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*Research Article*

# Annual-Cycle Movements and Phenology of Black Scoters in Eastern North America

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**ABSTRACT** Sea ducks exhibit complex movement patterns throughout their annual cycle; most species use distinct molting and staging sites during migration and disjunct breeding and wintering sites. Although research on black scoters (*Melanitta americana*) has investigated movements and habitat selection during winter, little is known about their annual-cycle movements. We used satellite telemetry to identify individual variation in migratory routes and breeding areas for black scoters wintering along the Atlantic Coast, to assess migratory connectivity among wintering, staging, breeding, and molt sites, and to examine effects of breeding site attendance on movement patterns and phenology. Black scoters occupied wintering areas from Canadian Maritime provinces to the southeastern United States. Males used an average of 2.5 distinct winter areas compared to 1.1 areas for females, and within-winter movements averaged 1,256 km/individual. Individuals used an average of 2.1 staging sites during the 45-day pre-breeding migration period, and almost all were detected in the Gulf of St. Lawrence. Males spent less time at breeding sites and departed them earlier than females. During post-breeding migration, females took approximately 25 fewer days than males to migrate from breeding sites to molt and staging sites, and then wintering areas. Most individuals used molt sites in James and Hudson bays before migrating directly to coastal wintering sites, which took approximately 11 days and covered 1,524 km. Males tended to arrive at wintering areas 10 days earlier than females. Individuals wintering near one another did not breed closer together than expected by chance, suggesting weak spatial structuring of the Atlantic population. Females exhibited greater fidelity (4.5 km) to previously used breeding sites compared to males (60 km). A substantial number of birds bred west of Hudson Bay in the Barrenlands, suggesting this area is used more widely than believed previously. Hudson and James bays provided key habitat for black scoters that winter along the Atlantic Coast, with most individuals residing for >30% of their annual cycle in these bays. Relative to other species of sea duck along the Atlantic Coast, the Atlantic population of black scoter is more dispersed and mobile during winter but is more concentrated during migration. These results could have implications for future survey efforts designed to assess population trends of black scoters. © 2021 The Wildlife Society.

**KEY WORDS** annual cycle, black scoter, *Melanitta americana*, migration, movement, phenology.

Understanding migration patterns is an essential component of developing long-term conservation strategies for wildlife that range widely (Webster et al. 2002, Berger 2004, Allen and Singh 2016). Migration in birds involves a delicate balance between resource acquisition and energetic expenditure to maximize long-term survival and reproductive output (Alerstam et al. 2003). As environmental conditions change, this balance may be disrupted, leading to unforeseen demographic consequences (Newton 2006, Møller et al. 2008). Further, migratory connectivity plays a key role in structuring populations by regulating gene flow among individuals in the absence of physical barriers. Individuals that overlap during parts of the year but occupy separate habitats during pair formation may experience shared environmental and anthropogenic pressures but operate as genetically distinct population units (Talbot et al. 2015). In addition, migratory

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patterns are structured by complex intrinsic and extrinsic factors including external cues, genetics, learned behavior, prior conditions, sex, and inter- and intra-specific competition (Liedvogel and Lundberg 2014, Petersen and Savard 2015). This fine-scale variation can result in individual fitness differences and heterogeneity in sensitivity to external conditions and risk factors (Bêty et al. 2004). Predicting how populations of migratory species will respond to current and future conditions therefore requires an understanding of the factors influencing migratory behavior at the individual level (Marra et al. 2011).

Although many species of birds undertake long-distance migrations, waterfowl including sea ducks (Tribe: Mergini) exhibit unusually complex patterns because of additional movements to distinct molt sites and pre-breeding and post-breeding staging sites (Jehl 1990, Brodeur et al. 2002, Robert et al. 2002, Petersen and Savard 2015). Sea ducks are vulnerable during post-breeding molt when they simultaneously molt their flight feathers and become flightless for several weeks, and they generally aggregate in large groups during this time (Guillemette et al. 2007, Savard and Peterson 2015). Migratory staging sites, especially those used during post-breeding, appear to provide habitat and connectivity functions (Lamb et al. 2019). The selective use of habitat by sea ducks during remigial molt (Fox et al. 2014, Derksen et al. 2015, Lamb et al. 2020*b*), combined with strong fidelity to molt sites in some species (Phillips and Powell 2006, Savard and Petersen 2015), suggests sea ducks may be less adaptable to loss or degradation of molt sites compared to either breeding or wintering areas. In addition to habitat requirements, individual factors also contribute to variation in migration timing, routes, and patterns (Oppel et al. 2009). Sex-based differences are especially important in sea ducks because males attend breeding sites only during egg-laying (i.e., days to weeks), whereas females may remain at breeding sites for several months to incubate eggs and raise young (Savard et al. 2007). Thus, males spend relatively more time than females at non-breeding and molt sites (Eadie and Savard 2015). Understanding migratory patterns for sea ducks requires assessing how individual variation interacts with spatial heterogeneity to structure year-round movement decisions.

The black scoter (*Melanitta americana*) is considered a sea duck species of concern because of unknown population trends and possible declines across its range (Sea Duck Joint Venture 2014, Bowman et al. 2015). Two separate and genetically distinct populations of black scoter are recognized in North America: an Atlantic population that winters along the Atlantic Coast and Great Lakes and breeds in eastern North America, and a Pacific population that winters along the Pacific Coast and breeds in western Alaska (Bordage and Savard 2011, Sonsthagen et al. 2019). The species is subject to threats that vary throughout its annual range, including the effects of climate change on their boreal and sub-Arctic breeding, molting, and marine wintering areas (Soja et al. 2007, Pinsky et al. 2013), offshore energy development and resource extraction at wintering sites (Zipkin et al. 2010, Loring et al. 2014), and harvest throughout the non-breeding period (Bordage and Savard 2011, Rothe et al. 2015, Koneff et al. 2017). Although recent studies have examined movements and habitat use by black scoters in wintering areas (Perry et al. 2009, Loring et al. 2014, Plumpton et al. 2020), factors influencing black scoter movements throughout the annual cycle remain unknown or less understood. To assess the effects of external stressors on black scoter populations, it is important to determine how various wintering areas are connected to staging, breeding, and molt sites, and how migration timing and routes vary among individuals within the broader population.

To determine individual-level migratory patterns of black scoters, we implanted satellite transmitters into individuals captured at non-breeding sites along the Atlantic Coast of North America and tracked them throughout the annual cycle across multiple years. Our primary goals were to identify key migratory routes and breeding areas for black scoters wintering in the Atlantic; to examine the timing and extent of among- and within-season movements and assess the degree of individual fidelity to specific sites and routes; to compare annual-cycle migratory patterns and site use between breeding and non-breeding males and females, and between apparently successful and unsuccessful breeding females; and to investigate spatial population structure by assessing migratory connectivity among wintering, staging, breeding, and molt sites.

## STUDY AREA

We tracked 113 black scoters marked during the boreal winters and springs (Jan–May) of 2002–2004 and 2009–2010 at several sites along the Atlantic Coast of North America. Given the tendency of black scoters to form large aggregations during the non-breeding period (Weller and Batt 1988), we targeted areas with large black scoter concentrations or at bottleneck areas in an attempt to sample the full Atlantic population and optimize capture efficiency. Capture efforts therefore focused primarily on pre-breeding staging sites on the Restigouche River Estuary and Chaleur Bay between New Brunswick and Québec, Canada, in the Gulf of St. Lawrence (48.0–48.1°N, 66.0–66.6°W; 2002–2010; $n = 93$; 48 males, 45 females) near the end of pre-breeding staging (2–19 May) to ensure we sampled early- and late-arriving individuals. We captured additional black scoters in winter along the coast of southern New England in Rhode Island (41.5°N, 71.3°W; Dec 2010–2011; $n = 17$; 10 males, 7 females) and in Chesapeake Bay, USA, (38.8°N, 76.4°W; Apr 2003; $n = 2$ females). Capture sites comprised primarily nearshore habitats with mixtures of sand, gravel, silt, and clay substrates and scattered rocky reefs (Loring et al. 2014). Subsequent movements by tracked black scoters covered a footprint of 300,000,000 ha, which encompassed portions of the taiga, Hudson plains, northern forests, and eastern temperate forests ecoregions (see Commission for Environmental Cooperation 1997 for descriptions of the flora and fauna of these regions), and nearshore marine and freshwater ecosystems. A complete analysis of seasonal habitat selection by tracked black scoters is presented in Lamb et al. (2020*b*).

