

ARTICLE

Environmental Drivers of Adult Atlantic Sturgeon Movement and Residency in the Delaware Bay

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Abstract

Animals utilize various habitats throughout their life to optimize growth, fitness, and survival. Identifying environmental conditions and locations where animals exhibit different movement behaviors can be used to infer the relative importance of habitat types. In the case of threatened and endangered species, such as the Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, critical habitat designations are a tool used to promote conservation and recovery. We utilized an extensive passive acoustic telemetry array, observed atmospheric conditions and river flow, modeled seawater conditions, and used generalized additive mixed modeling to determine environmental predictors of Atlantic Sturgeon movement and residency in the Delaware Bay on the U.S. East Coast. Our results suggested that shallower waters, warmer bottom temperatures, and areas toward the eastern portion of the Delaware Bay were predictive of residency, while movement was predicted by increased depth, cooler bottom temperatures, and areas toward the western portion of the bay. Our findings add to a growing body of evidence highlighting habitats at the Delaware Bay mouth, where Atlantic Sturgeon occur at heightened concentrations from late spring through fall. The Delaware River estuary once supported the largest population of Atlantic Sturgeon in North America, but that population is now critically imperiled (or endangered). Atlantic Sturgeon spend the vast majority of their life in marine, polyhaline waters, and without enhanced protection for these habitats, their recovery may never be realized.

Ecological theory asserts that species' distributions are determined by environmental states and that reasonable estimates of these states can be quantified (Austin 2007); this can be extended to drivers of animal movements. The movement ecology paradigm addresses four fundamental

questions: why movement occurs, when and where to move, how to move, and the consequences of movement (Nathan et al. 2008). Movement is fundamental to habitat selection, and its study gives insight into processes often affecting survival, growth, and fitness. Confounding the

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field of movement ecology is the fact that spatial and temporal observation scales can dictate the perceived habitat selection of an organism. To account for this scaling effect, Johnson (1980) suggested a four-order hierarchical approach when studying habitat selection: (1) species distribution, (2) home range, (3) sub-seasonal behavioral modes and residency patterns, and (4) forage selection. Understanding how environmental conditions and locations influence behavioral (including movement) modes has proven very useful in identifying habitats that are essential to a species' life history (Owen-Smith et al. 2010) and, by extension, its conservation.

One important factor for the conservation and recovery of threatened or endangered species in the United States is the designation of critical habitat. Critical habitat is defined as

the specific areas within the geographical area occupied by the species, at the time it is listed in accordance with the provisions of section 4 of this [Endangered Species] Act, on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection. [From USFWS and NMFS 2016.]

The determination of critical habitat requires an understanding on multiple levels, including documenting the species' use of that area, identifying whether and what essential features exist, and determining whether the area requires special management. For Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, the specific areas occupied in marine and estuarine environments—especially at scales appropriate to inform the second and third parts of critical habitat designation—are largely unknown (NMFS 2016).

Five distinct population segments (DPSs) of Atlantic Sturgeon were listed under the Endangered Species Act (ESA) on April 6, 2012, with the New York Bight, Chesapeake, Carolina, and South Atlantic DPSs listed as endangered and the Gulf of Maine DPS listed as threatened (NMFS 2012a, 2012b). Atlantic Sturgeon undergo large-scale coastal migrations, moving northward in the spring on the way to spawning and foraging grounds and moving southward in the fall to offshore overwintering areas (Collins et al. 2000). These migration routes increase their vulnerability to anthropogenic impacts, including fisheries bycatch. Incidental bycatch is highest in the fall, winter, and spring, when sturgeon utilize marine waters, and lowest in the summer months, when Atlantic Sturgeon enter estuarine and riverine habitats (Stein et al. 2004b). Fisheries-dependent bycatch records (Stein et al. 2004a) as well as fisheries-independent findings (Laney et al. 2007; Dunton et al. 2010; Erickson et al. 2011; Breece et al. 2016, 2017) suggest that Atlantic Sturgeon primarily occupy inshore areas of the continental shelf and that coastal

features, including inlets and mouths of bays, hold seasonally higher concentrations of Atlantic Sturgeon.

Although there has been a recent increase in the general understanding of Atlantic Sturgeon migration and occupancy in the mid-Atlantic region (Dunton et al. 2010, 2015; Oliver et al. 2013; Breece et al. 2017), there is still limited documentation of behavior modes in relation to these congregation areas and environmental conditions that could identify important features requiring special management. As such, identification of areas and environmental conditions where Atlantic Sturgeon are exhibiting a resident behavior may highlight foraging areas, while knowledge of locations of increased movement probability could highlight migration corridors, suboptimal habitat, or conditions associated with increased metabolic demands (Avgar et al. 2013).

Through a combination of generalized additive mixed models, passive acoustic telemetry, and environmental data, our study focuses on regions of increased movement or residency behaviors of Atlantic Sturgeon in the Delaware Bay on the U.S. East Coast. An improved understanding of the interaction among the physical attributes of habitat and sturgeon behavior is needed to further refine our understanding of key habitat features, as these areas likely meet the legal requirements of critical habitat under the ESA.

