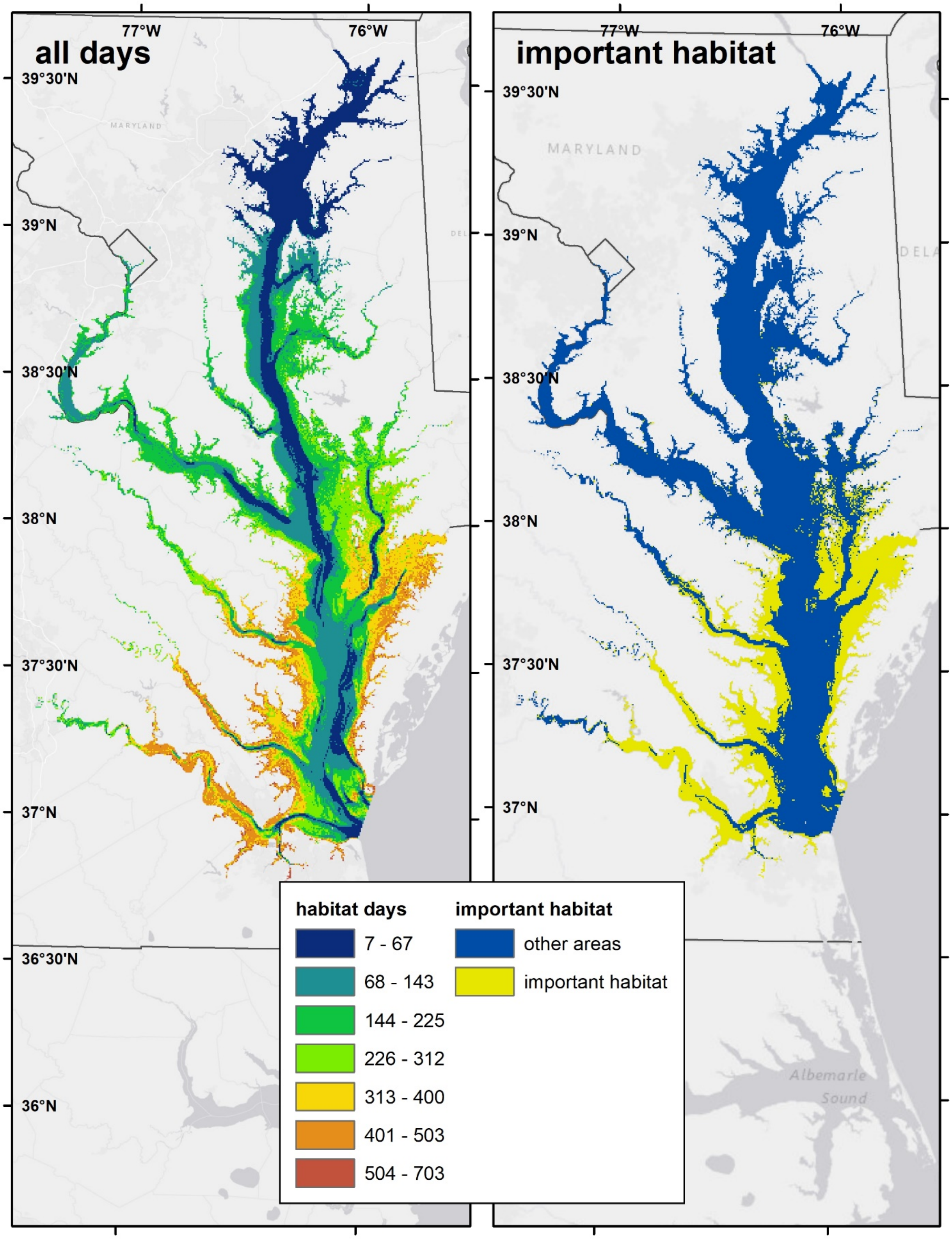

Figure 6. Number of suitable habitat days across the entire study period (2014–2018) and important habitat for the Kemp’s ridley random pseudo-absence model.

For the loggerhead model, a cutoff value 0.46 was used to partition daily habitat suitability predictions into habitat versus non-habitat. Values less than or equal to 0.46 were classified as non-habitat, and values greater than 0.46 were classified as habitat, which maximized the ratio of true positive to true negative predictions in ten tests where loggerhead locations and target group absences were randomly split into training and testing data sets.

Aggregating the daily habitat predictions by year, we saw the most suitable habitat, both total number of days and total area, in 2015, although 2016 and 2017 were similar, and the least in 2014 (**Figure 7**). The similarity between years was driven by the importance of bathymetry to the model, which was invariant between years. In all years, habitat was largely found in deeper, southern areas of the Bay. Some habitat did occur in Maryland waters and inland into some of the larger rivers, though the number of suitable habitat days generally decreased with increasing latitude, as salinity decreased. Riverine habitat appeared to be driven by depth, as shallower rivers did not have suitable habitat predicted.