## METHODS

### Transmitter Deployment

We captured subadult ($n = 10$ males, 9 females) and adult ($n = 48$ males, 45 females) black scoters with combinations of over-water mist nets and night-lighting. We determined age by bursa depth and external plumage characteristics (Iverson et al. 2003). For the purposes of the present analyses, we simplified age to 2 mutually exclusive categories: subadult (individuals classified as hatch year [<1 year old] during post-breeding captures or second year [1–2 years old] during pre-breeding captures), or adult (≥2 years old; i.e., individuals classified as after hatch year during post-breeding captures or after second year during pre-breeding captures). We then determined sex by cloacal examination or plumage characteristics and measured body mass with a Pesola spring scale (Pesola AG, Schindellegi, Switzerland; ±5 g) or digital hanging scale (HS-3000, Universal Weight Enterprises, Taipei Taiwan; ±2 g). Veterinarians, experienced in avian surgery, implanted 36-g coelomic-implant platform transmitter terminals (PTT; Microwave Telemetry, Columbia, MD, USA) into the right caudal coelomic cavity following the implantation technique described by Olsen et al. (1992) and Korschgen et al. (1996). Before transmitter implantation, the veterinarian verified health and condition and weighed all individuals to ensure that transmitters were <5% of body mass. We released birds at or near the capture site within 24 hours of capture. We handled and marked sea ducks under applicable permits using methods approved by the University of Rhode Island Institutional Animal Care and Use Committee (protocol number AN10-08-004).

We programmed transmitters to follow different duty cycles depending on deployment location. Most transmitters were programed with a single-season duty cycle consisting of 2–4-hour on periods followed by 72-hour off periods ($n = 103$). The duty cycles for the transmitters deployed in Rhode Island were programmed to collect high-resolution data in winter using a 2-period duty cycle: 4 hours on followed by 24 hours off during the first 116 cycles (20 Dec–29 Apr), and 4 hours on and 96 hours off thereafter ($n = 18$). Argos location data were processed and disseminated through Collecte Localisation Satellites (CLS) America (Lanham, MD, USA). Transmitter signals were received by equipment on polar-orbiting National Oceanic and Atmospheric Administration and MetOp satellites. Data were transferred to the CLS America processing center, where locations were estimated from the Doppler shift in the PTT's carrier frequency.

### Data Processing

Raw satellite telemetry data vary in quality of location estimates based on the configuration and number of satellites used to obtain each location. Argos Standard Service Processing assigned location estimates, in decreasing order of precision, to Argos location classes (LC) 3, 2, 1, and 0 or to auxiliary location codes (LC A, B, and Z). Accuracy (i.e., 1 SD) for location estimates with LC 3, 2, 1, and 0 were <250, 250–499, 500–1,499, and ≥1,500 m, respectively (Collecte Localisation Satellites 2016). In subsequent modeling, we incorporated all locations and assumed that each represented the center of an error ellipse based on the latitudinal and longitudinal error estimates associated with its location class (Jonsen et al. 2005). We evaluated every transmitter's sensor data to identify mortality events (by internal temperature sensor or activity sensor) or battery or tag failure (low voltage). When sensor data indicated mortality, we considered the last date the scoter was known to be alive as the last date of activity. For all transmitters that stopped transmitting for either low voltage or unknown reasons, we considered the day after last transmission as the last date of activity.

To define dispersive or stationary behavioral states based on observed locations, we used a switching state-space model (Jonsen et al. 2005). This model calculates the distributions of turning angles and step lengths between successive locations and combines a process model that accounts for variation in observation error associated with different Argos locations classes with an observation model of the underlying movement patterns that generate observed locations. We interpolated data to 1-day intervals based on probable tracking paths among locations. Interpolated locations were inexact and did not account for within-day movement; however, they allowed us to use available information to determine the most likely days when shifts in large-scale movement patterns occurred. We did not interpolate when successive locations were >7 days apart because longer temporal gaps produce unrealistic movement trajectories (Jonsen et al. 2005); we split any tracks with gaps >7 days into separate tracks before and after the gap. For individuals with few locations, models failed to converge or produced results with great uncertainty. We therefore excluded all individuals with <50 locations in LC 3–1 (typically, ≤1 month of location data) prior to analysis. Our final sample size was 74 adults (37 males, 37 females) and 12 subadults (3 males, 9 females).

We ran all models in the bsam package (Jonsen et al. 2005, Jonsen 2016) in R (version 3.6.2; R Core Team 2019). We selected a switching first-difference correlated random walk model with a 1-day timestep and trained the model using 5,000 burn-in samples. We then generated 5,000 posterior samples for analysis. We thinned posterior samples by selecting every fifth sample to reduce autocorrelation and computing time (Link and Eaton 2012) and used a 0.1 smoothing parameter to account for data sparsity. We used standard diagnostic plots (traceplots, density plots, autocorrelation plots, and shrink factor plots) in bsam to check the final models for convergence. Model outputs included probable daily locations with 2.5%, 50.0%, and 97.5% confidence intervals and a score (*b*) that ranged between 1 and 2, and indicated the average assignment of the location to either a dispersive (1; long step lengths and low turning angles) or stationary (2; short step lengths and high turning angles) behavioral state across all posterior samples post-thinning. Thus, smaller average values of $b$ indicated dispersive behavior, whereas larger values indicated stationary behavior. Overall, we obtained an average of $611 \pm 340$ (SD) locations/individual, including some duplicate locations within days, which we reduced to an average of $530 \pm 311$ daily locations/individual after state-space model interpolation and regularization.

### Migratory and Breeding Chronology and Site Use

Because female black scoters do not breed until ≥2 years of age, we excluded individuals captured as subadults from analyses of breeding chronology and success. To assess breeding chronology, we defined breeding site attendance as periods of ≥3 consecutive days classified as resident ($b > 1.5$) in terrestrial areas near an inland water body during the sea duck breeding season (May–Aug; Johnsgard 1978). To examine the influence of presumed breeding success on migration timing of female black scoters, we further defined a potentially successful breeding attempt when an adult female remained at a potential nest site for ≥40 days. Forty days represents the minimum duration for the combinations of laying eggs (range = 5–20 days), incubation (range = 27–31 days), and rearing broods (range = 7–21 days; Bordage and Savard 2011). By using this minimum duration threshold for successful breeding, we likely overestimated absolute breeding success but provided a consistent basis for comparing individual attendance patterns among years.

We also used the state-space modeling results to identify periods of dispersive or migratory movement ($b \leq 1.5$ for ≥3 consecutive days). We defined the first day when $b \leq 1.5$ as the initiation date of migration and calculated the duration of migratory movements as the number of days when $b \leq 1.5$ before reaching >3 consecutive days when $b > 1.5$. We assigned migratory movements to pre-breeding migration (i.e., among wintering sites and breeding or non-breeding summer sites), post-breeding migration (among breeding or molting areas and wintering sites), or within-season dispersal (among sites within seasons). For some individuals, the pre- and post- breeding migratory periods included additional distinct migratory movements, which we classified as breeding migration (between pre-breeding staging areas and breeding sites) or molt migration (between breeding and molt sites), respectively.