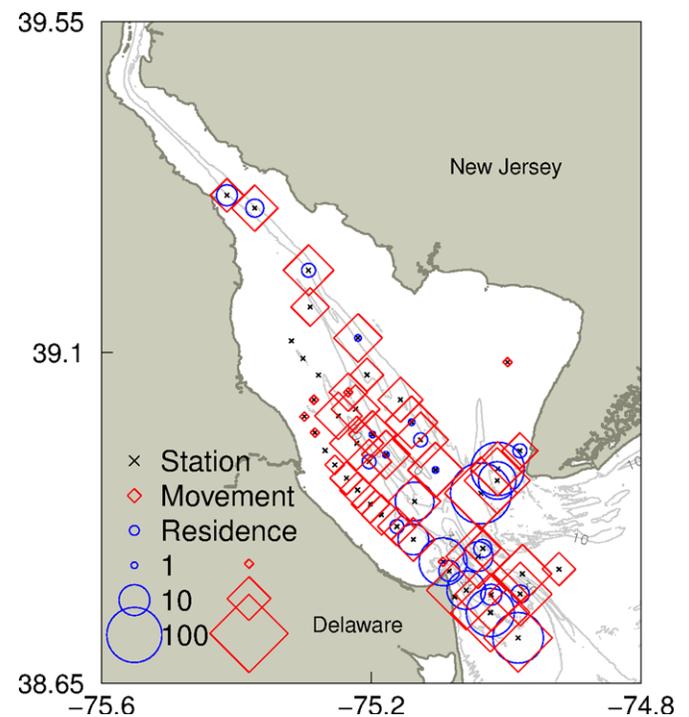


FIGURE 1. Map of the study area, showing the number of events by behavioral mode (movement and residency) for telemetered adult Atlantic Sturgeon recorded on passive acoustic receiver stations in the Delaware Bay and nearshore coastal waters; x- and y-axes indicate longitude and latitude, respectively.

METHODS

Atlantic Sturgeon biotelemetry acoustic detections were collected via a passive acoustic telemetry array consisting of VEMCO VR2W receivers ($n = 47$ stations; VEMCO Ltd., Halifax, Nova Scotia, Canada) deployed in the Delaware Bay and surrounding waters off Delaware and New Jersey (Figure 1). Typical maximum ranges for VR2W receivers and V16 transmitters in our study area are approximately 700–1,000 m depending on oceanographic conditions (Kilfoil 2014). Residency observations were confined to the Delaware Bay and the nearby coastal Atlantic waters of Delaware; however, additional receivers in the Delaware River and Atlantic Ocean (but not within the study domain) were utilized to capture observations of individuals that had left or not yet entered the study area.

Atlantic Sturgeon were collected from late March to mid-May 2009–2011 in the nearshore coastal Atlantic Ocean near Bethany Beach, Delaware, via large-mesh gill nets modeled on those used during the coastal intercept fishery prior to the moratorium on Atlantic Sturgeon harvest. Of the 324 Atlantic Sturgeon captured, 178 adults were anesthetized and received a coded acoustic transmitter (VEMCO V-16-6H; battery life ~6.4 years; mean transmission rate = 90 s) that was surgically implanted in accordance with the protocol of Fox et al. (2000). Individuals were measured for FL (mean = 156 cm; range = 63–230 cm), weighed (mean = 42 kg; range = 2–136 kg), fitted with an external spaghetti tag for visual identification, injected with a PIT tag, photographed, and released at the capture location upon recovery from the anesthesia, typically less than 1 h after capture.

Data management and analysis were performed in R (R Core Team 2015). Periods of residency and movement were calculated and catalogued using the behavioral event qualifier in the R package V-Track (Campbell et al. 2012). A period of residency was defined as a series of detections on a single receiver station for at least 12 h; this helped to ensure restricted movements and minimized the effects of tidal oscillations on detection fields. A residency event was terminated by either a detection of the individual at another receiver station or a period of 12 h without detection. Movement events were defined as movements between residency events and were censored to be between 10 min and 1 week to eliminate spurious detections from receivers that were several km apart and to only estimate movements during continuous observation periods in the Delaware Bay. Factorial variables (0 and 1) were given to residency and movement, respectively, for a binomial analysis.

For the purpose of distinguishing between residence and movement, residency periods were divided into three parts: start of residency, indicated by the first detection of the residency period; end of residency, indicated by the last detection of the period; and residency, being the entire residency period. Movement periods consisted of

times between residencies and when Atlantic Sturgeon spent less than 2 h at a receiver station. Swimming speed of sturgeons can be relatively slow (0.5–2.7 m/s; Thiem et al. 2015). To distinguish between slow-moving transient and resident Atlantic Sturgeon, detection events greater than 2 h but less than 12 h were not considered in this analysis to ensure correct classification of movement and residency events.