Aggregating the daily habitat predictions by month, we saw the most suitable habitat, both total number of days and total area, in August and the least in June (**Figure 8**). In general, suitable habitat was in the southern Bay in spring and early summer, extending northward into Maryland as the summer progressed, and retreating into deeper areas in November. In July-September, habitat was predicted farther north than loggerheads are generally seen. This is likely driven by the importance of depth to the model and loggerhead's occurrence in less saline conditions compared to Kemp's ridleys (**Figures 2 and 3**). In the southern Bay, shipping channels, which are dredged, were clearly highlighted as habitat as in all months except July and August (**Figure 8**).

Aggregating all the daily habitat predictions into a single surface, we found the areas with the highest suitability had over 1,008 days where suitable habitat was found over the course of the study period, or over 200 per year. The areas with the highest number of habitat days were in the southern, central Bay with the deepest depths, moderately high temperature, and relatively higher salinity. Some suitable habitat was identified in Maryland waters, but that area, in general, was predicted to be less suitable than lower portions of the Bay. The small amount of important habitat found in Maryland waters was limited to deep areas in the central Bay and the central reaches of a few larger rivers. The total predicted important habitat covered 2,775 km^2 (**Figure 9**) and was predominantly in the southern, central Bay.

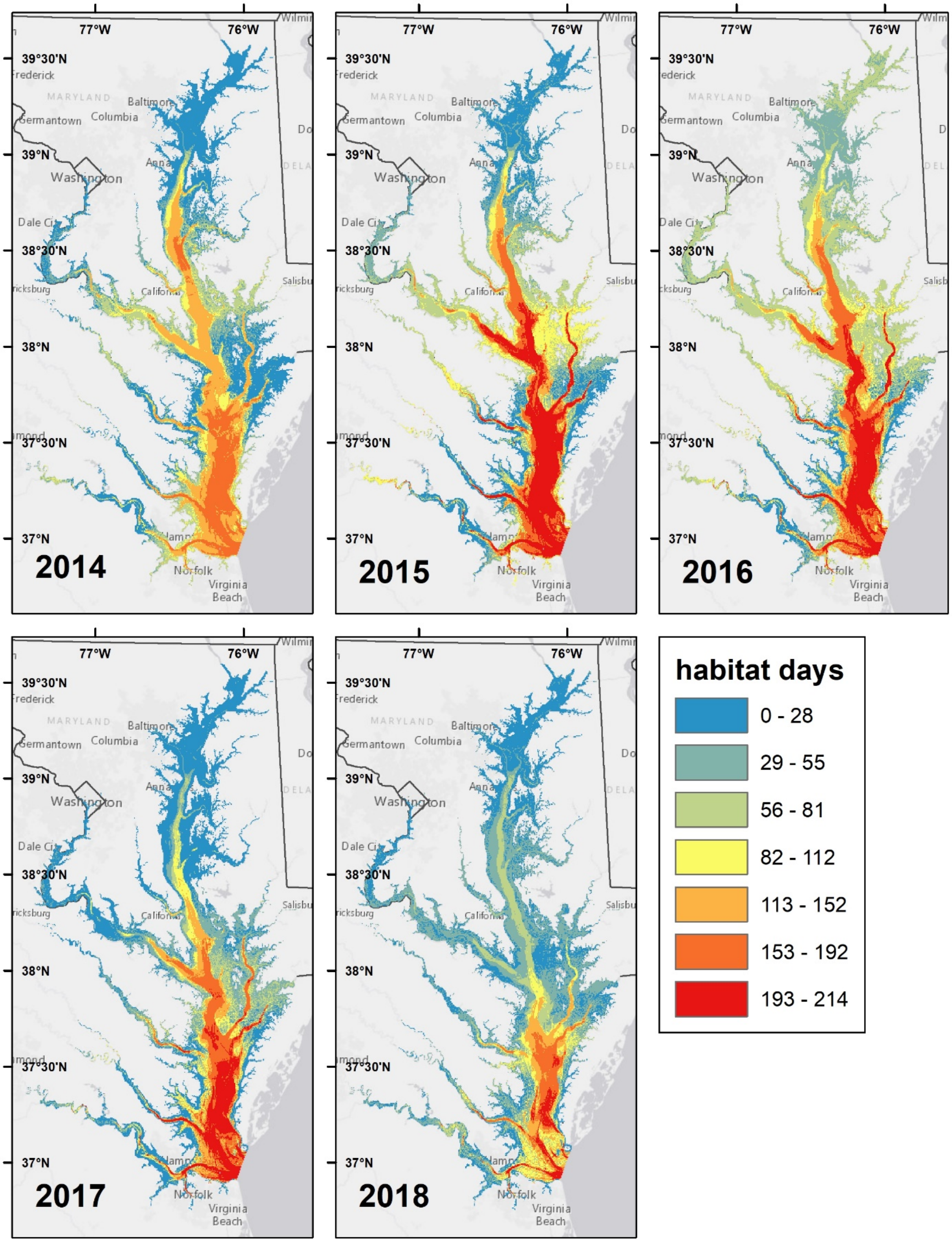

Figure 7. Number of suitable habitat days by year for the loggerhead turtle using the target-group absence model.