We classified periods of stationary behavior within migrations (i.e., $b > 1.5$ for ≤7 consecutive days; De La Cruz et al. 2009) as stopovers and divided longer periods of stationary behavior into 5 categories according to their positions in the annual cycle. Wintering included all non-breeding sites occupied between the end of post-breeding migration and the start of the subsequent pre-breeding migration. Pre-breeding staging included sites occupied for >7 days during pre-breeding migration. Breeding included inland sites occupied immediately following pre-breeding migration for ≥3 days as described above. We classified coastal or inland habitats occupied following breeding or, if breeding was not attempted, pre-breeding migration as either molting or post-breeding staging. To distinguish remigial molt sites from post-breeding staging areas, we used criteria derived from observations of closely related scoter species and defined molt sites as those used for ≥48 consecutive days, with arrival dates between July and September and departure dates between August and October (Dickson et al. 2012, Meattey et al. 2018). In all cases, we excluded the season in which a bird was captured from analysis; for individuals captured during winter, we assessed chronology and site use beginning with pre-breeding migration, and for individuals captured at pre-breeding or post-breeding staging sites we began with the subsequent breeding or wintering season. This allowed us to exclude from our analysis effects of capture and tagging on local-scale movement; however, because individuals with transmitters may also exhibit altered phenology beyond the season of capture (Lamb et al. 2020*a*), we included years since capture as a covariate when comparing movement among individuals (described in detail at the end of this section).

We defined each distinct group of stationary locations between 2 movement events (i.e., migration or dispersal) as a breeding, molting, wintering, staging, or stopover site. For each site, we assigned arrival and departure dates as the first and last days of stationary behavior following or preceding a migration or dispersal event. We then calculated the centroid for each site and used cluster analysis to group site centroids into clusters of occupied sites (i.e., regions) by season. We used the NbClust function in the R package NbClust (Charrad et al. 2014) to simultaneously evaluate partitioning using multiple clustering techniques and select the consensus cluster solution. We used Euclidean distance matrices and constructed clusters using Ward's method (Ward and Hook 1963), which minimizes within-cluster variance by merging sequentially smaller clusters into larger ones and minimizing increases in variance. For each season, we evaluated solutions ranging from 2–50 clusters and selected the solution supported by the largest number of clustering methods.

To compare chronology among individuals, we fit generalized linear mixed models for seasonal start date, end date, and duration for each season as a function of sex, age, breeding status (i.e., if the individual attended a breeding site in that year), cycle (i.e., years since capture), and year as fixed effects. We specified individual as a random effect to account for repeated sampling of individuals within and among seasons. We included cycle to account for effects of capture and tagging (Lamb et al. 2020*a*) and year to account for interannual variation. To model among-region differences, we fit the same models but with site-specific arrival and departure dates and durations as the response variables and included region as a predictor variable. We assessed model fit using Q-Q plots for random terms and generalized chi-square tests of residual variance. We considered any predictor variable significant if the 95% confidence intervals for its coefficient (β) value did not include zero.

### Migration Routes and Migratory Connectivity

We determined primary migration routes and calculated migration distances by connecting subsequent locations identified as transient by the state-space model (i.e.,

$b < 1.5$). In cases with long temporal gaps (>7 days) between locations, we assumed the quickest (straight-line) route between points for distance calculations but did not map this approximate route. We calculated seasonal and annual travel distances by summing the linear distances among daily locations as interpolated by the state-space model. Because some species of sea ducks may make substantial within-day movements (e.g., between foraging and resting areas; Reed and Flint 2007), this measurement likely represents a conservative estimate of distance traveled, particularly within stationary periods. Thus, whereas measurements of travel distances presented here are useful for broad comparisons among individuals, finer-scale observations would be needed to measure absolute travel distances accurately. We modeled among- and within-season daily and total travel distances as a function of sex, age, breeding status, year, and cycle, with individual as a random factor. To assess overlap in migration routes, we used the spatstat package in R (Baddeley et al. 2015) to create line density kernels for pre-breeding and post-breeding migrations representing the summed linear distance of migration routes for all individuals within each 0.5 × 0.5-degree (~2,500 $km^2$) grid cell.

We defined migratory connectivity as the degree to which individuals with closer locations or more similar departure dates during a given season arrive or group closer together during the subsequent season than expected by chance. We calculated connectivity by comparing pairwise distances among individuals between consecutive seasons using the Mantel test in the R package ade4 (Dray and Dufour 2007). This method is based only on distance matrices between individual locations, and thus has the advantage of not assuming any particular population groupings *a priori*. Complete segregation among groups of individuals produces correlation values closer to 1, whereas values closer to 0 indicate random mixing (Ambrosini et al. 2009). To avoid duplicating individuals in the sample, we retained only the final site used in the previous season and the first site used in the subsequent season (i.e., the sites used immediately before and after migration) and eliminated any individuals whose transmitters went offline during a given season because of mortality or transmitter failure. We also calculated temporal connectivity using the departure dates associated with the final location from each season and the arrival dates at the subsequent location. Given breeding attendance may be affected immediately after transmitter attachment (Lamb et al. 2020*a*), we calculated separate connectivity indices for the first and second years of data following transmitter attachment. Sea ducks spend long periods of time at staging and molting areas between breeding and wintering (Savard and Peterson 2015); therefore, in addition to conducting Mantel tests of direct connectivity between breeding and wintering sites (i.e., breeding-wintering and wintering-breeding), we also measured connectivity via migratory staging and molt areas (i.e., winter-pre-breeding staging, pre-breeding staging-breeding, breeding-molt, and molt-winter). We determined statistical significance at $P < 0.05$ after 9,999 random permutations.

### Interannual Site Fidelity and Carryover Effects

Because transmitters collected data across multiple years, we also examined interannual patterns in site use and reproduction. To assess interannual fidelity to specific sites, we measured linear distances between the centroid of each site used by each individual and the centroid of the nearest site used by that individual in the previous year. To determine whether individual interannual movements were different than expected by chance, we used a paired *t*-test to compare the distance between each site centroid and the centroid of the nearest site used by the same individual during the previous year with the average distance to the nearest sites used by all other individuals in the population. We also examined region-level site fidelity using the principal stage-specific regions identified by cluster analyses. For individuals with multiple years of data, we calculated interregional transition probabilities between each available pair of years. Finally, for adult females with multiple years of data, we examined potential carryover effects of reproduction by assessing the probability of breeding site attendance and presumed successful breeding (i.e., attendance at a breeding site for ≥40 consecutive days) in a given year as a function of the previous year's breeding status (presumed successful, presumed unsuccessful, or did not attempt).

## RESULTS

### Wintering

The wintering period lasted approximately 5 months from early November to late March (Table 1). Males arrived at and departed from wintering areas about 1 week earlier than females (start: β 95% CI = −13.3–−2, 8; end: β 95% CI = −14.3–−0.1; Fig. 1A–B, winter); however, duration of wintering was similar between sexes (Fig. 1C, winter). Males also used a greater number of distinct wintering sites (2.5 ± 1.2) than females (1.1 ± 1.1; β 95% CI = 0.1–1.1; Table 1). Individuals using multiple wintering sites arrived at their second site in mid-December ($n = 102$), their third site in mid-January ($n = 50$), and their fourth site in late January ($n = 13$).

Black scoter site use during winter was clustered in 6 main regions (Fig. 2A), with most individuals using multiple regions within or among years. Distinct wintering regions included the Canadian Maritimes (used by 4% of 83 individuals), southern New England (57%), Long Island Sound (58%), Delaware Bay (35%), Chesapeake Bay (36%), and the South Atlantic Bight between North Carolina and Florida (31%; Table 2). Duration of site occupancy was similar among regions (β = 0 for all regions). Arrival and departure dates were earlier in southern New England than in the other 5 regions (arrival: β 95% CI = 10.2–55.5; departure: β 95% CI = 1.6–58.9; Table 2). The ratio of males to females was above average in Delaware Bay and the Canadian Maritimes, and below average in the South Atlantic Bight (Table 2). Cumulative within-winter movements were the longest of any season (Table 1).

