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RESEARCH ARTICLE

Supportive wind conditions influence offshore movements of Atlantic Coast Piping Plovers during fall migration

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ABSTRACT

In advance of large-scale development of offshore wind energy facilities throughout the U.S. Atlantic Outer Continental Shelf (OCS), information on the migratory ecology and routes of federally threatened Atlantic Coast Piping Plovers (*Charadrius melodus melodus*) is needed to conduct risk assessments pursuant to the Endangered Species Act. We tagged adult Piping Plovers (n = 150) with digitally coded VHF transmitters at 2 breeding areas within the southern New England region of the U.S. Atlantic coast from 2015 to 2017. We tracked their migratory departure flights using a regional automated telemetry network (n = 30 stations) extending across a portion of the U.S. Atlantic Bight region, a section of the U.S. Atlantic coast, and adjacent waters of the Atlantic Ocean extending from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. Most adults departed within a 10-day window from July 19 to July 29, migrated nocturnally, and over 75% of individuals departed within 3 hr of local sunset on evenings with supportive winds. Piping Plovers migrated offshore directly across the mid-Atlantic Bight, from breeding areas in southern New England to stopover sites spanning from New York to North Carolina, USA, over 800 km away. During offshore migratory flights, Piping Plovers flew at estimated mean speeds of 42 km hr^{-1} and altitudes of 288 m (range of model uncertainty: 36–1,031 m). This study provides new information on the timing, weather conditions, routes, and altitudes of Piping Plovers during fall migration. This information can be used in estimations of collision risk that could potentially result from the construction of offshore wind turbines under consideration across large areas of the U.S. Atlantic OCS.

Keywords: automated radio telemetry, *Charadrius melodus melodus*, migration, offshore wind energy, Piping Plover

LAY SUMMARY

- The Atlantic coast population of the Piping Plover is listed as "Threatened" under the U.S. Endangered Species Act.
- Previously, little was known about exactly when, under what conditions, and along which routes these shorebirds undertake their migration from nesting areas along the Atlantic coast to wintering sites extending to eastern Caribbean islands.
- To help fill these information gaps, we attached miniature digitally coded VHF transmitters to 150 adult Piping Plovers at nesting areas in southern New England and constructed 35 radio antenna towers along the Atlantic coast to track their routes during fall migration.
- Most of the Piping Plovers in our study departed from southern New England in late July, at sunset, with tailwinds supporting offshore migratory flights across the mid-Atlantic Bight to stopover areas spanning from coastal New York to North Carolina.
- During offshore migratory flights, Piping Plovers flew at estimated mean speeds of 42 km hr^{-1} and at altitudes of 288 m.
- Our results provide the first empirical data on Piping Plover flight routes, altitudes, and weather conditions during fall migration.
- This information can be used to estimate collision risk from offshore wind turbines currently under consideration across large areas of the U.S. Atlantic Ocean.

Las condiciones del viento de apoyo influencian los movimientos en alta mar de *Charadrius melodus melodus* durante la migración de otoño

RESUMEN

Antes del desarrollo a gran escala de emprendimientos de energía eólica en alta mar a lo largo de la plataforma continental exterior (PCE) del Atlántico de EEUU, se necesita información de la ecología y las rutas migratorias de la especie amenazada a nivel federal *Charadrius melodus melodus* para realizar evaluaciones de riesgo conforme a la Ley de Especies en Peligro de Extinción. Marcamos adultos de *C. m. melodus* (*n* = 150) con transmisores VHF codificados digitalmente en dos áreas reproductivas en la región sur de Nueva Inglaterra de la costa atlántica de EEUU desde 2015 a 2017. Seguimos sus vuelos de partida migratoria usando una red regional de telemetría automatizada (*n* = 30 estaciones) dispuesta a lo largo de una porción de la región de la ensenada del Atlántico de EEUU, una sección de la costa atlántica de EEUU y las aguas adyacentes del Océano Atlántico que se extiende desde el Cabo Cod, Massachusetts hasta el Cabo Hatteras, Carolina del Norte. La mayoría de los adultos partieron dentro de una ventana temporal de 10 d del 19 al 29 de julio, migraron de noche y más del 75% de los individuos partieron durante las últimas 3 hr del atardecer local en tardes con vientos de apoyo. *C. m. melodus* migró a alta mar directamente a través de la ensenada del Atlántico medio, desde las áreas de cría en el sur de Nueva Inglaterra hasta los sitios de parada comprendidos entre Nueva York y Carolina del Norte, EEUU, a más de 800 km de distancia. Durante los vuelos migratorios en alta mar, los individuos de *C. m. melodus* volaron a velocidades estimadas promedio de 42 km hr^{-1} y altitudes de 288 m (rango de incertidumbre del modelo: 36–1,031 m). Este estudio brinda nueva información sobre las fechas, las condiciones temporales, las rutas y las altitudes de *C. m. melodus* durante la migración de otoño. Esta información se puede usar en estimaciones del riesgo de colisión que podría resultar de la construcción de turbinas eólicas en alta mar bajo consideración a lo largo de grandes áreas de la PCE del Atlántico de EEUU.

Palabras clave: Charadrius melodus melodus, energía eólica en alta mar, migración, radio telemetría automatizada

INTRODUCTION

In the U.S. Atlantic Outer Continental Shelf (OCS), over 5,492 km^2 is presently under lease agreement with the Bureau of Ocean Energy Management (BOEM) for development of commercial-scale offshore wind energy facilities and an additional 12,976 km^2 is in the planning stages for potential leases (BOEM 2019). The only offshore wind energy facility currently operating in North America is a 5-turbine, 30-megawatt (MW) demonstration-scale facility near Block Island, Rhode Island, USA, that started operations in 2016 (Wilber et al. 2018). The potential adverse effects of offshore wind energy developments on avian species include collision mortality, behavioral changes near turbines in response to visual stimuli, and impacts from physical alteration of habitat in response to construction of turbines and other infrastructure (Fox et al. 2006). With large areas of the Atlantic OCS under consideration for development of offshore wind energy facilities, information on offshore movements and flight characteristics of high-priority bird species is needed for estimating exposure of birds to collision risks with wind turbines, and for developing strategies to manage adverse effects (BOEM 2017).

There is considerable variation among avian species in their vulnerability to offshore wind energy developments (Furness et al. 2013), thus quantifying species-specific traits that influence collision risk factors is critical (May et al. 2017). Although much is known about flight characteristics (e.g., flight altitude, avoidance behaviors) of many species of marine birds in offshore habitats (Furness et al. 2013, Johnston et al. 2014), less is known about small-bodied (<100 g) shorebirds that migrate nocturnally. This is primarily due to technological limitations of monitoring their movement ecology. Much of the information that has been previously documented on offshore movements of shorebirds is from radar-based tracking studies (Richardson 1976, Williams and Williams 1990, Dirksen et al. 2000, Langston and Pullan 2003). However, radar technology used to study bird movements is limited by the operational range of the radar and often lacks the resolution required to identify birds to the species level (Desholm et al. 2006). The use of individual-based tracking technologies, such as radio or satellite transmitters, can provide more detailed information on the movements and behavior of known individuals across time and space (Robinson et al. 2010). However, only recently has tracking technology become available for monitoring movements of small-bodied avian species across large spatial extents (Taylor et al. 2017), such as the U.S. Atlantic region (Loring et al. 2017, 2018, 2019).