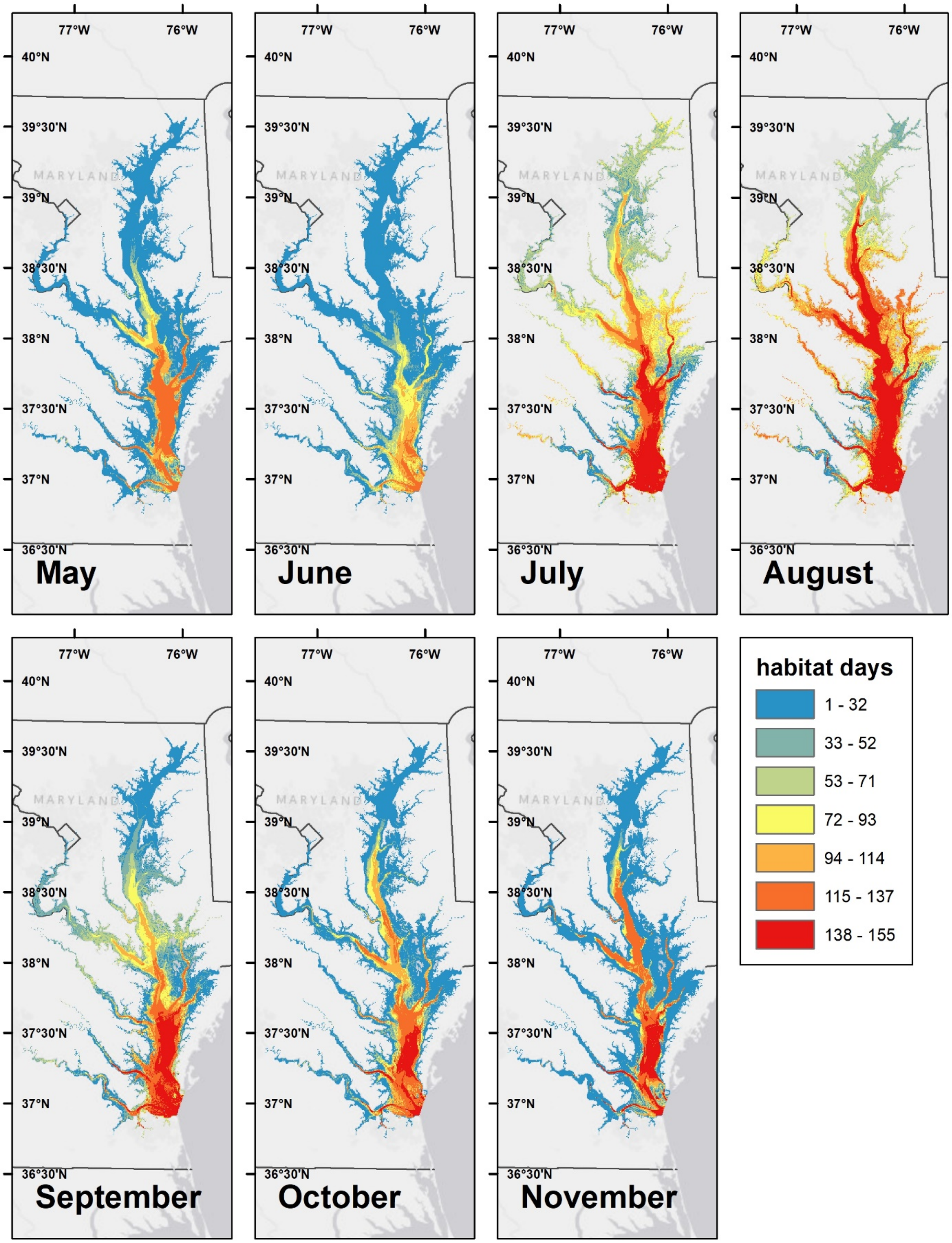

Figure 8. Number of suitable habitat days by month for the loggerhead turtle using the target-group absence model.