### Pre-Breeding Migration

Pre-breeding migration consisted of 2 distinct migration events separated by a prolonged pre-breeding staging period

**Table 1.** Seasonal start and end dates, duration, number of sites used, and distance traveled ($\bar{x} \pm$ SD) for black scoters in eastern North America, 2002–2013. Average values are shown separately for each sex (F = females, M = males) where parameters differed by sex (generalized linear mixed model, 95% CI did not overlap 0).

| | *n* | | | | | | Distance (km) | |
|---|---|---|---|---|---|---|---|---|
| | F | M | Start | End | Duration (days) | Number of sites used | Total[a] | Daily[a] |
| Winter | 45 | 38 | F: 7 Nov ± 9<br>M: 1 Nov ± 15 | F: 29 Mar ± 16<br>M: 19 Mar ± 18 | 140 ± 16 | F: 1.1 ± 1.1<br>M: 2.5 ± 1.2 | 1,256 ± 651 | 8.5 ± 10.0 |
| Pre-breeding migration | | | | | | | | |
| Winter-staging | 37 | 26 | F: 1 Apr ± 19<br>M: 25 Mar ± 19 | 5 Apr ± 16 | 9 ± 7 | 0.2 ± 0.4 | 1,027 ± 585 | 132.7 ± 92.1 |
| Staging | 43 | 32 | 5 Apr ± 15 | 30 May ± 36 | 45 ± 33 | 2.1 ± 0.8 | 532 ± 486 | 9.4 ± 6.9 |
| Staging-breeding | 41 | 28 | 22 May ± 14 | F: 11 Jun ± 14<br>M: 3 Jun ± 15 | F: 20 ± 11<br>M: 11 ± 6 | F: 1.0 ± 0.9<br>M: 0.3 ± 0.6 | 1,585 ± 888 | 111.2 ± 42.6 |
| Breeding | 38 | 14 | F: 11 Jun ± 12<br>M: 2 Jun ± 6 | F: 30 Jul ± 17<br>M: 28 Jun ± 20 | F: 49 ± 17<br>M: 26 ± 22 | 1.1 ± 0.2 | 345 ± 237<br>M: 11.2 ± 12.1 | F: 4.7 ± 3.5 |
| Post-breeding migration | | | | | | | | |
| Breeding-molt | 36 | 17 | F: 5 Aug ± 16<br>M: 7 Jul ± 30 | F: 11 Aug ± 18<br>M: 14 Jul ± 29 | 7 ± 5 | 0.2 ± 0.4 | 590 ± 465 | 90.7 ± 51.6 |
| Molt | 42 | 31 | F: 1 Aug ± 25<br>M: 30 Jun ± 27 | F: 6 Oct ± 19<br>M: 10 Sep ± 21 | 70 ± 22 | 1.0 ± 0.0[b] | 362 ± 214 | 5.6 ± 2.9 |
| Staging | 42 | 31 | F: 29 Jul ± 29<br>M: 18 Jun ± 27 | F: 26 Oct ± 7<br>M: 14 Oct ± 12 | F: 86 ± 25<br>M: 107 ± 28 | F: 2.1 ± 0.9<br>M: 2.4 ± 0.9 | 373 ± 285 | F: 20.3 ± 22.1<br>M: 13.3 ± 14.0 |
| Staging-wintering | 39 | 29 | F: 26 Oct ± 8<br>M: 16 Oct ± 11 | F: 6 Nov ± 9<br>M: 28 Oct ± 13 | 11 ± 7 | 0.2 ± 0.5 | 1,524 ± 560 | 152.5 ± 70.1 |

[a] Distance measurements are presented primarily for comparison among seasons and individuals; however, the temporal scale of data collection (1 location every 2–3 days) is not sufficient to capture diel foraging movements, meaning that these values are minimal estimates.

[b] Because black scoters are flightless during remigial molt, molt occurred at a single site by definition.

(Fig. 1A–B, pre-breeding), for an average duration of 66 days (Fig. 1C). Northward migrants followed the coast from wintering sites along the Atlantic seaboard, taking a direct route through the Bay of Fundy with a short overland crossing over the Chignecto Isthmus between New Brunswick and Nova Scotia before arriving at staging sites in the Gulf of St. Lawrence (Figs. 2B and 3A). From there, some individuals (apparent breeders) dispersed overland to boreal breeding areas, whereas others (apparent non-breeders) migrated directly from staging to molt sites in James and Hudson bays (Figs. 2D and 3A). Migration from wintering to staging sites lasted an average of 9 ± 6 days, with an average distance of 1,027 ± 585 km, or 132.7 ± 92.1 km/day. Subsequent migration to breeding sites lasted 16 ± 11 days and covered 1,585 ± 888 km, or 111.2 ± 42.6 km/day. Although the timing of breeding migration initiation was similar between males and females, few tracked males traveled to the westernmost breeding areas; thus, males spent less time migrating to breeding sites (β 95% CI = −11.3–−4.0), migrated shorter distances (β 95% CI = −974–−414), completed migration earlier (β 95% CI = −9.6–−1.0), and used fewer stopover sites than females (β 95% CI = −0.9–−0.3; Table 1, staging-breeding migration).

Within pre-breeding migration, individuals spent an average of 45 days at staging sites between early April and late May (Table 1, staging; Fig. 1, pre-breeding). Individuals used an average of 2.1 ± 0.8 staging sites in pre-breeding, with no evidence of differences between sexes. Individuals using multiple pre-breeding staging sites arrived at their second (*n* = 97) and third sites (*n* = 24) in early May, and their fourth site in mid-May (*n* = 3). Most pre-breeding staging sites were in the Gulf of St. Lawrence (92% of sites; 99% of individuals; Fig. 2B). The remaining 8% of staging sites were along the Atlantic Coast from Chesapeake Bay to the Gulf of Maine (Fig. 2B). Birds from these regions also used short-term stopover sites, mainly in James Bay and Western Hudson Bay (Fig. 2B). Arrival and departure dates were earlier in the Atlantic (β 95% CI = −62–−45), the Gulf of St. Lawrence (β 95% CI = −43–−28), and James Bay (β 95% CI = −17–−1) than in Western Hudson Bay (Table 2). Durations of occupancy were longer in the 2 more southerly coastal regions (15–18 days) than in James Bay and West Hudson Bay (5 days; β 95% CI = 5.3–17.9; Table 2). Individuals moved an average of 532 ± 486 km during pre-breeding staging, or 9.4 ± 6.9 km/day during stationary periods (Table 1).

## Breeding

Breeding lasted from early June to late July (Table 1). Males departed earlier (β 95% CI = −44–−23) and spent less time at breeding sites (β 95% CI = −36–−12; Fig. 1, breeding) than females. Sites used during breeding were divided among 3 main regions: to the west of Hudson Bay in Nunavut and the Northwest Territories (37% of 52 individuals), centered along the northern edge of the boreal forest from northern Manitoba to Hudson Bay (37%), and to the east of Hudson Bay in Quebec (31%; Fig. 2C). More females than males attended breeding sites across all regions (Table 2). Arrival and departure dates varied among regions and were earlier at near-west and eastern sites compared to far-west sites (β 95% CI = −16–−3; Table 2), whereas