Recently, biologists have used digitally coded VHF transmitters to assess migration departure decisions and stopover ecology of smaller shorebirds (Anderson et al. 2019, Holberton et al. 2019). During preconstruction monitoring, assessments of the exposure risk of migratory birds to offshore wind energy facilities require species-specific information on migratory routes, flight altitudes, temporal (diel and seasonal) variation in movement patterns, and variation in environmental conditions associated with offshore movements. Information about meteorological conditions associated with offshore flights is especially important for risk assessments, as birds may be at higher risk of collision with offshore wind turbines during inclement weather (e.g., high winds, precipitation, low visibility) due to impaired visibility and avoidance responses (Exo et al. 2003).

Migratory shorebirds may be especially susceptible to the potential effects of wind energy development due to their use of coastal habitats and migratory routes that may occur offshore (O'Connell et al. 2011). One species of concern is the federally threatened Atlantic coast population of the Piping Plover (*Charadrius melodus melodus*; U.S. Fish and Wildlife Service 1985). This population nests from North Carolina, USA, to Newfoundland, Canada (Elliott-Smith and Haig 2020), and winters ~800–2,000 km from its breeding grounds, from North Carolina to Florida, as well as on islands in the Caribbean (Gratto-Trevor et al.

2012, 2016; Cohen et al. 2018, Weithman et al. 2018). Little is known about factors that affect the departure decisions and specific migratory routes that Atlantic Coast Piping Plovers take from their breeding grounds to stopover sites and wintering areas (Burger et al. 2011). Further, there is a lack of information regarding the degree to which Piping Plovers utilize shorter coastal flights (1–100 km) between migratory stopover areas or intermediate-distance offshore migratory flights (100–2,000 km; O'Reilly and Wingfield 1995, Hedenström et al. 2013). A large proportion of Atlantic Coast Piping Plovers winters in the Bahamas, or Turks and Caicos (Haig and Plissner 1993, Gratto-Trevor et al. 2016); therefore, these individuals must undertake sustained offshore flights during their annual cycle. However, their migratory routes between breeding or stopover sites and wintering areas have not yet been described (O'Connell et al. 2011).

To help address these information gaps, we assessed movements of adult Piping Plovers during fall migration in relation to demographic, temporal, and meteorological covariates. We tracked Piping Plovers using digitally coded VHF transmitters monitored by a regional array of automated telemetry stations along the U.S. Atlantic coast, extending from Cape Cod, Massachusetts, to Back Bay, Virginia, USA. We conducted this study in collaboration with the Motus Wildlife Tracking System, a coordinated network of tagging projects and automated telemetry stations, with project-specific regional nodes distributed across the western Hemisphere (Taylor et al. 2017). Our specific objectives were to (1) model migratory departure decisions of Piping Plovers relative to demographic variation, temporal (diel and seasonal) variation, and meteorological conditions (i.e. wind speed, wind direction, barometric pressure, temperature, visibility, precipitation); (2) model trajectories of migratory departure flights from breeding areas; and (3) summarize routes, flight metrics, and weather conditions of migratory flights.

METHODS

Study Area

Our study area extended along the U.S. Atlantic coast and adjacent waters of the Atlantic OCS that had coverage from our regional array of automated radio telemetry stations; it extended from Cape Cod, Massachusetts, to Back Bay, Virginia (Figure 1). As of January 2020, there were 11 BOEM Commercial Renewable Energy Lease Areas covering 4,997 km^2 within the study area (Figure 1). These Renewable Energy Lease Areas were located in Rhode Island Sound and adjacent offshore waters of Massachusetts (2,106 km^2), New York Bight (321 km^2), and adjacent waters offshore of New Jersey (1,391 km^2), Delaware (390 km^2), Maryland (322 km^2), and Virginia (467 km^2). Additional Renewable Energy Planning Areas (under consideration for designation as lease areas) were located within our study area off the coast of Massachusetts (1,578 km^2) and New York (7,188 km^2).

Tagging sites in Massachusetts included Monomoy National Wildlife Refuge (NWR; 41.6004°N, 69.9911°W) and adjacent South Beach in the town of Chatham, on Cape Cod. In 2017, these sites collectively supported 61 pairs or about 9% of the Massachusetts population of 668 pairs of Piping Plovers (Levasseur 2017). In Rhode Island, tagging sites included several locations along the state's southern coast, ranging from Napatree Point in Westerly (41.3103°N, 71.8742°W) to Sachuest NWR in Middletown (41.4862°N, 71.2524°W). Across all sites in Rhode Island, the highest trapping effort for Piping Plovers was on Trustom Pond NWR (41.3695°N, 71.5809°W). Trustom Pond NWR contains the highest nesting population of Piping Plovers in Rhode Island, accounting for 31% of nesting pairs monitored by USFWS staff in 2017 (J. White, USFWS, Rhode Island Wildlife Complex, Charlestown, Rhode Island, personal communication).

Tagging and Tracking Piping Plovers

From 2015 to 2017, field staff surveyed potential Piping Plover nesting habitat in each breeding area 3–5 days per week to monitor breeding chronology and nest success of Piping Plovers from early May to early August. From May 9 through June 27, we trapped adult Piping Plovers during the incubation period (3–14 days prior to estimated hatching dates) during daylight hours (approximately 0800 to 1600 hours) on days with no precipitation, fog, or windy (>15 km hr^{-1}) conditions. At Rhode Island beaches, site managers placed circular wire anti-predator exclosures over selected nests to minimize egg depredation (Melvin et al. 1992). For exclosed nests, we used a modified trap design by attaching hardware cloth with a mist-net funnel to the exterior of the exclosure. For nests that were not exclosed, we trapped adult plovers using walk-in funnel traps (Hall and Cavitt 2012).

Each plover was banded with a single, dark blue Darvic leg band on the right tibiotarsus and a green flag engraved with a unique 3-digit alphanumeric code on the opposite tibiotarsus. Coded flags were issued in collaboration with researchers at Virginia Polytechnic Institute and State University (Blacksburg, Virginia) as part of a larger population dynamics study. We measured morphometrics on all individuals including mass (±0.1 g), and collected 3–5 contour feathers from each bird for molecular-based determination of sex (Avian Biotech, Gainesville, Florida, USA). We then attached a digitally coded VHF transmitter ("nanotag"; Lotek Wireless, Ontario, Canada) by clipping a small area of feathers from the interscapular region and