Environmental predictors from several sources were matched with discrete movement events and the start and end of residency periods, while mean conditions were matched to the entire duration of residency. Additionally, we matched changes in environmental predictors that may affect behavior, end condition minus start condition for residency, and change over the previous 24 h for all other events. Lunar phase was matched using the function `lunar.phase` (“lunar” package; Lazaridis 2014). Delaware River flow was taken from U.S. Geological Survey gauging station 01463500 at Trenton, New Jersey. Water depth was obtained through the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information, U.S. Coastal Relief Model (National Geophysical Data Center 1999). Barometric pressure observations were recorded on station BRND1-8555889 (Brandywine Shoal Light) in the middle of the Delaware Bay. To obtain estimates of surface water temperature, bottom water temperature, salinity, and current (direction and magnitude) at each receiver station, we utilized Regional Ocean Modeling System (ROMS; www.myroms.org) model outputs of the Delaware Bay from 2009 to 2011 (provided by J. Wilkins, Rutgers University). The ROMS modeled circulation in the Delaware Bay using the three-dimensional hydrostatic primitive equations (Shchepetkin and McWilliams 2005) in terrain following vertical coordinates with external forcing from six major tributaries, air–sea fluxes estimated using the North American Regional Reanalysis, and sea-level and barotropic velocity at the continental shelf open boundary specified from a regional tidal model (Mukai et al. 2002). The Delaware Bay ROMS has been used extensively to study ecological processes, such as larval dispersal and salinity inundation in the bay (Narváez et al. 2012; Wang et al. 2012; Munroe et al. 2013), performs very well (high skill and high correlation), and is summarized in detail by Wang et al. (2012). Matched predictor variables were tested for collinearity between variables (“`cor`” function in the “stats” package) with a threshold value of 0.70 to determine high correlation (Wegmann et al. 2016). If correlations were above 0.70, then only one of the two predictors was chosen to be included in the model based on interpretability and ecological relevance.

Three initial generalized additive mixed models (GAMMs) were developed to determine whether there were significant differences between environmental

predictors (day of year, water temperature, salinity, barometric pressure, river flow, current [direction and magnitude], depth, lunar phase, and changes in water temperature and salinity) and the three behavioral response variables (i.e., start of residency, end of residency, and total residency period). Generalized additive models (Hastie and Tibshirani 1990; Wood 2006) and their extension, GAMMs (GAMM4 package; Wood and Scheipl 2015), account for nonlinear relationships and individual effects while maintaining interpretability that can be lost in more complex or underdocumented models. A GAMM sums smoother functions (penalized regression splines) to model the binomial variable of behavior. To account for uneven sampling of individuals, we used individual Atlantic Sturgeon as the random effect (Lin and Zhang 1999); we also included projected longitude and latitude (spTransform; Bivand et al. 2014; Universal Transverse Mercator system datum = WGS84) for receiver stations to account for spatial trends in the data (Dormann et al. 2007; Gilles et al. 2016). Penalized thin-plate regression splines (“ts” function in GAMM4) were implemented as an automatic alternative to forward and backward model selection of the environmental predictors; penalized thin-plate regression splines incorporate a penalty, which may shrink all of the coefficients of a smoother to zero, effectively penalizing the predictor out of the model (Marra and Wood 2011). Day of year and lunar phase are circular predictors, and we therefore implemented cyclical smoothers (“cp” function; Wood 2006) for these variables. Number of knots was initially limited to five for each single-variable smooth predictor to prevent overfitting (Wegmann et al. 2016). Once the analyses between stages of residency were completed, we analyzed residency versus movement by using a GAMM comparing residency and continuous movement events with the same predictor variables as above. To reduce unnecessary complexity, nonsignificant ($P > 0.05$) predictors that had little contribution to the model and that had estimated degrees of freedom (EDF) close to their lower limit were removed, and the model was refitted based on the remaining predictors (Wood and Augustin 2002). Additionally, predictors that were always within 1 SE of zero were also removed, and the model was refitted (Wood and Augustin 2002). Akaike’s information criterion (AIC) was used to ensure that model trimming did not result in a loss of information (Wood 2006).

To determine whether model complexity and overfitting were problems, we used fivefold cross-validation on the top-performing model. To obtain a cross-validated prediction for each observation, we split the data randomly into five subsets, reiteratively fitting the model to four of the five subsets and then using the fifth subset for model prediction (Wegmann et al. 2016). We also calculated the explained deviance (r^2), sensitivity (correctly classified

presences), specificity (correctly classified absences), and the optimal threshold (point of maximum combined sensitivity and specificity) for each model via the R package “PresenceAbsence” (Freeman and Moisen 2008).

RESULTS

Continuous movements and/or residency periods were observed for 157 of the 178 telemetered Atlantic Sturgeon between April 4 and November 24 during this 3-year study. There were 7,133 total detection events, with the longest lasting 42.3 d. A total of 609 of the detection events met the criterion (>12 h) to be considered residency, of which 539 were matched to environmental data on 26 receiver stations. We documented a total of 2,218 movements, with 976 covering less than 2 h; the vast majority (885) were matched to environmental data at 44 receiver stations (Figure 1).

Surface and bottom temperatures were the only highly correlated predictors ($r = 0.71$, slope = 1.0; Figure 2); as a result, bottom temperature was used, as Atlantic Sturgeon are thought to occur in bottom habitat the majority of the time (Erickson et al. 2011). This also showed that the environment was relatively well mixed. Residency and movement occurred over a wide range of bottom temperatures, with a mean of 19.2°C (range = 8.9–28.8°C) and 18.5°C (range = 8.8–27.3°C), respectively (Figure 3). Salinity also varied widely, with a mean of 26.8‰ (range = 0–31.8‰) and 28.0‰ (range = 4.3–32‰), respectively. The majority of observations for magnitude of currents and river flow for both residency and movement were at low velocities. Mean depth varied between residency (13.9 m; range = 4.1–24.6 m) and movement (16.2 m; range = 2.2–24.3 m). Barometric pressure was similar between residency (mean = 1,014 millibars [mb]; range = 992–1,032 mb) and movement (mean = 1,015 mb; range = 991–1,034 mb). Salinity anomalies (difference from mean over the previous 14 d) ranged from –6.6‰ to 9.8‰ for residency and from –7.3‰ to 8.7‰ for movement. Changes in temperature over the previous 24 h ranged from –2.7°C to 1.8°C for residency and from –1.7°C to 3.2°C for movement. Environmental observations matched to telemetry observations are plotted in Supplemental Figure S.1 (available separately online).