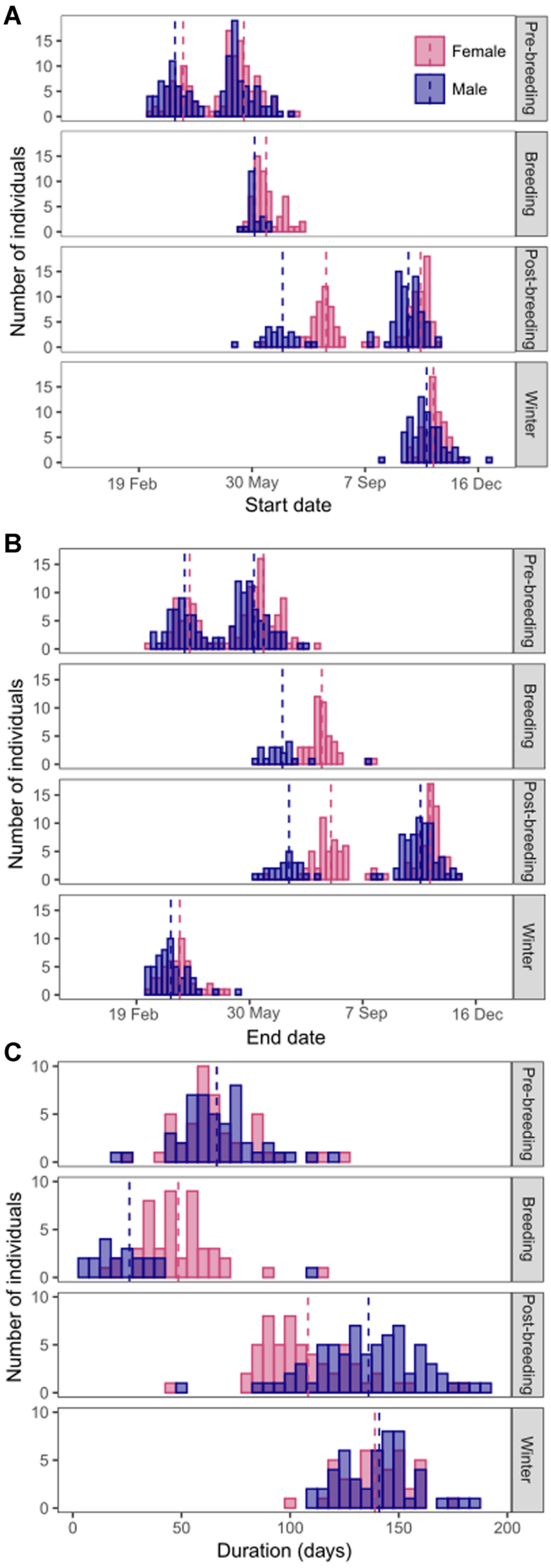

**Figure 1.** Start dates (A), end dates (B), and durations of stay (C) by season for black scoters in eastern North America, 2003–2013. Histogram bars show numbers of males (M; purple) or females (F; pink), with dashed lines showing sex-specific average values. Within migrations, mean start and end dates are shown separately for migration to staging (pre-breeding, first line) and molt (post-breeding, first line) sites, and from staging to breeding (pre-breeding, second line) or wintering (post-breeding, second line) sites.

duration of stay and breeding success rates were similar among regions (Table 2). Individual movements at breeding sites averaged 345 ± 237 km, with males averaging greater daily movement during stationary periods than females (β 95% CI = 4–29; Table 1). Compared to individuals that did not attend breeding sites, breeders departed pre-breeding staging sites earlier (β 95% CI = −21–−11), arrived at post-breeding staging sites later (β 95% CI = 34–48), and spent less time in pre-breeding and post-breeding staging areas (pre-breeding duration: β 95% CI = −19–−2; post-breeding duration: β 95% CI = −44–−29).

Adult females that remained at breeding sites long enough to presumably raise ducklings arrived at breeding sites earlier (β 95% CI = −21–−12) than those that were presumed unsuccessful. Among females that remained at nest sites long enough to presumably breed (*n* = 14), most (86%) also attended breeding sites during the following season, and 79% were apparently successful (Table 3). Most females (77%) who attended breeding areas but were apparently unsuccessful (*n* = 9) also visited breeding sites during the following season, with an apparent success rate of 44%. Among individuals that did not attend breeding sites (*n* = 11), 73% attended breeding sites during the following year, with an apparent success rate of 55% (Table 3).

## Post-Breeding Migration

Post-breeding migration consisted of 2 movements: from breeding areas to molt and staging sites, and from molt and staging sites to wintering areas (Fig. 1A–B, post-breeding), with an average duration of 110 days for females and 135 days for males (Fig. 1C, post-breeding). After ducks left breeding areas, they generally converged at molt sites in James and Hudson bays before migrating overland through southern James Bay following the Ottawa River Valley, passing just east of Lake Ontario and over New York to coastal wintering sites. This briefer post-breeding overland migration to the New England coast differed from the longer coastal pre-breeding migration through the Bay of Fundy and the Gulf of St. Lawrence (Fig. 3). Migration from breeding to molt sites lasted 7 ± 5 days and covered 590 ± 465 km or 90.7 ± 51.6 km/day (Table 1). Migration to molt sites started and ended almost 1 month earlier for males than for females (start: β 95% CI = −48–−25; end: β 95% CI = −47–−24; Table 1; Fig. 1A–B, post-breeding). Migration from post-breeding staging to wintering areas lasted 11 ± 7 days and covered 1,524 ± 560 km or 152.5 ± 70.1 km/day (Table 1). Migration to wintering areas occurred about 10 days earlier for males than for females (start: β 95% CI = −14–−5; end: β 95% CI = −15–−7; Table 1; Fig. 1A–B, post-breeding). Durations, distances traveled, and number of sites used did not differ between sexes for either migration (Table 1).

Post-breeding migration included the molt and post-breeding staging period and lasted from early July to late-October (Table 1). Individuals occupied an average of 2.2 sites (range = 1–5), and typically included 1 molt site and ≥1 staging site (Table 1), with staging sites clustered in similar regions to those used during pre-breeding staging