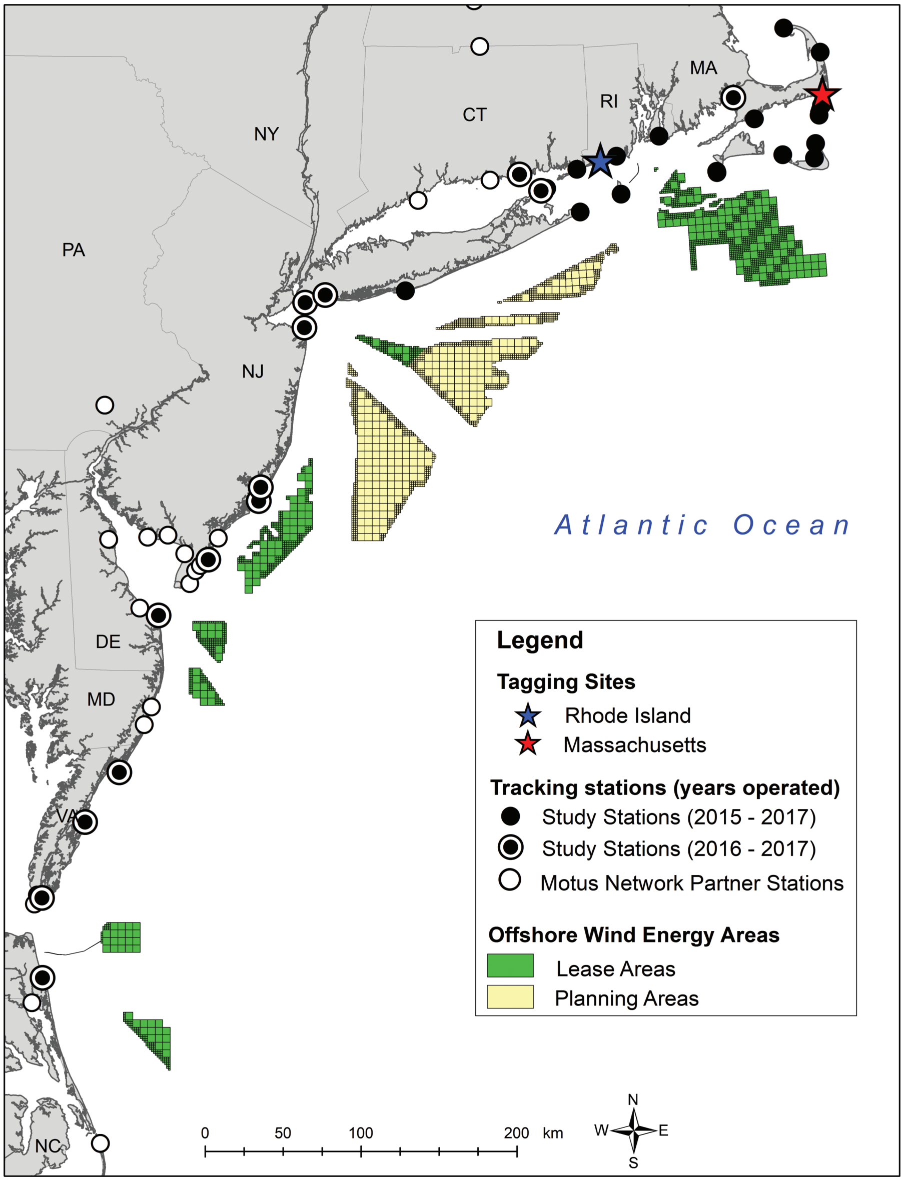

FIGURE 1. Map of study area (2015–2017) in U.S. mid-Atlantic Bight region, showing locations of tagging sites at breeding areas in Rhode Island (RI; blue star) and Massachusetts (MA; red star). Locations of tracking stations operated for study shown as either black dots (for stations operated from 2015 to 2017) or black and white dots (for stations operated from 2016 to 2017). Stations within the study area that were operated by partners in the Motus Wildlife Tracking System between 2015 and 2017 are shown as white dots. Potential areas for offshore wind energy development (as of January 2020) within the study area are shown in green (Lease Areas) and yellow (Planning Areas).

gluing the tag to the feather stubble, skin, and overlaying contour feathers with cyanoacrylate gel. In 2015 and 2016, each plover was fitted with a 1.1-g nanotag (Lotek NTQB-4-2; transmitter body: 12 × 8 × 8 mm). In 2017, each plover was fitted with a 0.67-g nanotag (Lotek NTQB-3-2; 12 × 6 × 5 mm). Both tag models had a 16.5-cm antenna. The transmitter and attachment materials weighed <3% of the body mass of tagged plovers; <2% for the 0.67-g model. Handling time, from capture to release, was ~15–30 min per bird.

All transmitters were programmed to emit signals at fixed burst intervals on a shared frequency of 166.380 MHz from activation through the end of battery life. Burst intervals were unique to each transmitter and ranged from 4 to 6 s. The expected life of the 1.1-g nanotags ranged from 146 days (4-s burst interval) to 187 days (6-s burst interval). The expected life of the 0.67-g nanotags ranged from 72 days (4-s burst interval) to 92 days (6-s burst interval). There was no evidence that trapping or tagging plovers affected their productivity as measured by the number of chicks fledged per nesting attempt (Stantial et al. 2018) or their apparent annual survival rates (Stantial et al. 2019).

A targeted array of automated radio telemetry stations tracked tagged birds, in coordination with the broader Motus Wildlife Tracking Network (Taylor et al. 2017). In 2015, we operated an array of 16 coastal telemetry stations in Massachusetts, Rhode Island, and New York. During 2016, 14 additional coastal stations tracked plovers at sites ranging from Cape Cod, Massachusetts, to Back Bay, Virginia. During each year of the study, we downloaded data from all stations approximately every 2 weeks from April through November to ensure that the stations operated continuously from tag deployment through migratory departure. Loring et al. (2019) provides a detailed description of the locations, specifications, and operational dates of each tracking station.

Most of the stations operated for this study had a 12.2-m radio antenna mast that supported six 9-element (3.3 m) Yagi antennas mounted in a radial configuration at 60° intervals. At some sites, stations consisted of up to 4 Yagi antennas, or a single omni-directional antenna, attached to existing structures. At each of the tracking stations, the antennas were connected to a receiving unit (Lotek SRX) via coaxial cables. We operated each receiving station 24 hr per day using one 140-watt solar panel and two 12-volt deep-cycle batteries. When tagged birds were within detection range, the receivers automatically recorded transmitter ID number, date, time stamp, antenna (defined by monitoring station and bearing), and signal strength value of each detection.

Detection range of each station varied with the height of the receiving antennas (meters above sea level: m.a.s.l.), altitude of the tagged bird, and the signal gain properties of the transmitter and receiver (Loring et al. 2019). The maximum estimated detection range of our configuration, with receiving antennas at 12.2 m.a.s.l. was ~20 km to birds flying at altitudes of 25 m.a.s.l. (lower limit of rotor swept zone [RSZ] of offshore wind turbines), and ~40 km to birds flying at altitudes of 250 m.a.s.l. (upper limit of RSZ of offshore wind turbines). Birds flying at higher altitudes (>1,000 m.a.s.l.) may be detected at ranges exceeding 80 km (Loring et al. 2019). Stations operated by partners in the Motus network had a variety of configurations of antennas and receiving equipment, with a typical detection range of ~15 km (Taylor et al. 2017).

Post-processing of Telemetry Data

We used the program R 3.4.1 (R Core Team 2017) and associated packages to post-process and analyze detection data. To filter detection data, we used an algorithm in the R package *Sensorgnome* (Brzustowski 2015) that removed false detections from the raw VHF telemetry data (Loring et al. 2019). The algorithm was based on the following default parameters applied to each unique transmitter: minimum of 3 consecutive bursts required to comprise a "run" (i.e. run length), a maximum of 20 consecutive missed bursts allowed within each run, and a maximum deviation of 4 ms from a tag's unique burst interval between its consecutive bursts (Brzustowski 2015). We selected these parameters according to conservative recommendations from Motus network developers (Taylor et al. 2017). In addition to data from the automated radio telemetry stations that we operated for the present study, we also incorporated detection data from stations that partners operated, as part of the Motus Wildlife Tracking System (Motus 2016).