Investigative GAMMs between residency behavioral modes revealed no distinction in environmental predictors between the three periods of residency: start of residency, end of residency, and the entire residency period. All three models had very low r^2 values (<0.0001), and no predictors had a significant impact on the models (Supplementary Tables S.1–S.3).

The initial GAMM comparing residency and movement, including all of the environmental predictors as well as an interaction term to account for spatial trends in the

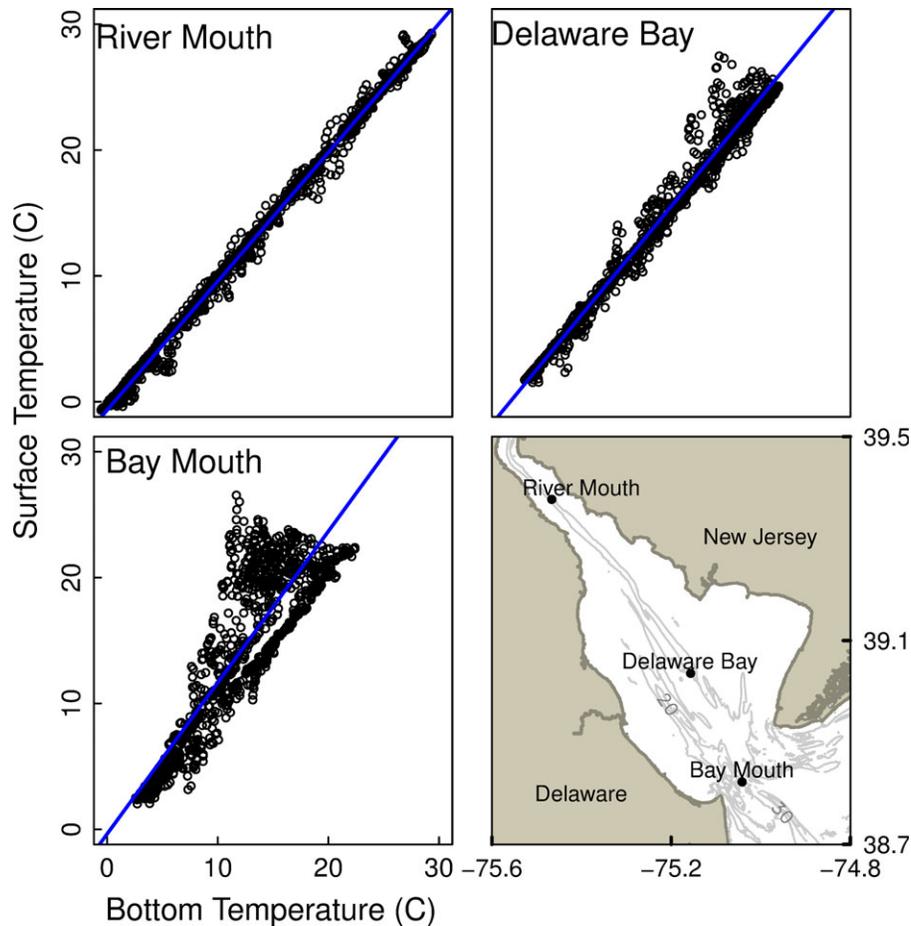


FIGURE 2. Modeled surface temperature ($^{\circ}\text{C}$) versus bottom temperature at acoustic receiver stations located at the mouth of the Delaware River, in mid-Delaware Bay, and at mouth of the Delaware Bay. The blue line represents a slope of 1. The x - and y -axes of the bottom right panel indicate longitude and latitude, respectively.

data, indicated that bottom temperature ($P < 0.0001$), day of year ($P < 0.0001$), depth ($P < 0.0001$), current velocity ($P = 0.003$), moon phase ($P = 0.047$), and the spatial component ($P < 0.0001$) significantly influenced behavioral transitions between residency and movement states in adult Atlantic Sturgeon. The other nonsignificant predictors' EDF were penalized to at or near zero, essentially removing their influence on the model (Table S.4). To simplify model interpretation and complexity, the GAMM was then re-run utilizing only the significant terms while excluding predictors with EDF of approximately zero from the first model. The results indicated that current velocity, day of year, and moon phase were no longer significant predictors of behavioral states (i.e., residency and movement). Reduction in AIC scores from the first to second iteration confirmed that the reduced complexity outweighed the information lost when only the subset of predictors was used (AIC = 1,523–1,335) and that the second, simpler model was more appropriate. The final model was refitted by using only the significant terms of bottom

temperature, depth, and the spatial component as predictors for residency and movement. All predictors were significant, and the AIC was again reduced during this refit (from 1,335 to 1,249), providing support for our decision (Table 1) to use the final, simplest model:

$$\text{behavior mode} \sim s(\text{bottom temperature}) + s(\text{depth}) + s(\text{longitude, latitude}) + (1|\text{individual}),$$

where $s()$ indicates a smoother was used.