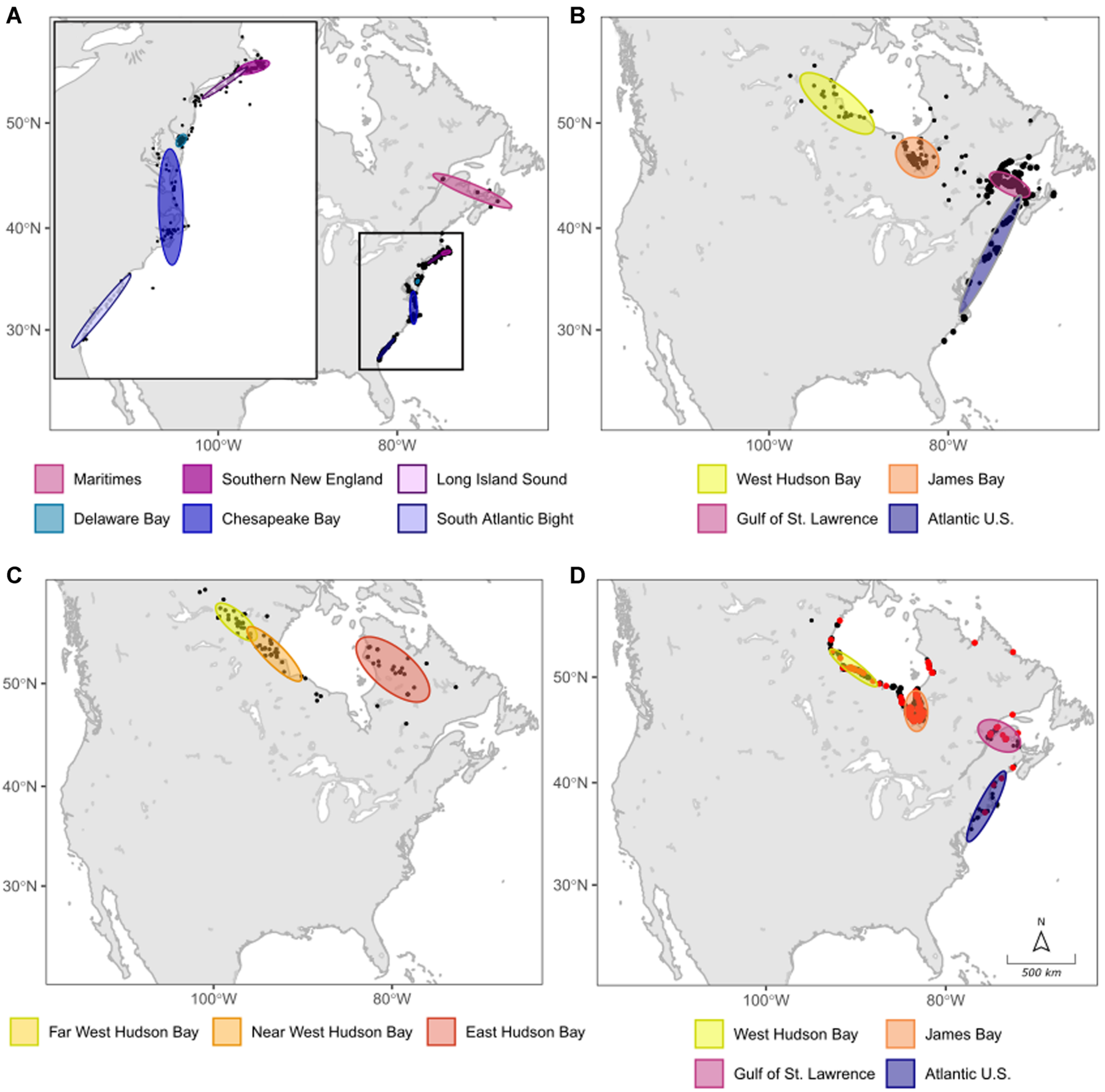

**Figure 2.** Sites used during A) wintering, B) pre-breeding migration (staging = large points; stopover = small points), C) breeding, and D) post-breeding migration (molt = red points; staging = large points; stopover = small points) for black scoters in eastern North America, 2002–2013. Shaded areas represent 90% confidence ellipses for clusters of occupied sites.

(Fig. 2D vs. 2B). Individuals that used >1 staging site arrived at their second site around mid-August (*n* = 112), their third site (if used) in mid-September (*n* = 50), and their fourth site (if used) in late September (*n* = 12). During molt, James Bay was occupied by 79% of individuals, including males and breeding and non-breeding females (Table 2). Gulf of St. Lawrence (21%) and Atlantic Coast sites (2%) were used primarily by non-breeders, whereas Western Hudson Bay (29%) was used primarily by post-breeding adult females (Table 2). Average arrival date at principal molt sites was about 1 month earlier for males (start: β 95% CI = –41–-23; end: β 95% CI = –33–-19); however, all other parameters were similar among sites and between sexes (Table 1). During staging, 89% of individuals used sites in James Bay, 44% in Western Hudson Bay, 26% in the Gulf of St. Lawrence, and 19% at Atlantic Coast sites (Table 2). Western Hudson Bay and Atlantic Coast sites were used mainly for stopovers, whereas sites in James Bay and the Gulf of St. Lawrence were occupied for longer durations (β 95% CI = 9–33; Table 2). Birds arrived at staging areas on the Atlantic Coast earlier than at other sites (β 95% CI = –118–-17) and birds departed Western Hudson Bay and James Bay sites earlier than at the 2 more southerly coastal staging areas (β 95% CI = –114–-33; Table 2). Females moved greater daily distances than males at staging sites and each moved greater distances at staging sites compared to molt sites (5.6 ± 2.9 km/day; Table 1).

**Table 2.** Proportion of tracked individuals and sexes, proportion of distinct sites, duration of site use, and arrival and departure dates for seasonal regions used by black scoters in eastern North America, 2002–2013. Associated breeding statuses are shown for the breeding season (proportion of breeding attempts in the region classified as successful based on attendance lasting ≥ 40 consecutive days) and remigial molt (proportion of individuals using the region that attended breeding sites before arrival).

| | Proportion individuals[a] | Proportion male | Proportion sites | Duration of occupancy in days ($\bar{x} \pm SD$) | Site arrival date[b] ($\bar{x} \pm SD$) | Site departure date[b] ($\bar{x} \pm SD$) | Breeding status (adult females) |
|---|---|---|---|---|---|---|---|
| Winter (83 individuals; 295 sites) | | | | | | | |
| Canadian Maritimes | 0.05 | 0.75 | 0.02 | 58 ± 58 | 24 Nov ± 31 | 21 Jan ± 78 | |
| Southern New England | 0.57 | 0.53 | 0.26 | 53 ± 47 | 10 Nov ± 32 | 6 Jan ± 56 | |
| Long Island Sound | 0.58 | 0.54 | 0.24 | 49 ± 43 | 12 Dec ± 44 | 30 Jan ± 60 | |
| Delaware Bay | 0.35 | 0.66 | 0.17 | 51 ± 42 | 24 Dec ± 41 | 14 Feb ± 40 | |
| Chesapeake Bay | 0.36 | 0.57 | 0.14 | 63 ± 49 | 5 Dec ± 37 | 10 Feb ± 51 | |
| South Atlantic Bight | 0.31 | 0.23 | 0.17 | 54 ± 40 | 7 Dec ± 26 | 30 Jan ± 30 | |
| Pre-breeding staging and stopover (75 individuals; 387 sites) | | | | | | | |
| Atlantic Coast | 0.32 | 0.29 | 0.10 | 18 ± 20 | 7 Apr ± 26 | 24 Apr ± 33 | |
| Gulf of St. Lawrence | 0.99 | 0.42 | 0.68 | 15 ± 13 | 24 Apr ± 21 | 14 May ± 21 | |
| James Bay | 0.53 | 0.28 | 0.16 | 5 ± 4 | 27 May ± 10 | 1 Jun ± 10 | |
| Western Hudson Bay | 0.24 | 0.17 | 0.06 | 5 ± 4 | 5 Jun ± 11 | 9 Jun ± 12 | |
| Breeding (42 individuals; 73 sites) | | | | | | | Presumed successful |
| East Hudson Bay | 0.31 | 0.38 | 0.33 | 38 ± 19 | 4 Jun ± 10 | 12 Jul ± 22 | 0.41 |
| Near West Hudson Bay | 0.37 | 0.37 | 0.36 | 38 ± 18 | 8 Jun ± 10 | 17 Jul ± 21 | 0.50 |
| Far West Hudson Bay | 0.37 | 0.11 | 0.31 | 43 ± 22 | 17 Jun ± 13 | 30 Jul ± 21 | 0.48 |
| Molt (73 individuals; 144 sites) | | | | | | | Attended breeding site |
| Atlantic Coast | 0.03 | 0.50 | 0.02 | 71 ± 6 | 7 Jul ± 15 | 15 Sep ± 21 | 0.00 |
| Gulf of St. Lawrence | 0.21 | 0.47 | 0.11 | 77 ± 26 | 11 Jul ± 36 | 26 Sep ± 26 | 0.18 |
| James Bay | 0.78 | 0.47 | 0.69 | 72 ± 22 | 13 Jul ± 31 | 23 Sep ± 24 | 0.42 |
| Western Hudson Bay | 0.29 | 0.48 | 0.17 | 57 ± 16 | 22 Jul ± 26 | 15 Sep ± 17 | 0.84 |
| Post-breeding staging and stopover (73 individuals; 381 sites) | | | | | | | |
| Atlantic Coast | 0.19 | 0.50 | 0.06 | 14 ± 24 | 17 Oct ± 44 | 31 Oct ± 22 | |
| Gulf of St. Lawrence | 0.26 | 0.53 | 0.08 | 55 ± 34 | 9 Aug ± 49 | 3 Oct ± 28 | |
| James Bay | 0.89 | 0.43 | 0.70 | 40 ± 31 | 5 Aug ± 48 | 14 Sep ± 46 | |
| Western Hudson Bay | 0.44 | 0.22 | 0.16 | 28 ± 27 | 3 Aug ± 28 | 31 Aug ± 26 | |

[a] Because individuals used multiple sites or regions among and across years, proportions add to >1.

[b] Arrival and departure dates include within-season movement.