Movement Models

A 2-beam radio propagation model estimated locations and altitudes of tagged birds (Janaswamy 2001, Janaswamy et al. 2018) following methods described in Loring et al. (2019). This approach allowed for automated location estimation across individuals and accounted explicitly for variation relative to beam orientation and flight altitudes (Janaswamy 2001, Janaswamy et al. 2018). Model workflow proceeded in 6 steps (Loring et al. 2019). In the first 2 steps, the target bird's location was estimated as the weighted mean among sequential locations: this we weighted by the inverse-square discrepancy in signal strength among all near-simultaneous detections, resulting in the lowest discrepancy between measured and predicted signal strength. We constrained these calculations by differentiating between local movements (at breeding or stopover areas) and nonstop flight (regional or migratory) movements. The constraints included (1) limits to a bird's possible flight speeds in the horizontal and vertical planes and (2) the assumption that, during directed flight, a bird limits variation in its horizontal and vertical speed. We constrained maximum flight speeds at 12 m s^{-1} for Piping Plovers (Hedenström et al 2013, Stantial and Cohen 2015). For the third step, we interpolated the estimated locations to 1-min time steps using a Brownian Bridge movement model to interpolate the temporally irregular detection sequences to regular intervals (Horne et al. 2007). We selected a 1-min time window to estimate locations as it represented movements at approximately a 1-km scale (given maximal flight speeds). This also helped to optimize the tradeoff between the advantage of adding more information (detections) to co-locate position, and the disadvantage of the bird's actual position changing within the time window.

In the fourth step, we downloaded meteorological data from the National Centers for Environmental Prediction North American Regional Reanalysis (NARR; National Oceanic and Atmospheric Administration 2017), which covered the study area at ~32-km^2 spatial resolution and 3-hr temporal resolution. We interpolated this

3-dimensional meteorological data to each 1-min record, and derived orientation and airspeed from flight speed and wind data (Kemp et al. 2012). In the fifth model step, we quantified occurrence in offshore waters using the output from the Brownian Bridge model, and calculated uncertainty as the standard deviation of location estimates in the horizontal plane. Finally, in the sixth model step, we extracted the magnitude of all meteorological and flight speed–related covariates to assess incidence in offshore waters, including flight direction and heading, wind support, and crosswinds.

Timing of Migratory Departure

We classified migratory departure events as nonstop southbound departure flights from breeding areas to nonbreeding grounds that were tracked by 2 or more stations within the telemetry array. Departure dates were assigned (day of year, with January 1 = day 1) corresponding to the onset of each departure event. To examine the timing of departure relative to daylight, we used the R package *maptools* (Bivand and Lewin-Koh 2016) to calculate the local time (in hours, EST) of sunset at each modeled location estimate. We then calculated the difference in time (in hours) between the local sunset and onset of migratory departure events. We used a 2-sample Mann–Whitney *U*-test in base R (function: *wilcox.test*) to compare timing of departure relative to the timing of local sunset between breeding locations (Massachusetts and Rhode Island).

Covariate Analysis of Migratory Departure Decisions

We performed an integrated analysis of all covariates (temporal, demographic, and meteorological) to predict migratory departure events using a nonlinear binomial logistic regression method, boosted generalized additive models (GAMs, R package *mboost* using function *gamboost*; see also Bühlmann and Hothorn 2007). The nonlinear specification of these models allowed for flexibility in the response–covariate relationships and aligned with our objective of prioritizing explanatory over predictive power. We included the following covariates in the boosted GAM model: bird ID (random intercept), day of year, wind direction (circular, in degrees true N), wind speed ($m\ s^{-1}$), precipitation accumulation ($kg\ m^{-2}$), visibility (m), Δ air temperature (the change in air temperature over the preceding 24-hr period, in °C), and Δ pressure (the change in pressure over the preceding 24-hr period, in Pa). We also included 2 first-order interaction terms: date*location (MA or RI) and date*sex (male or female).

We chose an inverse logit-link regression formulation, calculating daily migratory departure events (coded as 1) and nonevents (coded as 0) for each individual, starting on the conclusion (fledge or fail date) of their final nesting attempt and ending on the date that occurred 24 hr prior to the onset of migratory departure. For days when birds did not depart (i.e. nonevents), we calculated the daily mean of each meteorological covariate within ±3 hr of local sunset to represent conditions when birds could have left because 78% of actual departure events occurred within this time window. For departure events, we calculated the mean of each meteorological covariate within 3 hr prior to the onset of departure, to represent conditions that plovers experienced prior to takeoff. We calculated means of meteorological covariates using the R packages *plyr* (Wickham 2011) and *lubridate* (Grolemund and Wickham 2011). We calculated the mean wind direction that the wind was blowing toward based on the circular distribution using the package *Circular* (Agostinelli and Lund 2017).

The boosted GAM approach allowed us to estimate both the relative "influence" of covariates on migratory departure (i.e. the percentage reduction in deviance attributable to each predictor), and the "relative" response to these covariates (Hastie et al. 2009). In this formulation, we incorporated probability of migratory departure as an "inverse logit-link," with responses to each covariate presented as partial contributions to the likelihood (log-transformed odds ratio) of a migratory departure event occurring (i.e. the higher the contribution, the increased predicted likelihood of a migratory departure event). Responses represent the contribution of a given covariate to the likelihood of migratory departure, quantified by log-transformed odds ratio of migratory departure.

Additional advantages of this boosted GAM method are that, in being additive, it fits nonlinear and independent responses to each covariate. The boosted GAM approach iteratively summed simple regressions based on single-covariate "learner" functions, each chosen to minimize an equivalent loss function based on binomial predictors (see Bühlmann and Hothorn 2007). The additive approach facilitated estimation of the relative "influence" of each covariate, using the number of boosts choosing that covariate, to minimize the current loss. We selected model parameters to reduce possible bias and overfitting (Bühlmann and Hothorn 2007), an additional advantage of boosted methods over (non-boosted) GLMs or GAMs, which can be prone to overfitting (Randin et al. 2006). We fit the model incrementally using small step sizes or "shrinkage" (default 0.25) of each iterative sub-model (Maloney et al. 2012). We used 1,000 boosts per analysis and verified that this was a reasonable number of iterations using the function *cvrisk* (cross-validated risk) with a specific number of separate "folds" (i.e. 4 independently sampled fits). We fit responses to the categorical covariates (sex and location) using linear learner functions (resulting in fixed effects for each category). Responses to each individual (bird ID) were treated as random intercepts, and responses to all the meteorological covariates were fit using cubic p-splines. The package also allowed cyclical responses to the periodic covariates (wind direction). Finally, to assess the significance of the predicted covariate responses, we performed a bootstrap analysis using function *confint* with 1,000 model fits to produce 95% confidence intervals for each covariate response.

We mapped migratory trajectories of all Piping Plovers tracked during departure from breeding areas that had nonstop flight speeds ≥5 m s^{-1}. We used these tracks to calculate summary statistics (mean, SD, range) of migratory flights in the mid-Atlantic Bight region. Flight metrics included duration (hr), distance (km), speed (km hr^{-1}), and altitude (in m.a.s.l.). We report summary statistics of meteorological conditions associated with nonstop migratory flights (i.e. wind direction, wind speed, wind support, visibility, air temperature, and atmospheric pressure).

RESULTS

Tag Attachment and Retention

From 2015 to 2017, we tagged 50 adult Piping Plovers annually at Monomoy NWR and adjacent beaches in Chatham, Massachusetts (n = 25 per year), and on beaches in southern Rhode Island (n = 25 per year) from Napatree Point in Westerly to Sachuest NWR in Middletown. Based on genetic analysis of contour feathers, 52% (n = 150) of tagged plovers were females, 45% were male, and the sex of the remaining 3% was undetermined; sex ratios were unbiased across sites. Based on observations by field staff, 25% of plovers in the study dropped their transmitters on the breeding grounds prior to post-breeding migration (range: 16–32% of plovers observed with dropped tags annually). The number of dropped transmitters was lowest in 2017 when we used a lighter (0.67 g) model of transmitter. We detected plovers with active transmitters by the tracking array for a mean of 46 days (SD = 27 days, range: 0–102 days).