The cross-validated scores (area under the receiver operating characteristic curve [AUC] = 0.78; $r^2 = 0.31$) were similar to the full model scores (AUC = 0.73; $r^2 = 0.20$), suggesting that our model was not overfitted (Wegmann et al. 2016). Optimal threshold analysis (PresenceAbsence package; Freeman and Moisen 2008) revealed the optimal threshold (maximization of sensitivity and specificity) to be 0.64, indicating that estimates above this value were predictive of movement and estimates below this value were predictive of residency. Our model

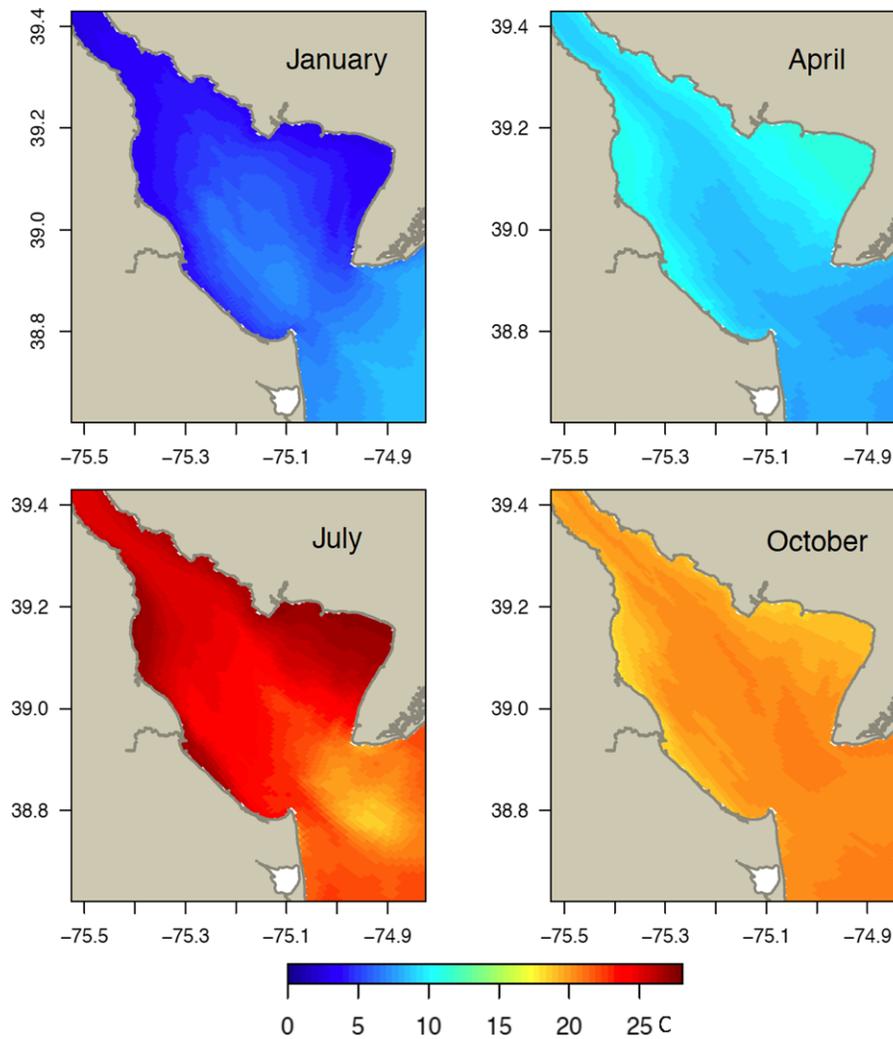


FIGURE 3. Modeled Delaware Bay bottom temperatures ($^{\circ}\text{C}$) for four representative monthly periods during the study. In general, the bay is well mixed throughout the year; x - and y -axes indicate longitude and latitude, respectively.

TABLE 1. Predictive generalized additive mixed model for adult Atlantic Sturgeon movement and residency in the Delaware Bay and nearshore coastal waters (EDF = estimated degrees of freedom), $s()$ indicates a smoother was used.

Residence/movement model	Estimate	SE	EDF	χ^2	Z	P
Intercept	0.6029	0.1402			4.299	<0.0001
$s(\text{bottom temperature})$			1.225	44.38		<0.0001
$s(\text{depth})$			3.386	33.41		<0.0001
$s(\text{longitude, latitude})$			1.820	52.96		<0.0001

performed well in correctly classifying residencies (specificity = 80.3%) and movements (sensitivity = 58.2%) and correctly identified 66.6% of the entire data set with both behavioral modes.