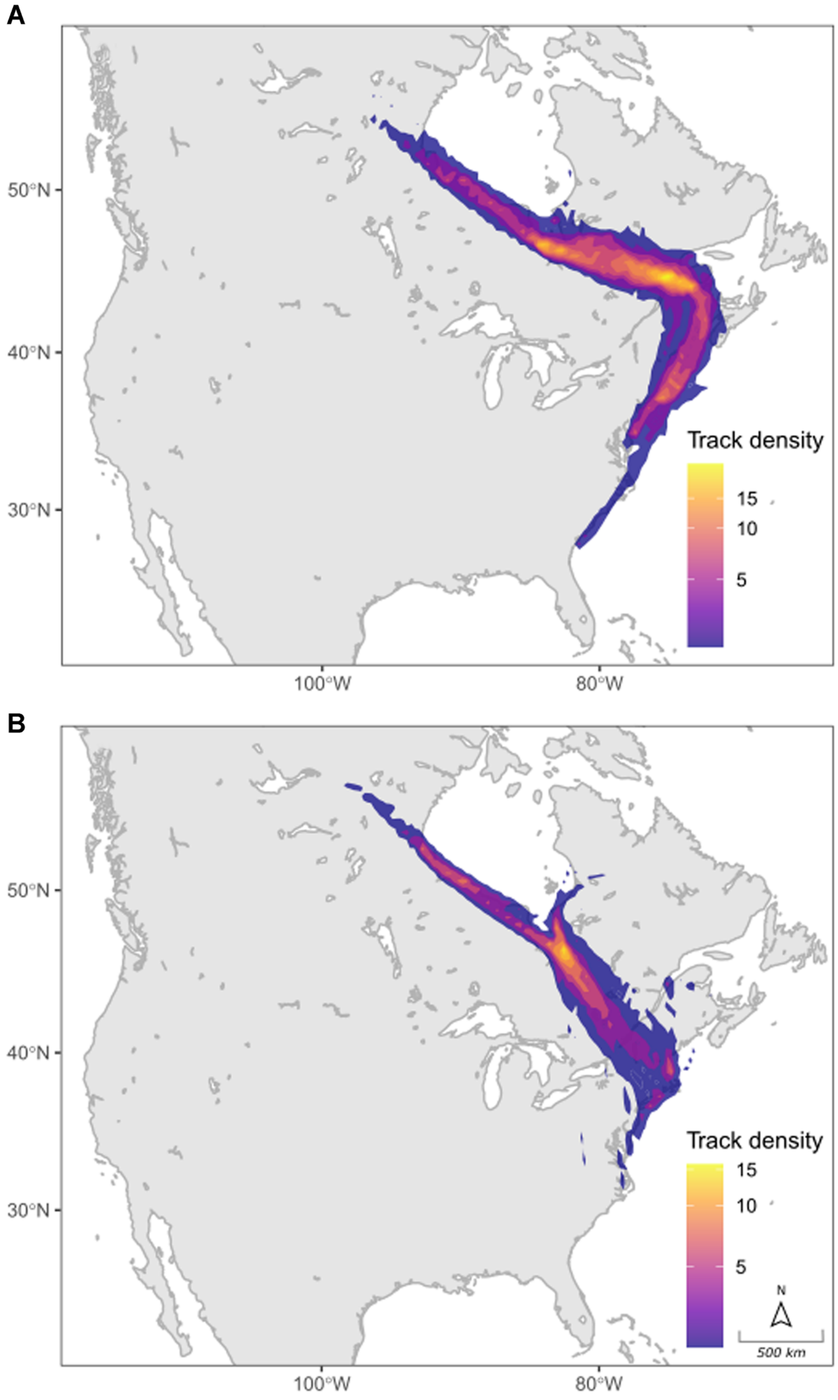

**Figure 3.** Linear density (km/2,500 km$^2$) of A) pre-breeding and B) post-breeding migration tracks of tagged black scoters in eastern North America, 2002–2013. Densities are displayed on a log10 scale to highlight variation along routes used most frequently.

**Table 3.** Breeding statuses of adult female black scoters tracked across multiple years in eastern North America, 2002–2013. Presumed breeding success is based on duration of stay at breeding sites (≥40 consecutive days = presumed successful; <40 consecutive days = presumed unsuccessful). Values represent numbers of individuals in each breeding class.

| | | **Year 2 breeding status** | | | |
|---|---|---|---|---|---|
| | *n* | **Presumed successful** | **Presumed unsuccessful** | **Attended breeding site; duration unknown** | **Did not attend breeding site** |
| Year 1 breeding status | | | | | |
| Presumed successful | 14 | 11 | 0 | 1 | 2 |
| Presumed unsuccessful | 9 | 4 | 1 | 3 | 1 |
| No breeding attempt | 11 | 6 | 0 | 2 | 3 |

**Table 4.** Mantel test results for spatial and temporal migratory connectivity between pairs of seasons for black scoters in eastern North America, 2003–2013. Higher values indicate greater migratory connectivity between seasons (i.e., individuals with closer locations or more similar departure dates during a given season arrive or group closer together during the subsequent season than expected by chance).

| | | | | Spatial connectivity (location-location) | | | Temporal connectivity (departure date-arrival date) | | |
|---|---|---|---|---|---|---|---|---|---|
| **From** | **To** | **Year** | ***n*** | **Value** | **Variance** | ***P*** | **Value** | **Variance** | ***P*** |
| Breeding | Winter | 1 | 31 | 0.06 | 0.00 | 0.17 | 0.14 | 0.02 | 0.15 |
| | | 2 | 17 | 0.01 | 0.01 | 0.43 | 0.02 | 0.01 | 0.40 |
| Winter | Breeding | 1 | 33 | 0.03 | <0.01 | 0.26 | −0.05 | 0.01 | 0.57 |
| | | 2 | 18 | 0.03 | 0.01 | 0.35 | 0.02 | <0.01 | 0.40 |
| Winter | Pre-breeding staging | 1 | 60 | 0.12 | <0.01 | 0.03 | 0.71 | <0.01 | <0.01 |
| | | 2 | 31 | 0.65 | 0.02 | <0.01 | 0.45 | <0.01 | <0.01 |
| Pre-breeding staging | Breeding | 1 | 35 | −0.06 | <0.01 | 0.79 | 0.08 | <0.01 | 0.17 |
| | | 2 | 35 | 0.03 | 0.01 | 0.32 | 0.04 | 0.01 | 0.30 |
| Breeding | Post-breeding staging and molt | 1 | 35 | 0.37 | <0.01 | <0.01 | 0.94 | <0.01 | <0.01 |
| | | 2 | 22 | 0.54 | <0.01 | <0.01 | 0.66 | <0.01 | <0.01 |
| Post-breeding staging and molt | Winter | 1 | 65 | −0.09 | 0.01 | 0.88 | 0.53 | <0.01 | <0.01 |
| | | 2 | 34 | 0.06 | 0.01 | 0.29 | 0.14 | 0.01 | 0.12 |

## Migratory Connectivity and Site Fidelity

Direct spatial and temporal migratory connectivity between breeding and wintering sites were weak (<0.06 for all pairs) and non-significant ($P > 0.10$ for all pairs; Table 4). But when we considered pre-breeding intermediate staging and post-breeding molt sites, we observed significant, moderate connectivity values between wintering and pre-breeding staging sites (0.12–0.65; $P < 0.05$) and between breeding and molt sites (0.37–0.54, $P < 0.01$; Table 4). Connectivity remained weak and non-significant between pre-breeding staging and breeding sites and between molt and winter sites when we included intermediate staging locations (Table 4).