Timing of Migratory Departure

The automated telemetry array detected migratory departures of 65 Piping Plovers from 2015 to 2017 (2015: n = 19; 2016: n = 20; 2017: n = 26), with flights for 39 plovers from breeding areas in Massachusetts (n = 20 females, n = 19 males) and 26 plovers from breeding areas in Rhode Island (n = 13 females, n = 13 males). Overall, most tagged plovers departed in a 10-day window between July 19 and July 29 (25th–75th quartiles; Figure 2).

Most (78%) departure flights from breeding areas were initiated within 3 hr of local sunset, with variation in timing of departure relative to sunset by location (W = 304, P = 0.006; Figure 3). Plovers from Massachusetts departed an average of 1.91 hr before timing of local sunset (SD = 2.67 hr, range: 4.57 hr before to 8.01 hr after local sunset). Plovers from breeding areas in Rhode Island departed an average of 0.69 hours before timing of local sunset (SD = 3.3 hr, range: 10.72 hr before to 6.01 hr after local sunset).

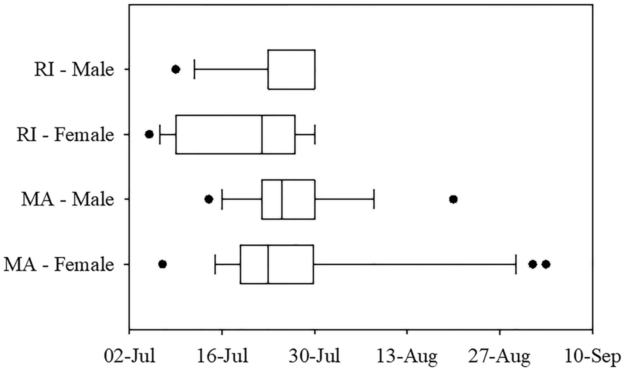

FIGURE 2. Boxplots of migratory departure dates by sex for Piping Plovers tagged in Massachusetts (MA; n = 20 females and 19 males) and coastal Rhode Island (RI; n = 13 females and 13 males), USA, from 2015 to 2017, showing median (bold midline), third and first quartiles (upper and lower limits of the box), interquartile range × 1.5 (whiskers), and outliers (points).

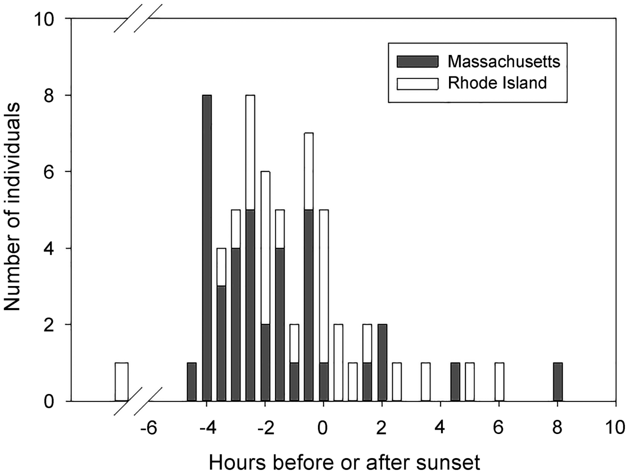

FIGURE 3. Timing of migratory departure of tagged Piping Plovers (n = 65) from breeding areas in Massachusetts and Rhode Island, USA, relative to timing of local sunset (hours EST), 2015 to 2017.

Covariate Analysis of Migratory Departure Decisions

Wind direction and date were the strongest predictors of migratory departure of Piping Plovers from their breeding grounds based on the boosted GAM covariate analysis (Table 1). Peak departures occurred when winds were blowing to the southwest (Figure 4A), from late July through early August (Figure 4B). Interaction terms with breeding area and date indicated that plovers from Massachusetts departed slightly later (through early September) relative to plovers from Rhode Island (Figure 4C), and that males were more likely to depart later relative to females (Figure 4D). There were weak associations with migratory

TABLE 1. Fitting functions and selection frequencies of environmental and temporal covariates utilized in a binomial Boosted GAM analysis of migratory departures of tagged Piping Plovers (*n* = 65) from breeding areas in Massachusetts and Rhode Island, USA, 2015–2017.

Covariate (units)	Fitting function	Selection frequency
Wind direction (degrees true N)	cyclical p-spline	0.35
Date	p-spline	0.27
Date * Location	p-spline * categorical interaction	0.13
Date * Sex	p-spline * categorical interaction	0.12
Δ Air temperature (°C)	p-spline	0.11
Δ Pressure (Pa)	p-spline	0.01
Bird ID	Random intercept	0.00
Wind speed (m s^{-1})	p-spline	0.00
Precipitation (kg m^{-2})	p-spline	0.00
Visibility (m)	p-spline	0.00

departures during decreasing air temperatures (Figure 4E) and increasing atmospheric pressure (Figure 4F) over the preceding 24-hr period.

Migratory Departure Trajectories

The array tracked migratory trajectories for 33 plovers from breeding areas in Massachusetts and 19 plovers from breeding areas in Rhode Island (Figures 5 and 6). Among plovers tracked during departure from breeding areas in Massachusetts, 91% (*n* = 30) followed a south-southwest trajectory across Nantucket Sound, and the remaining 9% (*n* = 3) departed to the west across Rhode Island Sound toward Long Island, New York. Most (67%, *n* = 22) plovers tracked during departure from breeding areas in Massachusetts were last detected by the telemetry array while in flight over waters south of Nantucket, due in part to limited numbers of stations in the mid-Atlantic region during 2015 (Figure 5). The telemetry array tracked flights of the remaining 33% (*n* = 11) offshore across the mid-Atlantic Bight to coastal areas ranging from Long Island, New York, to North Carolina.

All Piping Plovers tracked during migration from breeding areas in Rhode Island (*n* = 19) departed on south-southwest trajectories between Block Island Sound and eastern Long Island Sound and 68% (*n* = 13) were last detected within this region. The remaining 32% (*n* = 6) were tracked offshore across the mid-Atlantic Bight to coastal areas ranging from New Jersey to North Carolina.

Migration Routes Across the Mid-Atlantic Bight

The automated radio telemetry array tracked migratory flights of 17 plovers (*n* = 11 from Massachusetts and *n* = 6 from Rhode Island) across the mid-Atlantic Bight (Figure 6). Mean model uncertainty (68th percentile error) in the x and y coordinates was 23 km (SD = 13 km, range: 9–53 km). Mean distance of flights tracked across the mid-Atlantic Bight was 579 km (SD = 209 km, range: 163–811 km). Mean duration of flights tracked was 17.5 hr (SD = 10.4 hr, range: 3.0–39.8 hr), with a mean estimated flight speed of 42 km hr^{-1} (SD = 17 km hr^{-1}, range: 20–72 km hr^{-1}). Based on model estimates, mean altitude of offshore flights across the mid-Atlantic Bight was 288 m.a.s.l. (SD = 79 m.a.s.l., overall range of model uncertainty: 36–1,031 m.a.s.l.).

Piping Plovers crossed the mid-Atlantic Bight when winds were blowing to the southwest (circular mean = 238°) at a mean wind speed of 7.8 m s^{-1} (SD = 3.0 m s^{-1}; range: 2.6–13.5 m s^{-1}), which provided a mean wind support of 4.3 m s^{-1} (SD = 5.7 m s^{-1}; range: −5.8 to 11.8 m s^{-1}; Appendix Table 2). During offshore flights, visibility was high (mean = 18 km; SD = 19 km, range: 14–20 km), precipitation was variable (mean = 0.27 kg m^{-2}; SD = 0.39 kg m^{-2}, range: 0–1.27 kg m^{-2}), mean air temperature was 22°C (SD = 3°C; range: 19–28°C), and mean atmospheric pressure was 101,295 Pa (SD = 389 Pa; range: 100,709–102,139 Pa).