Variable importance of the final model indicated that depth had the most influence on the model (37%), followed by longitude (32%), temperature (30%), and latitude, which had little effect (1%). The EDF of the three

predictors revealed that the relationships between predictors and responses were nonlinear. Factorial variables (0 and 1) were assigned to residency and movement, respectively; therefore, an increase in the response variable indicated that Atlantic Sturgeon behavior was more likely to be movement, whereas a decrease in the response variable indicated residency behavior. The bottom temperature response curve had a generally decreasing trend with

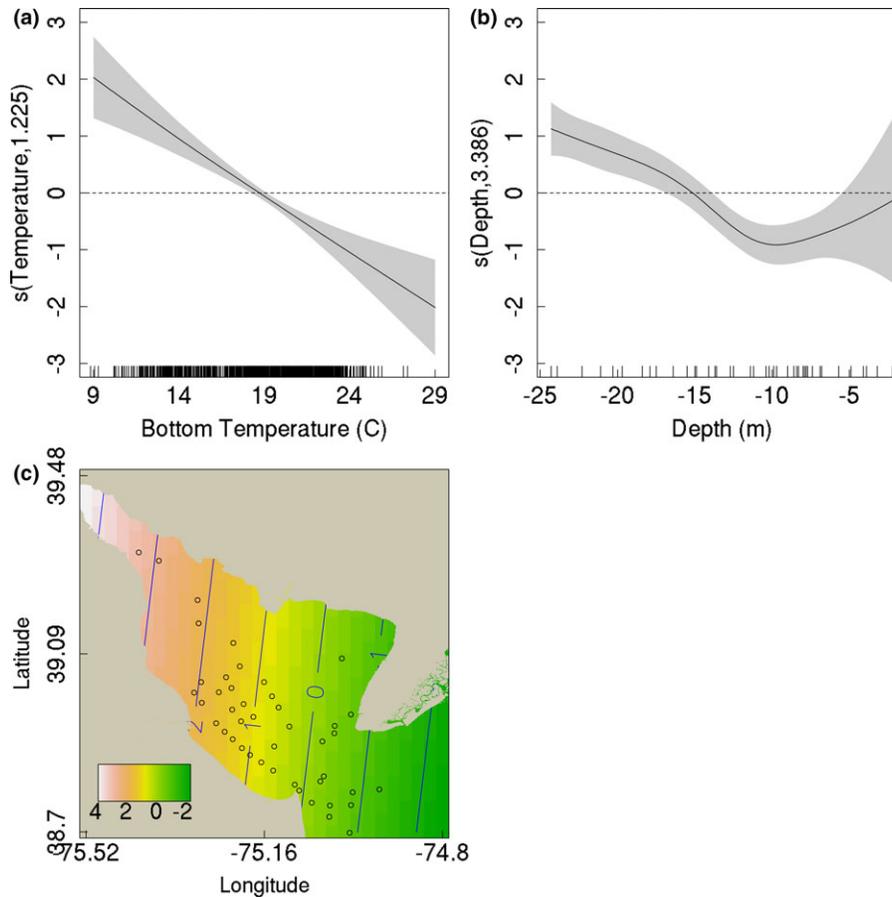


FIGURE 4. (A) Bottom temperature ($^{\circ}\text{C}$), (B) depth (m), and (C) spatial response functions for the final generalized additive mixed model of Atlantic Sturgeon movement (+) versus residency (-). Circles in (C) represent locations of acoustic receivers.

increased temperature, indicating that Atlantic Sturgeon residency was more likely at higher temperatures and transitioned to movement as temperatures fell below 18–19 $^{\circ}\text{C}$ (Figure 4A). The response curve for depth predicted that movements were more likely in deeper waters, while waters less than 14 m in depth were associated with increased residence; it is important to note that the confidence intervals for the shallowest depths contained zero and therefore were inconclusive (Figure 4B). The spatial (longitude, latitude) response function suggested that Atlantic Sturgeon were more likely to exhibit the movement pattern in the western or upper portions of the Delaware Bay (Figure 4C).

Extrapolating the GAMM output onto four representative scenarios revealed a seasonal change in the behavioral patterns of Atlantic Sturgeon in the Delaware Bay. In the winter, when water temperatures were coldest, movement of sturgeon was predicted for the entire study area. In the spring (April), the majority of the area was still dominated by the movement of sturgeon, with small, isolated pockets of sturgeon residency in deeper water near the mouth of the Delaware Bay. During the summer

and fall, when the waters were warmer overall, these small pockets expanded, and there was a larger—but still isolated—area of Atlantic Sturgeon residency at the Delaware Bay mouth that aligned with cooler, upwelled waters. The behavior of sturgeon in the remainder of the study area was estimated to be movement or was undetectable (Figure 5).

DISCUSSION

Predicting behavioral modes for large, highly mobile species like adult Atlantic Sturgeon can be very challenging due to their size and difficulty of capture. By utilizing an extensive telemetry array, observed and modeled environmental predictors, the R package V-Track, and a GAMM, we were able to identify habitats where environmental factors predicted the behavior of adult Atlantic Sturgeon in the Delaware Bay. Decreased bottom temperature, increased depth, and decreasing longitude all had similar effects and were associated with increased predictions of movement. Fine-scale behaviors like those associated with foraging or migration over large expanses can