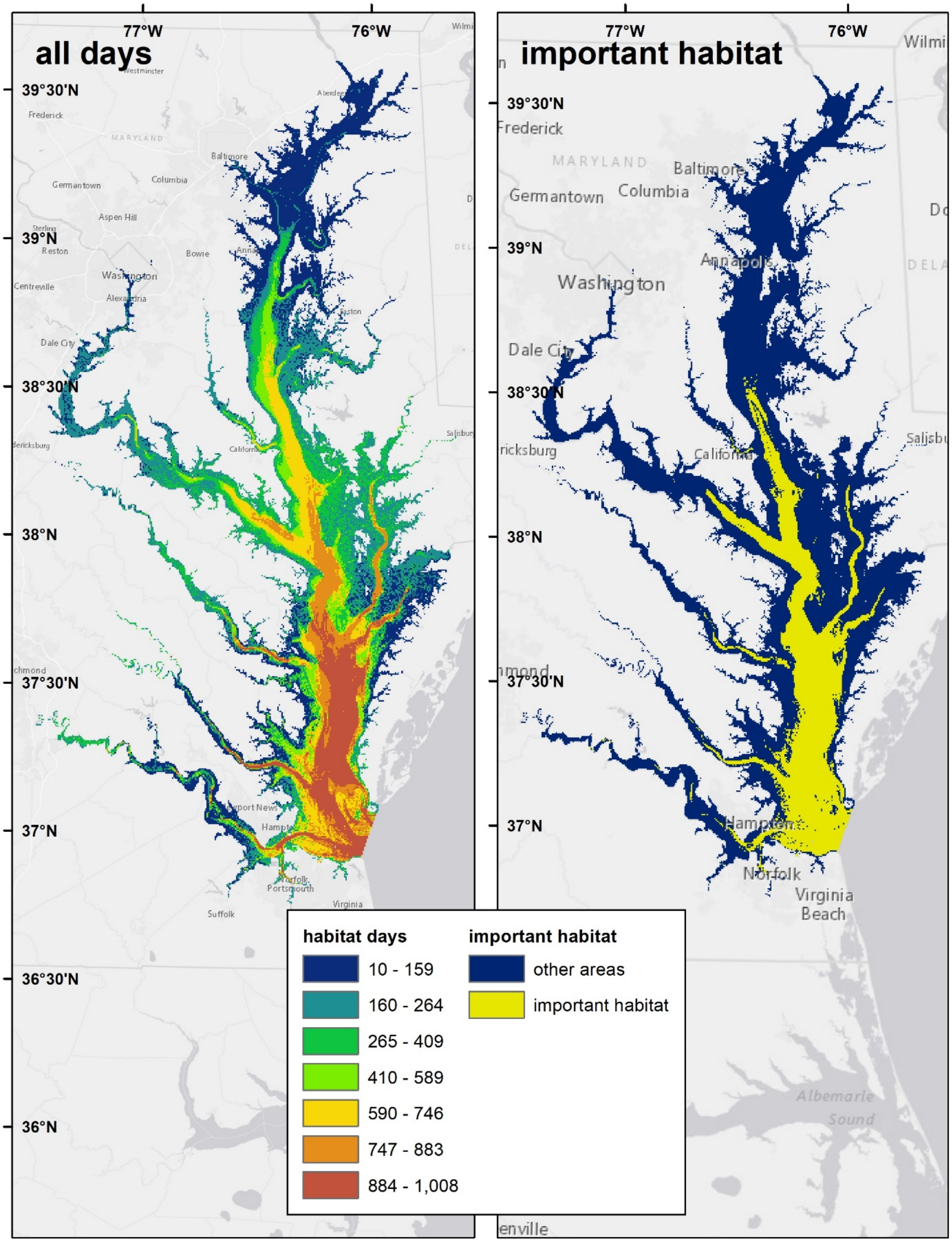

Figure 9. Number of suitable habitat days across the entire study period (2014–2018) and important habitat for the loggerhead turtle using the target-group absence model.

Comparing the Kemp's ridley randomly generated pseudo-absence model and the loggerhead target-group absence model, the Schoener's D score was 0.52 and Hellinger's Distance (I) was 0.82. These scores indicate there is some evidence that these two species are inhabiting different areas.

The Syrjala's test *P* values were less than 0.0001 for both the Cramer-von Mises and Kolmogorov-Smirnov tests (1000 permutations). Rejection of the null hypothesis indicates that the spatial distribution of the two species is significantly different. If we assume our habitat model accurately represents spatial distribution in the region, this is strong evidence that the species are partitioning habitat and using different resources. Overlaying animal locations on top of predicted habitat (**Figures 10 and 11**), the assumption that our models reflect species' distributions appears to be reasonable.

Considering the evidence from the D and I metrics and Syrjala's test, we propose there is habitat partitioning occurring between these two species, even given the assumption that our habitat suitability models are equivalent to occupancy (which would have to be derived from surveys).