DISCUSSION

We used a network of automated telemetry stations to model the fall migration ecology of the federally threatened Atlantic Coast Piping Plover in relation to proposed offshore wind energy developments in the region. Most Piping Plovers initiated migration during the post-breeding period in mid- to late July, within 3 hr of local sunset, when winds were blowing to the southwest. These wind conditions supported direct, offshore flights from breeding areas in southern New England to stopover areas in the mid-Atlantic. Our study provides the first empirical evidence that Piping Plovers migrate across the Atlantic OCS, rather than taking a more circuitous route along the coast, addressing a key information gap for this species (Burger et al 2011).

As with many other avian species, Piping Plovers in the present study initiated migration near sunset on evenings with meteorological conditions advantageous to sustained flight, such as wind assistance and the passage of fronts

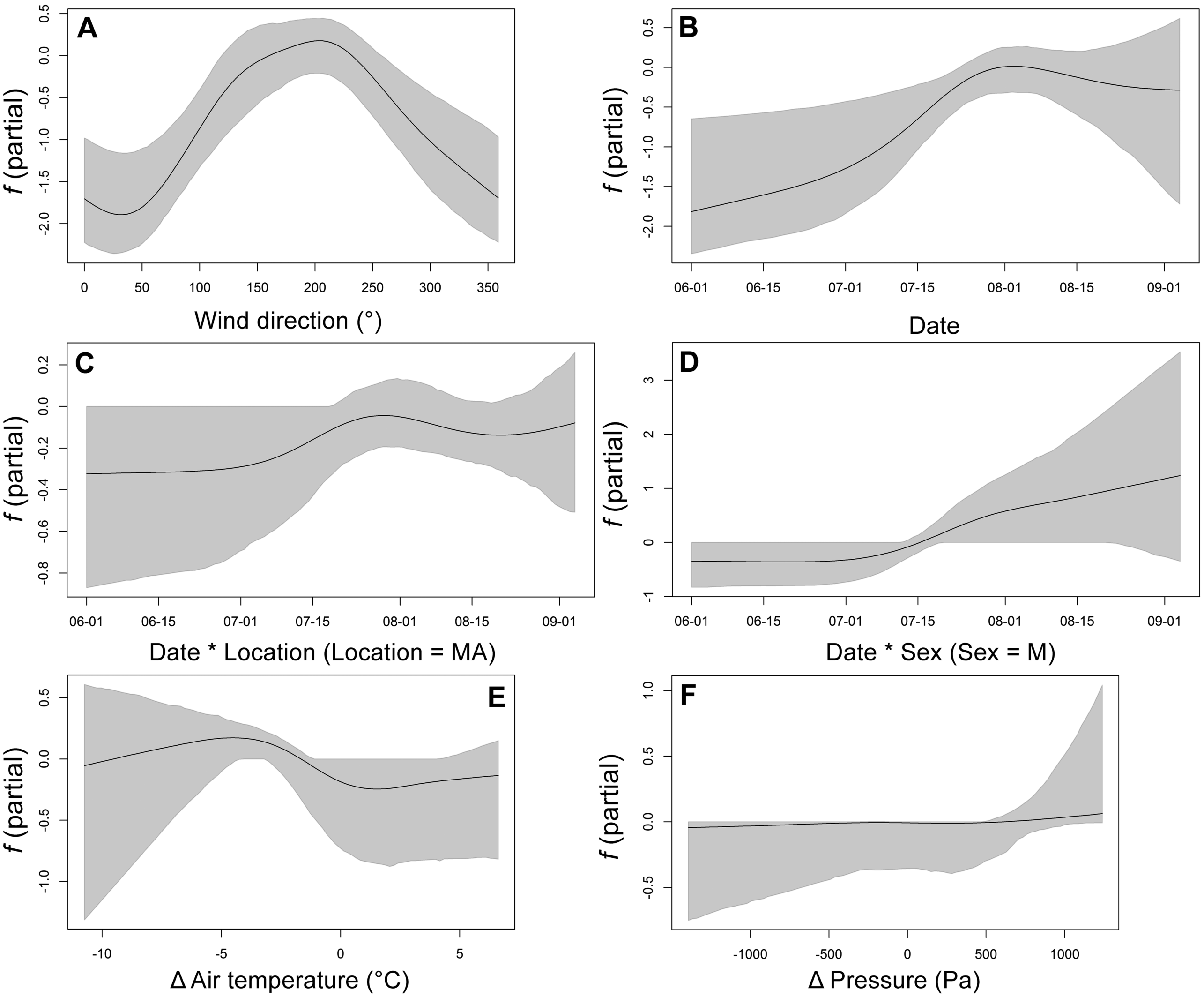

FIGURE 4. Predicted effects of covariates on migratory departure decisions of Piping Plovers ($n = 65$) from breeding areas in Massachusetts (MA) and Rhode Island (RI), USA, from 2015 to 2017: (**A**) wind direction (in degrees clockwise from geographic north that the wind is blowing toward); (**B**) date; (**C**) date*location interaction term (with location "MA" shown); (**D**) date*sex interaction term (with sex "male" shown); (**E**) Δ air temperature (change in °C over the preceding 24-hr period, where negative values indicate decreasing temperatures and positive values indicate increasing temperatures); (**F**) Δ air pressure covariate (change in Pa over the preceding 24-hr period, where negative values indicate decreasing pressure and positive values indicate increasing pressure). The *x*-axis shows the Boosted GAM prediction for the partial contribution of each covariate. The *y*-axis shows the likelihood (log-transformed odds ratio or *f*-partial) of migratory departure among Piping Plovers. The gray-shaded area represents the 95% confidence interval for the response based on 1,000 bootstrapped models.

(e.g., falling air temperatures, rising atmospheric pressure; Brooks 1965, Able 1973, Richardson 1978, Gill et al. 2014, Shamoun-Baranes et al. 2017, Anderson et al. 2019). Wind assistance reduces energy expenditure during long-distance flights, thus wind selectivity prior to departure is thought to be one of the primary factors determining departure decisions (Richardson 1978, Butler et al. 1997, Dossman et al. 2016, McCabe et al. 2017, Wright et al. 2018). Nocturnal migration is also thought to be advantageous for some species due to increased diurnal foraging opportunities prior to and after a migration bout, and reduced predation risk from raptors (Kerlinger and Moore 1989, Lank 1989, Alerstam 2009). In addition, atmospheric conditions may be more favorable to migratory flights at night due to reductions in turbulence and evaporative water loss, relative to daytime conditions when winds tend to be stronger and the air less humid (Kerlinger and Moore 1989). These conditions supported a shorter direct ocean crossing to stopover areas in the mid-Atlantic, rather than a longer route following the coast.