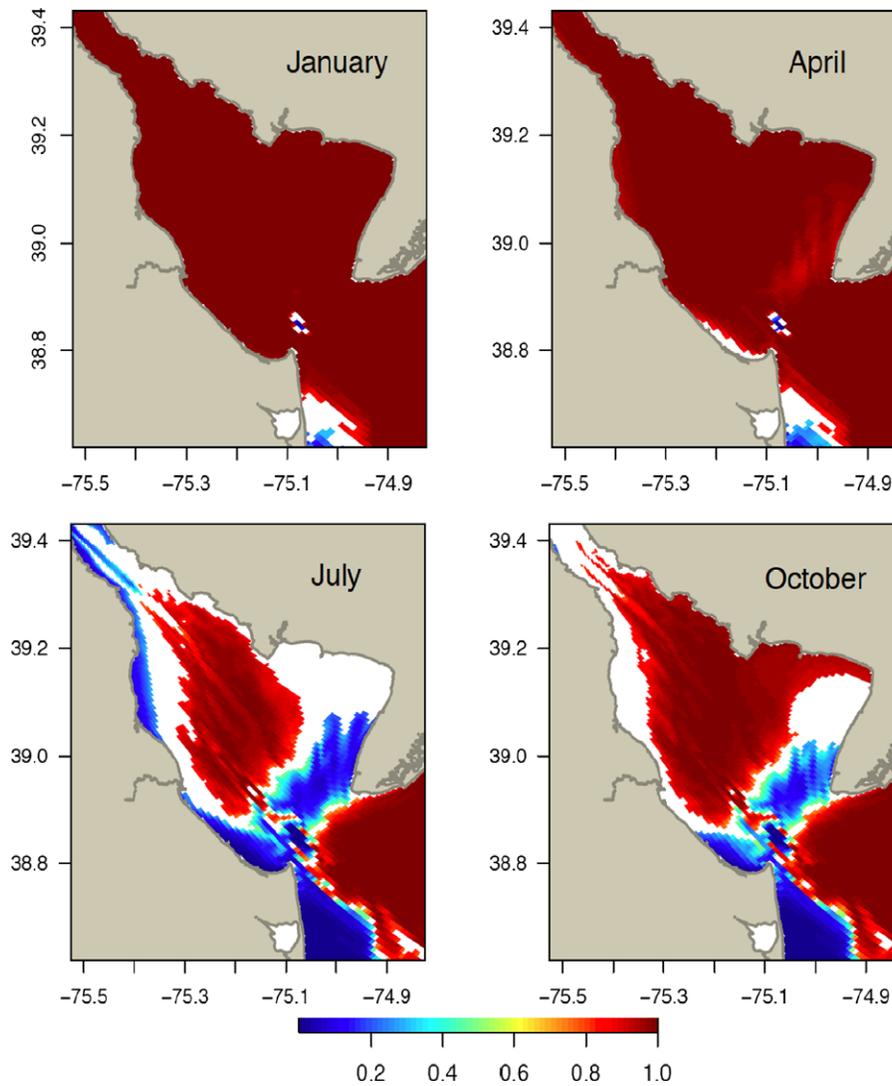


FIGURE 5. Generalized additive mixed model predictions of adult Atlantic Sturgeon behavior at four representative time periods during the study in the Delaware Bay. Predictions were extrapolated to areas where no telemetry receivers were deployed (red = high probability of movement; blue = high probability of residency; white = nonsignificant predictions); x - and y -axes indicate longitude and latitude, respectively.

be difficult to observe in marine environments. Estimation of behavioral modes (e.g., movements versus residency) at coarser scales allows us to infer conditions or features that may be critical to the conservation and recovery of what was once the largest population of Atlantic Sturgeon (Secor and Waldman 1999). For example, as the rate of an animal's movement slows, the likelihood that it is experiencing ideal habitat or favorable conditions is increased; conversely, as the movement rate increases, habitat conditions are likely to be less favorable or to be taxing on the individual (Avgar et al. 2013).

Our findings suggest that depth and longitude, which are both static variables, are of the highest importance when predicting Atlantic Sturgeon behavioral mode in the Delaware Bay, while varying bottom temperatures

are needed to visualize changes in behavioral patterns. Our model predicts that at colder temperatures, Atlantic Sturgeon exhibit increased movement and reduced residency in the Delaware Bay. As temperatures rise, regional conditions within our study area promote different behaviors. The effect of longitude is likely a proxy for distance from the mouth of the estuary (eastern area), which becomes a prominent area of residency for Atlantic Sturgeon—likely due to persistent upwelling that keeps these bottom waters comparatively cooler (Garvine 1991; Voynova et al. 2013). The model also forecasts increased periods of residency in the shallow waters on the southwest side of the Delaware Bay, although these areas are within the depth range where the model has poor performance.

Anadromous sturgeons are known to concentrate at the mouths of estuaries and inlets, but documentation of their behavior in these areas is limited. All major estuaries in the mid-Atlantic region have known concentration areas of Atlantic Sturgeon: the Chesapeake Bay (Erickson et al. 2011), the Delaware Bay (Breece et al. 2013, 2016), the mouth of the Hudson River (Dunton et al. 2015), and Long Island Sound (Savoy and Pacileo 2003). Likewise, Green Sturgeon *A. medirostris* on the U.S. West Coast (Adams et al. 2002; Kelly et al. 2007; Moser and Lindley 2007) and Gulf Sturgeon *A. oxyrinchus desotoi* (Fox et al. 2002) occupy major estuaries, with many being designated as critical habitat (USFWS and NMFS 2003). Salinity was not a significant predictor of adult Atlantic Sturgeon behavior; however, our results highlight the mouth of the Delaware Bay as an area where individuals maintain residency at given stations for up to 6 weeks without leaving and where many other individuals remain from May to October. Appropriate water depths and comparatively cooler bottom temperatures create suitable habitat in a narrow band at the Delaware Bay mouth, where extended residency of Atlantic Sturgeon makes them vulnerable to environmental disasters or habitat degradation in an area that is in proximity to high population centers and receives large amounts of commercial vessel traffic.