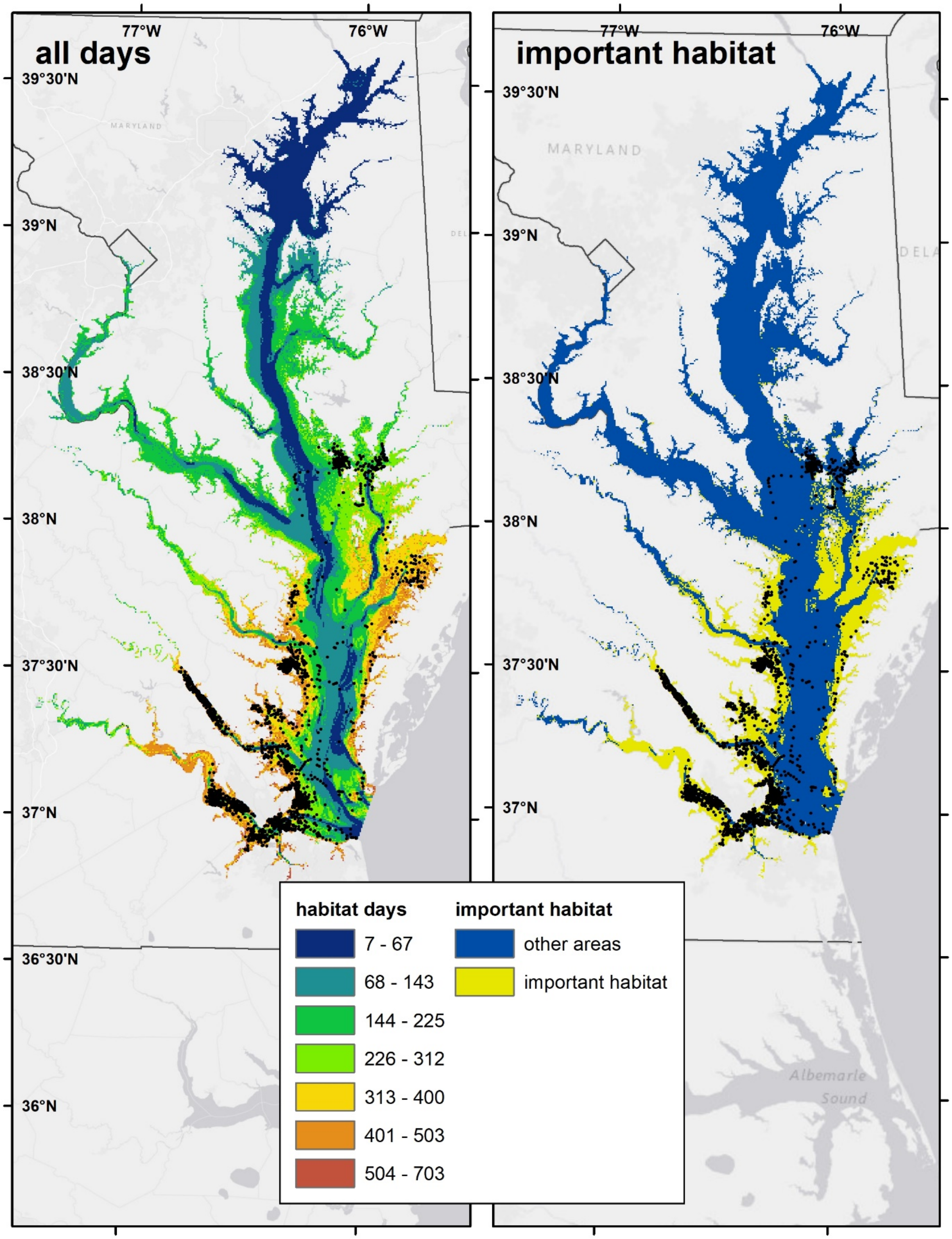

Figure 10. Number of suitable habitat days across the entire study period (2014–2018) and important habitat for the Kemp's ridley turtle using the randomly generated pseudo-absence model with hSSM locations overlaid.