Assessments of avian collision risk with offshore wind turbines require information on flight relative to the

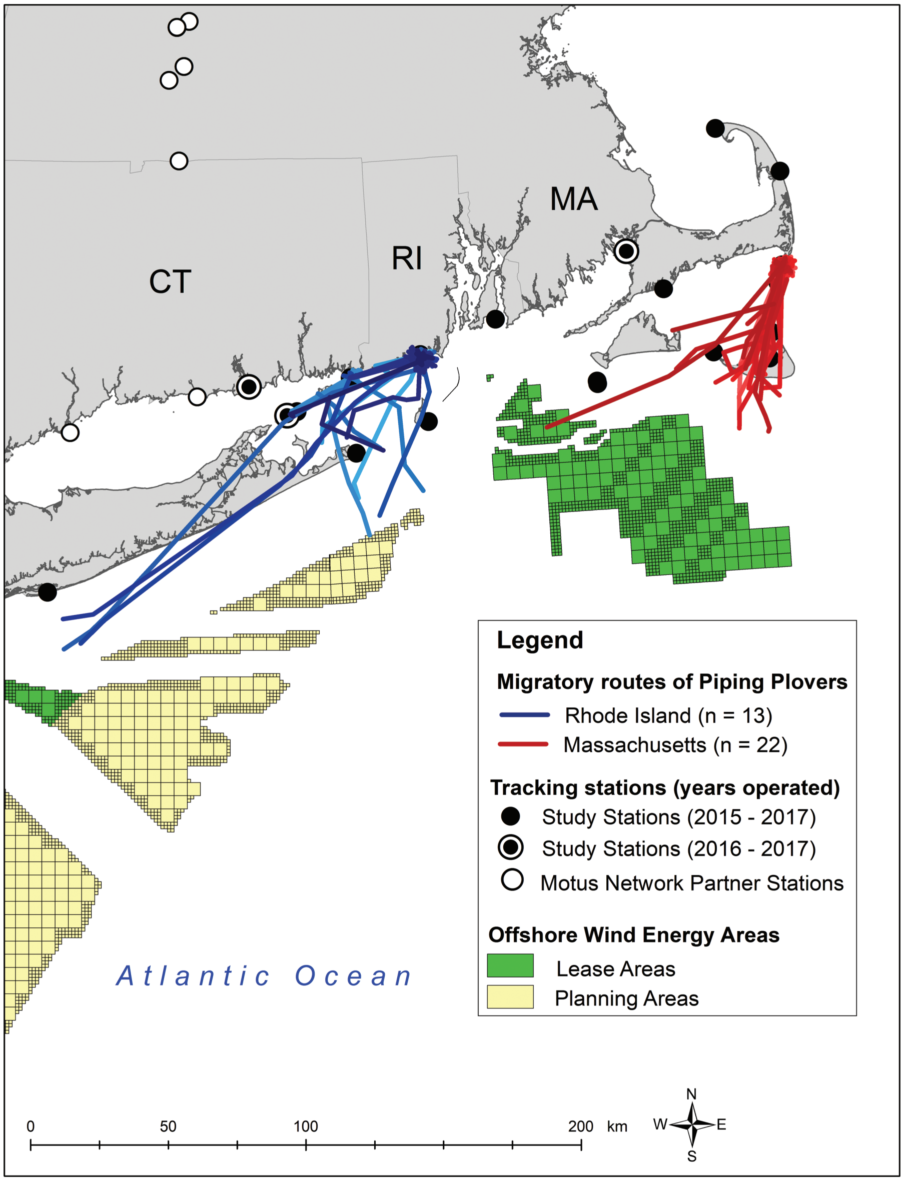

FIGURE 5. Modeled trajectories of tagged Piping Plovers from breeding areas in Rhode Island (RI; *n* = 13 in blue) and Massachusetts (MA; *n* = 22 in red), 2015–2017, showing individuals that were tracked through migratory departure from breeding areas.

Rotor Swept Zone (RSZ; Masden and Cook 2016), generally 25–250 m.a.s.l. Flight altitudes of Piping Plovers during migration have not been previously described, and this represents a significant information gap in assessments of risk from offshore wind energy developments to this species (Burger et al. 2011). In the present study, we applied models based on the theoretical relationship between horizontal detection range of signals received by automated radio telemetry stations, which increases with transmitter height above ground, to coarsely estimate flight altitudes when plovers were detected by 2 or more spatially separated stations simultaneously. These estimates indicated that mean offshore migratory flight altitudes of Piping Plovers crossing the mid-Atlantic Bight were mostly within or above the RSZ of offshore wind turbines. However, due to the coarse scale at which flight altitude was estimated, the estimates of exposure to the RSZ should be interpreted in the context of the model range (uncertainty) in plausible altitudes, which generally exceeded the range in estimated altitudes (Appendix Table 2). Thus, more detailed information on the migratory altitudes of Piping Plovers is needed to fully assess risks associated with developing offshore wind turbines throughout their migratory range.

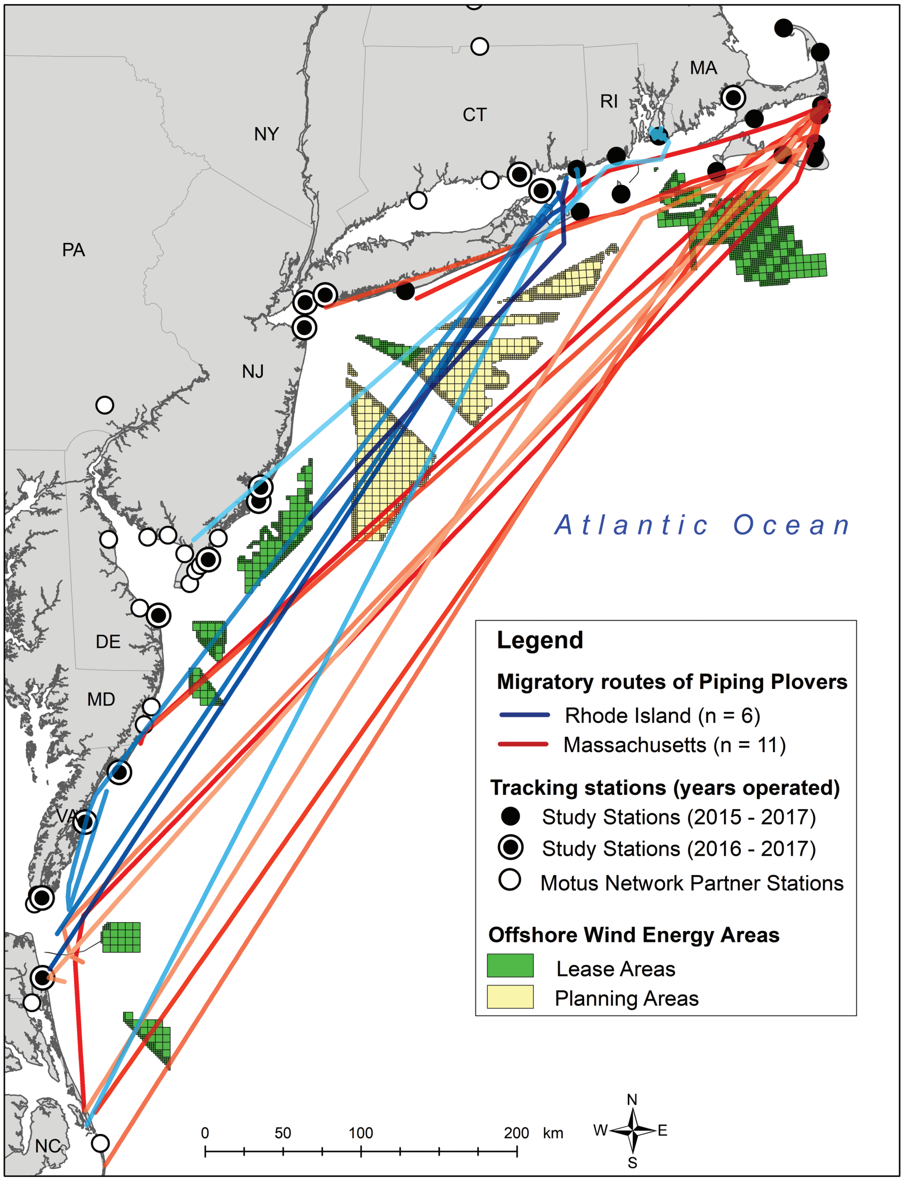

FIGURE 6. Modeled migratory routes of tagged Piping Plovers from breeding areas in Rhode Island (RI; *n* = 6) and Massachusetts (MA; *n* = 11), 2015–2017, showing individuals that were tracked across a broader portion of the mid-Atlantic Bight.