There are two phenomena that may be responsible for the shift in Atlantic Sturgeon behavior from movement to residency in the Delaware Bay: physiology and physical oceanography. For Atlantic Sturgeon, the optimal metabolic temperature is approximately 18°C, and metabolic demand increases sharply as temperatures increase above 18°C in polyhaline waters (Niklitschek and Secor 2009). This thermal response may drive Atlantic Sturgeon to seek out cooler waters during the summer months (Moser and Ross 1995; Hightower et al. 2002). The mouth of the Delaware Bay provides near-metabolically optimal water temperatures when a combination of strong tidal mixing (Münchow et al. 1992) and southwest summer winds creates upwelling, which brings in cooler, nutrient-rich, highly oxygenated offshore waters (Garvine 1991; Voynova et al. 2013). Our findings provide evidence of adult Atlantic Sturgeon exploiting the cooler bottom temperatures during the summer months when they have taken up residency in the lower bay and near-shore coastal waters.

In addition to physiological demands and physical oceanography, sturgeons also utilize the interface between estuary and marine waters for foraging during coastal migrations and extended residency periods to maximize growth and replenish energy stores for gonadal recrudescence after spawning. Highly productive feeding grounds have been documented in the Bay of Fundy (Dadswell et al. 2016), where trajectories of Atlantic Sturgeon show tortuous, confined movements during feeding bouts from

May to October (McLean et al. 2014). The closely related Gulf Sturgeon forage in the mouths of estuaries and in coastal marine waters at their interface (Fox et al. 2002; Harris et al. 2005). On the west coast of the United States and Canada, Green Sturgeon are also found to forage in aggregations in the coastal ocean near (Lindley et al. 2008) and within estuaries (Moser and Lindley 2007; Lindley et al. 2011), where more productive habitat is likely to exist. Upwelling of offshore waters increases productivity (Voynova et al. 2013) in the areas of increased residency of adult Atlantic Sturgeon within the Delaware Bay and creates identifiable and predictable conditions similar to those in areas where foraging has been found for other sturgeons in other estuaries. High abundance of benthic invertebrates that are known food items for Atlantic Sturgeon (Collins et al. 2000; Guilbard et al. 2007; McLean et al. 2013) has been shown in these areas of the Delaware Bay (Kinner and Maurer 1978; Maurer et al. 1978). Atlantic Sturgeon exhibiting increased residency at the Delaware Bay mouth are at a critical stage when energy demands are high, and this area may provide the resources needed to meet those demands.

The focus of this study was to estimate key features mediating the behaviors of adult Atlantic Sturgeon in the Delaware Bay and not their occurrence or distribution. However, if we match the findings of this study with the results of previous distributional studies (Breece et al. 2016, 2017), we discover that the area at the Delaware Bay mouth is an area not only of high residency but also of high occurrence. During migration into the area in the spring, the probability of occurrence increases from April to June and then again in September and October (Breece et al. 2017), while this study predicts increased movement during that same time frame. As water temperatures increase, occurrence seems to decrease; however, Breece et al. (2017) noted that this is likely due to the increase in use of areas not covered by the acoustic receiver array. Our findings provide additional support for the idea that when temperatures throughout most of the Delaware Bay are highest, Atlantic Sturgeon shift to a residency behavior in an isolated region with optimal-temperature waters near the mouth of the Delaware Bay (an area where receiver coverage was limited).

The Delaware Bay mouth not only has a high occurrence of Atlantic Sturgeon, it also has a high occurrence of commercial vessel traffic, such as oil tankers, ferries, and cargo vessels. Additionally, this area is impacted by dredging for maintenance and channel deepening, which could alter sediment, benthic communities, and Atlantic Sturgeon habitat. This overlap of Atlantic Sturgeon occurrences and high volume of commercial traffic and impacts greatly increases the risk of vessel strikes (Simpson and Fox 2009; Fisher 2011) and destruction of critical habitat from events such as oil spills in the Delaware Bay (DRA-BOSA Committee 2010). The Delaware Bay and

nearshore coastal waters constitute a vital aggregation area that once supported the largest population of sturgeon in North America (Secor and Waldman 1999) and that currently is utilized by adult Atlantic Sturgeon from every DPS in the United States (Breece et al. 2017). Our results and previous research suggest that this area is of high importance for Atlantic Sturgeon, and the physical and biological/physiological features that occur here are essential to their conservation and recovery.

The study of movements and residencies in animals provides great insights into resource selection and habitat needs. We increased the utility of acoustic telemetry data by using V-Track to classify behavioral events and compare them to oceanographic conditions, allowing us to extrapolate predictions to unsampled areas. The study design and methods developed herein are readily transferable to many acoustic telemetry data sets worldwide to estimate how environmental conditions affect behavior. In addition, our methods help to highlight areas or conditions that should be investigated further to determine their importance for the life history of the species being studied. Going beyond a descriptive summary of Atlantic Sturgeon, we highlight important behavioral features that are likely being mediated by selection for essential habitat. The features identified here indicate where conservation efforts may have the greatest impacts and can improve the efficiency of resource management for this endangered 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.