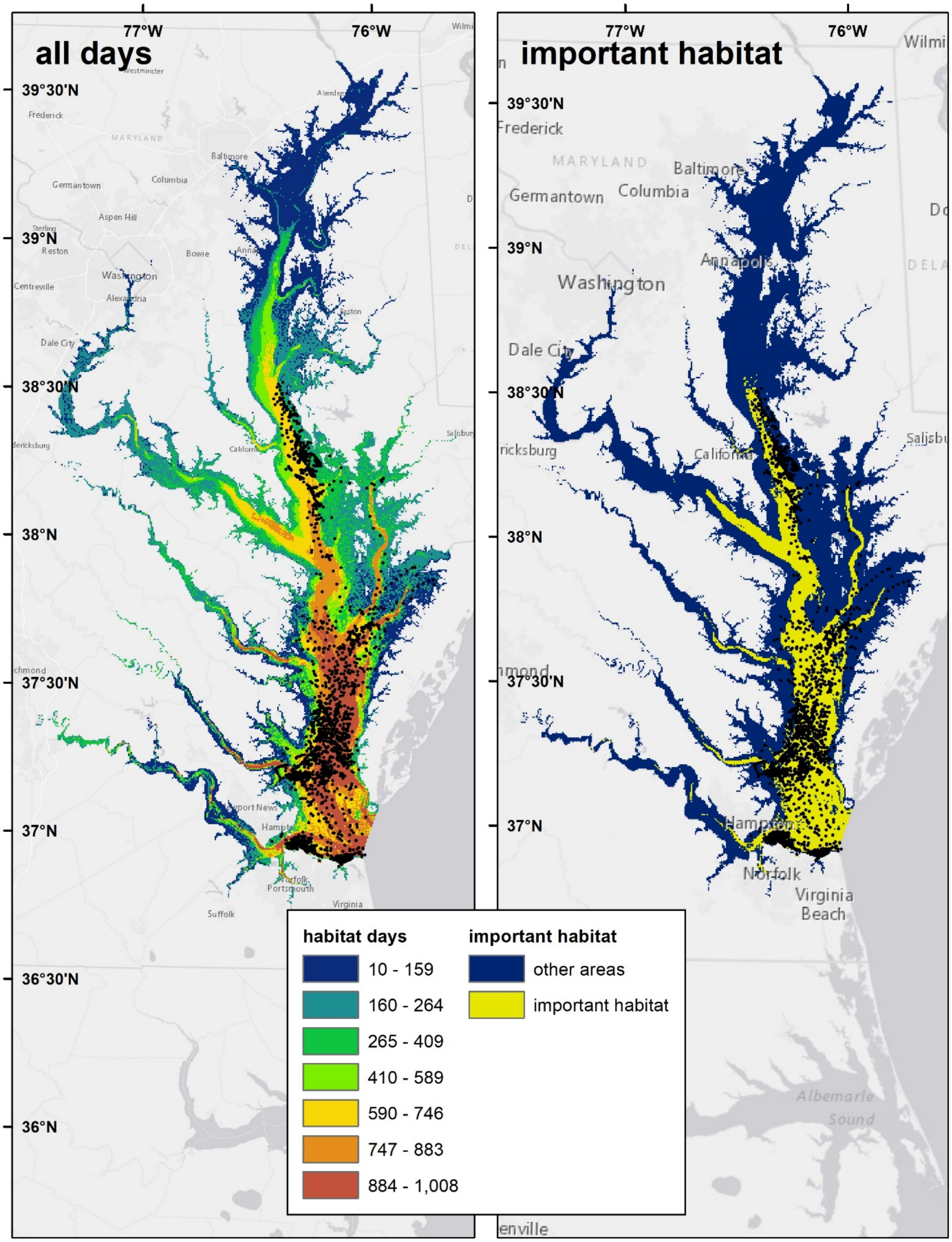

Figure 11. Number of suitable habitat days across the entire study period (2014–2018) and important habitat for the loggerhead turtle using the target-group absence model with hSSM locations overlaid.

3 Discussion

Examining reasons for why the Kemp's ridley target-group absence model predictions performed poorly, we saw that, like the loggerhead target-group absence model, bathymetry was by far the most important variable (51.4%). This meant that shallow areas in the north of the Bay were classified as suitable habitat even though animals have never been sighted there. We could have attempted to ameliorate this by limiting predictions to the southern Bay but one of the intents of this study was to identify possible habitat areas where animals have not been tracked. While it could be argued that the areas identified in the north of the Bay meet this goal, we felt the identified habitat was too extensive, and the artifact of a single covariate relationship, rather than a realistic depiction of unutilized habitat. This is supported by an examination of Kemp's ridley stranding data for Chesapeake Bay from 2008–2012 where only five of 224 Kemp's ridley strandings were north of the Potomac River, which divides the Maryland and Virginia portions of Chesapeake Bay, and no Kemp's ridley turtles stranded north of latitude 38.8 °N (Barco et al. 2015).

The functional relationships of the Kemp's ridley randomly generated absence model were more defined and the three variables had similar influence. We feel this may more accurately reflect Kemp's ridley preferences as the randomly generated absences sampled a broader range of the environmental covariates than the target group absences.

It may be that our model performance is limited by the available covariates. Temporally variable prey covariates, solar insolation, bottom temperature, or other covariates related to sea turtle physiology or prey could refine these predictions but are not currently available in the Bay at appropriate temporal or geographic resolutions. Likewise, prey availability in the form of crustacean distribution and abundance, which is likely the driving factor of distribution, is difficult to quantify overall and nearly impossible on small temporal and spatial scales.

The functional relationships from the Kemp's ridley randomly generated absence model predict that Kemp's ridleys avoid very warm surface temperatures (> 27°C). This may be true as juvenile Kemp's ridleys are small and may not be able to thermoregulate as well as larger turtles and may not have cold water refugia in the shallower depths they appear to prefer. Bottom temperatures would be a better reflection of the actual temperature turtles are exposed to while foraging but high-resolution bottom temperature data were not available for the spatial and temporal range of this study. This relationship, whether true or not, is likely the driving factor for lower suitably being predicted for Kemp's ridley turtles in the months of August and September, which are the warmest months in the Bay.

Of concern for loggerheads are the shipping channels being highlighted as suitable/important habitat. These channels are dredged regularly, and loggerheads are the primary species identified to be affected by dredging operations in the Bay (Mansfield and Musick 2003; NMFS 2018). If loggerheads do use these areas regularly, they are at increased risk from dredging operations and ship strike from the shipping and naval vessel traffic using these deep-water channels. The importance of depth to the loggerhead habitat model could be the reason that these areas are highlighted (e.g., an artifact of the model) but the relationship merits further investigation given the potential conservation implications.

It is worth noting that loggerheads may be recorded as the primary species impacted by dredges because they are larger and more likely to be reported. The Kemp's ridleys using river habitat may be susceptible to dredging in rivers. The Department of Defense regularly dredges the York River to ensure access to the Cheatham Annex and York River Weapons Depots naval facilities.