Information from offshore radar studies has recorded shorebirds migrating at altitudes exceeding 1–2 km (Richardson 1976, Williams and Williams 1990), whereas nearshore studies documented local and migratory flights of shorebirds occurring at altitudes <100 m (Dirksen et al. 2000, Langston and Pullan 2003). Risk of exposure to rotor swept altitudes may increase during takeoff and landing from stopover areas, emphasizing the need for determining setback distances when developing turbines near migratory stopover areas (Howell et al. 2019). In addition, flight altitudes of migratory birds may vary in response to weather as they search to find suitable tailwinds (Shamoun-Baranes et al. 2017, Senner et al. 2018). Migratory birds may also descend to lower altitudes during periods of limited visibility, low cloud ceiling, and/or inclement weather, increasing their risk of collision with offshore wind turbines (Hüppop et al. 2006, Senner et al. 2018). In addition, risk of collision is potentially higher at night due to reduced visibility of turbines (Exo et al. 2003) and attraction or disorientation effects from artificial lighting on turbine towers (Richardson 2000, Drewitt and Langston 2006). Future efforts to assess fine-scale movements of Piping Plovers will be of continued importance as additional wind energy facilities are developed in offshore waters and tracking technology continues to improve. Detailed tracking of flight altitudes and avoidance behavior is beyond the ability of current VHF technology within the Motus Network, although development of lightweight GPS transmitters (Senner et al. 2018) or VHF tags with embedded altimeters (Bowlin et al. 2015) may provide viable options for tracking fine-scale 3-D flight paths of small-bodied shorebirds in the near future.

Results from this study address high-priority information needs on the timing, conditions, and routes of Piping Plovers in offshore environments to support assessments of developing wind energy facilities throughout a portion of the U.S. Atlantic, extending from Cape Cod, Massachusetts, to Back Bay, Virginia. However, due to incomplete coverage from Motus network tracking stations along U.S. Atlantic coast, we limited the spatial scale of the analysis of movements to the bounds of the study area in the U.S. mid-Atlantic region. The study area contained a regional array of tracking towers that we strategically erected at coastal sites, spanning from Cape Cod, Massachusetts, to the north to Back Bay, Virginia, to the south, with direct line-of-sight to offshore areas of the U.S. mid-Atlantic Bight. Each tower was 10.2 m tall and had 6 high-range directional antennas arranged radially to track movements of birds in all directions. This design attempted to maximize the detection range and directionality of land-based towers but had limited coverage for detecting birds in offshore areas of the U.S. Atlantic OCS beyond 20 km from land. As offshore lease areas move into development phases, deployment of automated radio telemetry equipment on offshore structures offers a promising approach for collecting more detailed data needed for collision risk models, including information on passage rates through individual lease areas, diurnal vs. nocturnal flight activity, and coarse information on avoidance rates and flight altitudes.

Since large areas for development of offshore wind energy facilities are under consideration to the south of our regional telemetry array, including off the coast of North Carolina, USA, there is a need for more complete information on the movements of Piping Plovers throughout their entire migratory range to fully assess risk. Major migratory stopover areas for Piping Plovers in the mid-Atlantic include Ocracoke, North Carolina, where Weithman et al. (2018) estimated use by 15% of the Atlantic coast population with the first peak of migrants arriving in late July. Piping Plovers from breeding areas in New England remained at Ocracoke for over 40 days (Weithman et al. 2018), suggesting this may be an important stopover site for adults to complete prebasic molt-migration (Tonra and Reudink 2018) before moving on to wintering areas farther south (Gratto-Trevor et al. 2012, 2016; Cohen et al. 2018). Thus, Piping Plovers using this stopover area may be at risk of passing through lease areas off the coast of North Carolina, particularly if they depart along the direct route toward the Caribbean where over 30% of the population is estimated to winter (Gratto-Trevor et al. 2016).

Fully estimating exposure and collision risk of Piping Plovers to offshore wind turbines requires tracking technology capable of collecting high-resolution movement and altitude data throughout the entire migratory range and full annual cycle. GPS tracking technology may provide a viable solution for collecting high-resolution, 3-D movement data of small-bodied shorebirds in the near future, as lightweight transmitters become more widely available (Senner et al. 2018). Data on the migratory routes and flight altitudes of Piping Plovers from breeding areas throughout the Atlantic Coast is needed to fully assess population-level risks, as widespread development of offshore lease areas is planned throughout a large portion of the Atlantic OCS (BOEM 2019). There is presently a lack of information on the movements of Piping Plovers during spring (northbound) migration. Shorebirds may be more likely to migrate during inclement weather in spring due to less stable atmospheric conditions and time constraints to reach breeding areas (O'Reilly and Wingfield 1995). These conditions may lead to increased risk during spring relative to fall, including increased exposure to offshore wind turbines and other flight hazards (Richardson 2000). Future efforts to track full annual cycle movements of Piping Plovers and other avian species of conservation concern will be critical for assessments of cumulative impacts resulting from development of multiple offshore wind energy facilities throughout the migratory range.

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Data depository: Analyses reported in this article can be reproduced using the data provided by Loring et al. (2020).

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APPENDIX TABLE 2. Metrics of migratory flights across the mid-Atlantic Bight of Piping Plovers from U.S. Atlantic coast breeding areas in Massachusetts (MA) and Rhode Island (RI) in 2015 to 2017.

Aux	Sex	Loc	Start (EST)	End (EST)	Dist (km)	Length (hr)	Speed (km hr^{-1})	Alt (m)
6XW	F	RI	7/4/2015 19:41	7/5/2015 03:31	404	7.8	51	313
4NC	M	MA	7/15/2015 22:20	7/16/2015 01:20	163	3.0	55	272
2YK	M	MA	7/13/2015 19:10	7/14/2015 19:50	595	24.7	24	373
A8A	F	MA	9/2/2016 18:22	9/3/2016 22:12	811	27.8	29	342
KVV	F	MA	7/8/2016 17:23	7/8/2016 21:53	274	4.5	62	265
CAK	F	MA	7/19/2016 14:04	7/20/2016 9:34	803	19.5	41	284
AE9	M	RI	7/23/2016 21:16	7/24/2016 17:46	693	20.5	34	269
E4V	M	RI	7/23/2016 21:31	7/25/2016 1:31	635	28.0	23	92
CAK	F	MA	7/23/2017 15:32	7/24/2017 09:42	581	18.2	33	329
6VH	M	MA	7/23/2017 18:27	7/24/2017 06:37	359	12.3	33	99
KHM	M	MA	7/23/2017 17:04	7/25/2017 08:54	808	39.8	20	335
AAA	F	MA	7/23/2017 16:52	7/24/2017 20:42	719	27.8	26	329
UNN	M	MA	7/25/2017 15:42	7/26/2017 07:12	786	15.5	51	328
Y8M	M	MA	7/29/2017 21:41	7/30/2017 21:31	746	23.8	32	334
H3J	M	RI	7/29/2017 19:09	7/30/2017 03:18	585	8.2	72	281
XAP	M	RI	7/29/2017 19:14	7/30/2017 06:43	601	11.5	52	339
XMJ	F	RI	7/29/2017 18:44	7/29/2017 23:14	280	4.5	70	331