Comparing the selected Kemp's ridley and loggerhead models, we saw evidence that these species may be partitioning their habitat. We posit that this is driven by the distribution of the preferred prey of each species, blue crabs for Kemp's ridleys, compared with horseshoe crabs and other benthic invertebrates for loggerheads (Barco et al. 2015). In the Bay, blue crabs are found primarily in shallow, vegetated areas.

This habitat partitioning complicates conservation efforts as area closures or restrictions targeting one species may shift risks to the other. We recommend that any mitigation or conservation measures be applied to the entire southern Bay and southern rivers, as these will be the most effective for protection efforts of both species. Area closures that shift impacts into other areas of the Bay should be avoided based on the evidence that these species are partitioning habitat. The exception would be conservation measures that shift impacts to the northern areas of the Bay, where turtles do not appear to be present and where little suitable habitat exists. Given the economic importance of the region it is unlikely that conservation efforts that include outright closures will be reasonable. The timing of any restrictions should cover the core months of the foraging seasonal for both species (June–September). Of particular concern are the shipping channels into and out of the Bay which loggerheads may be utilizing as habitat.

4 References Cited

Barbet-Massin, M., Jiguet, F., Albert, C.H., and Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3: 327–338. doi:10.1111/j.2041-210X.2011.00172.x

Barco, S.G., Lockhart, G.G., Rose, S.A., Mallette, S.D., Swingle, W.M., and Boettcher, R. (2015). Virginia/Maryland Sea Turtle Research & Conservation Initiative. Final Report to NOAA for 2nd Award #NA09NMF4720033. VAQF Scientific Report 2015-05. Virginia Aquarium 3 Foundation, Virginia Beach, Virginia.

Barco, S.G., S.A. Rose, and G.G. Lockhart. (2017). Turtle Tagging and Tracking in Chesapeake Bay and Coastal Waters of Virginia: 2016 Annual Progress Report. Prepared for U.S. Fleet Forces Command. Submitted to Naval Facilities Engineering Command Atlantic, Norfolk, Virginia, under Contract No. N62470-15-D-8006, TO 0027 issued to HDR Inc., Virginia Beach, Virginia. June 2017.

Barco, S.G., S.A. Rose, G.G. Lockhart, and A. DiMatteo. (2018). Sea Turtle Tagging and Tracking in Chesapeake Bay and Costal Waters of Virginia: 2017 Annual Progress Report. Prepared for U.S. Fleet Forces Command. Submitted to Naval Facilities Engineering Command Atlantic, Norfolk, Virginia, under Contract No. N62470-15-8006, Task Order F4031, issued to HDR, Inc., Virginia Beach, Virginia. April 2018.

Bradley, A.P. (1997). The use of the area under the ROC curve in the evaluation of machine learning algorithms. Pattern Recognition 30(7): 1145–1159.

Byles, R.A. (1988). The behavior and ecology of sea turtles in Virginia. Ph.D. dissertation, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia. 112 pp.

Cerasoli, F., Iannella, M., D'Alessandro, P., and Biondi, M. (2017). Comparing pseudo-absences generation techniques in Boosted Regression Trees models for conservation purposes: A case study on amphibians in a protected area. PloS ONE 12(11): e0187589. https://doi.org/10.1371/journal.pone.0187589

DiMatteo, A. (2019). Unpublished data. Work performed under HDR, Inc. Project Number 1000300001270.

DiMatteo, A., Lockhart, G.G., and Barco, S.G. (Submitted). Normalizing home ranges of juvenile Kemp's ridley turtles (*Lepidochelys kempii*) in an important estuarine foraging area to better assess their spatial distribution. Marine Biology Research.

Douglas, D.C., Weinzierl, R., Davidson, S.C., Kays, R., and Wikelski, M. (2012). Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3: 999–1007. https://doi.org/10.1111/j.2041-210X.2012.00245.x

Elith, J., Leathwith, J.R., and Hastie, T. (2008). A working guide to boosted regression trees. Journal of Animal Ecology 77(4): 803–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Esri. (2019). ArcGIS Desktop: Release 10.7. Environmental Systems Research Institute, Redlands, California.

Hirzel, A.H., Hausser, J., Chessel, D., and Perrin, N. (2002). Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83: 2027–2036. doi:10.1890/0012-9658(2002)083[2027:ENFAHT]2.0.CO;2

Hosseinian Yousefkhani, S. S., Rastegar-Pouyani, E., and Aliabadian, M. (2016). Ecological niche differentiation and taxonomic distinction between *Eremias strauchi strauchi* and *Eremias strauchi kopetdaghica* (Squamata: Lacertidae) on the Iranian Plateau based on ecological niche modeling, Italian Journal of Zoology 83(3) 408–416, DOI: 10.1080/11250003.2016.1209581

Howell, E.A., Hoover, A., Benson, S.R., Bailey, H., Polovina, J.J., Seminoff, J.A., and Dutton, P.H. (2015). Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. Fisheries Oceanography 24: 57–68. doi:10.1111/fog.12092

Jonsen, I. (2016). Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Scientific Reports 6: 20625

Jonsen, I.D., Mills Flemming, J., and Myers, R.A. (2005). Robust state-space modeling of animal movement data. Ecology 86: 2874–2880

Keinath, J.A., Musick, J.A., and Byles, R.A. (1987). Aspects of the biology of Virginia's sea turtles: 1979-1986. Virginia Journal of Science 38: 329–336

Lefcheck, J. S., Orth, R.J., Dennison, W.C., Wilcox, D.J., Murphy, R.R., Keisman, J., Gurbisz, C., Hannam, M., Landry, J.B., Moore, K.A., Patrick, C.J., Testa, J., Weller, D.E., and Batiuk, R.A. (2018). Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. Proceedings of the National Academy of Sciences of the USA 115(14): 3658–3662. http://dx.doi.org/10.1073/pnas.1715798115.

Lutcavage, M., and Musick, J.A. (1985). Aspects of the biology of sea turtles in Virginia. Copeia 1985: 449–452. DOI: 10.2307/1444857

Mansfield, K.L. (2006). Sources of mortality, movements and behavior of sea turtles in Virginia. Ph.D. dissertation. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia. 343 pp.

Mansfield, K.L. and Musick, J.A. (2003). Loggerhead sea turtle diving behavior. Final report submitted to U.S. Army Corps of Engineers, Norfolk, VA. 41 pp.

Mansfield, K.L., Saba, V.S., Keinath, J.A., and Musick, J.A. (2009). Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. Marine Biology 156(12): 2555–2570. https://doi.org/10.1007/s00227-009-1279-x

National Centers for Environmental Information. (2017). NOAA NOS Estuarine Bathymetry - Chesapeake Bay (M130). National Centers for Environmental Information, NOAA. doi:10.7289/V5ZK5F0X. Accessed 15 September 2019.

National Marine Fisheries Service. (2011). Determination of nine Distinct Population Segments of loggerhead sea turtles as endangered or threatened. Federal Register 76: 58867–58592.

National Marine Fisheries Service . (2018). Endangered Species Act Biological Opinion. Construction and maintenance of Chesapeake Bay entrance channels and use of sand borrow areas for beach nourishment. Document F/NER/2018/14816. National Marine Fisheries Service, Greater Atlantic Regional Fisheries Office, Gloucester, Massachusetts.

National Marine Fisheries Service. (2020). Office of Habitat Conservation: Chesapeake Bay CMECS Component Geodatabase, https://inport.nmfs.noaa.gov/inport/item/29682.

Phillips, S.J., Dudik, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., and Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19(1): 181–197.

Preston, B. (2004). Observed winter warming of the Chesapeake Bay estuary (1949–2002): Implications for ecosystem management. Environmental Management 34: 125–139. https://doi.org/10.1007/s00267-004-0159-x

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Schoener, T.W. (1968). *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704–726.

Schofield, G., Bishop, C., Katselidis, K., Dimopoulos, P., Pantis, J., and Hays, G. (2009). Microhabitat selection by sea Turtles in a dynamic thermal marine environment. Journal of Animal Ecology 78(1): 14–21. Retrieved June 25, 2020, from www.jstor.org/stable/27696336

Seney, E. E., and Musick, J. A. (2005). Diet analysis of Kemp's ridley sea turtles (*Lepidochelys kempii*) in Virginia. Chelonian Conservation and Biology 4(4): 864–871.

Seney, E.E. and Musick, J.A. (2007). Historical diet analysis of loggerhead sea turtles (*Caretta caretta*) in Virginia. Copeia 2007: 478–489. https://doi.org/10.1643/0045-8511(2007)7[478:HDAOLS]2.0.CO;2

Spotila, J., and Standora, E. (1985). Environmental constraints on the thermal energetics of sea turtles. Copeia 1985(3): 694–702. doi:10.2307/1444763

Syrjala, S.E. (1996). A statistical test for a difference between the spatial distributions of two populations. Ecology 77: 75–80. doi:10.2307/2265656

Turtle Expert Working Group. (2009). An assessment of the loggerhead turtle population in the western North Atlantic Ocean. NOAA Technical Memorandum NMFS-SEFSC-575. National Marine Fisheries Service, Miami, Florida. 142 pp. http://www.sefsc.noaa.gov/seaturtletechmemos.jsp

Van der Vaart, A.W. 1998. Asymptotic statistics. Cambridge Univ. Press, Cambridge, U.K.

Warren, D.L., Glor, R.E. and Turelli, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883. doi:10.1111/j.1558-5646.2008.00482.x

Werdell, P.J., Bailey, S.W., Franz, B.A., Harding, L.W., Feldman, G.C., and McClain, C.R. (2009). Regional and seasonal variability of chlorophyll-a in Chesapeake Bay as observed by SeaWiFS and MODIS-Aqua. Remote Sensing of Environment113(6): 1319–1330. https://doi.org/10.1016/j.rse.2009.02.012.

Wessel, P., and Smith, W.H.F. (1996). A global self-consistent, hierarchical, high-resolution shoreline database, Journal of Geophysical Research 101: 8741–8743.This page intentionally left blank.