During all seasons, individuals for which multiple years of data ($n = 57$) were available used sites closer to their own previously occupied sites than to sites occupied by other individuals ($t_{478} = -16.1$, $P \leq 0.001$; Fig. 4). Site fidelity was greatest for breeding adult females, which occupied breeding sites a median distance of 3.0 km from their previously used sites compared to 60.1 km for adult males attending breeding areas (Fig. 4). During the non-breeding season, site fidelity was apparent at regional scales (200–300 km; Fig. 5), and males remained slightly closer to previously occupied sites (β 95% CI = −206–−19) and showed less variability in interannual movement distances than females (Fig. 4). Although individuals often used the

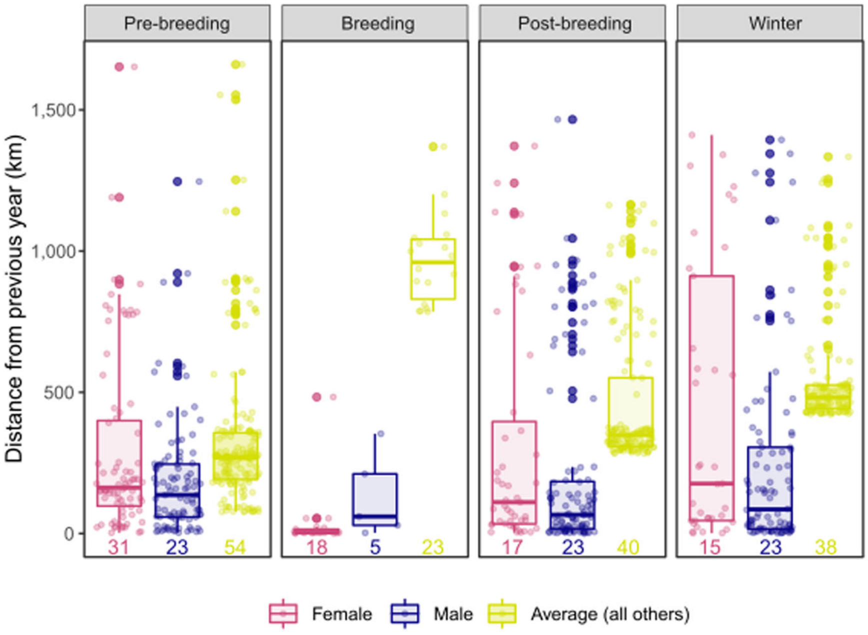

**Figure 4.** Interannual distances between centroids of sites occupied by black scoters by season in eastern North America, 2002–2013. Pink (female) and purple (male) boxes show medians and interquartile ranges of distances of each site from sites used by the same individual in the following year, while yellow boxes show the same parameters for the average distance of each site from all sites used by other individuals in the following year. Sample sizes are below each box.

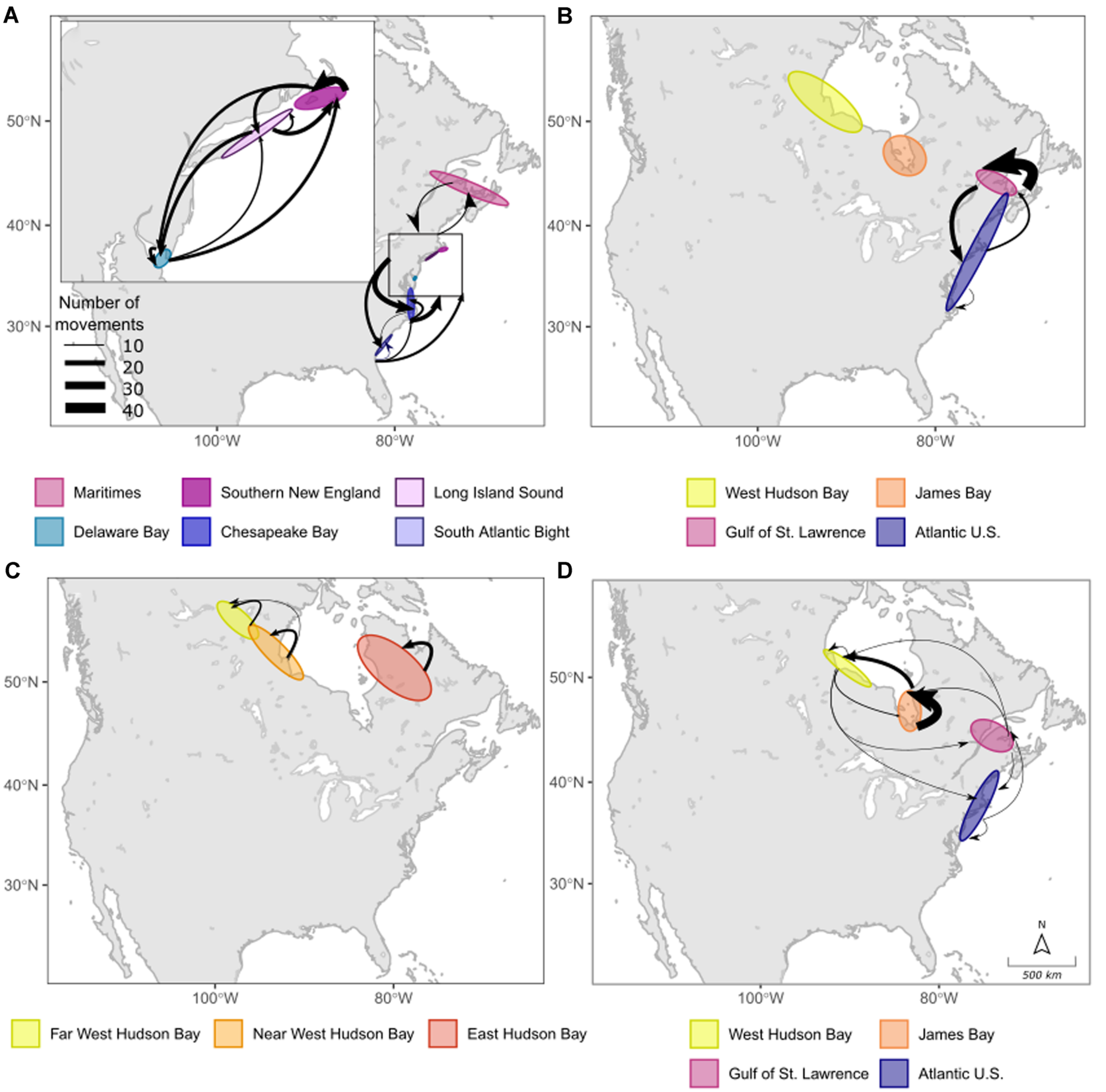

**Figure 5.** Interannual movement among sites occupied by black scoters in eastern North America during A) winter, B) pre-breeding staging, C) breeding, and D) molt, 2002–2013. Shaded areas represent 90% confidence ellipses for clusters of occupied sites. Arrow widths correspond to the number of individual movements recorded. Arrows that return to the same cluster indicate individuals that occupied sites within the same region during consecutive years.

same region in consecutive years, interannual movements among neighboring regions were also frequent, particularly during molt and winter (Fig. 5).

## DISCUSSION

Our study reinforces the value of using individual tracking to fill knowledge gaps in habitat use, distribution, and demography of mobile wildlife that occupy inaccessible areas, such as Arctic-breeding species (Davidson et al. 2020). This large-scale satellite tracking effort for black scoters in eastern North America provides detailed information on annual-cycle movements, which had previously been absent for this species (Bordage and Savard 2011). Aside from timing of seasonal site use and migratory movements, which would be difficult to observe directly, tracking black scoters across seasons and years allowed us to examine seasonal site fidelity, spatial and temporal aspects of distribution, and interannual variation in site fidelity and breeding site attendance, each of which we will discuss in turn.

### Wintering

As in most sea ducks (Savard and Peterson 2015), black scoters spent nearly half the annual cycle in wintering areas. Wintering lasted approximately 5 months, compared to 2.5 months for pre-breeding migration, 1.5 months for breeding, and 3 months for molt and post-breeding migration. Males arrived at and departed from wintering areas earlier than females, and were also more mobile within wintering areas, using 2–3 wintering sites per year. These differences are likely related to several factors including a male-biased sex ratio, which may require males to move more widely during winter to seek out breeding opportunities with unpaired females (Rodway 2007, Rodway et al. 2015). The southernmost wintering areas were used predominantly by females, suggesting a potential latitudinal gradient in sex ratios during winter as has previously been observed in canvasbacks (*Aythya valisineria*) in the same wintering region (Haramis et al. 1994). In addition, trapping bias likely favors capture of unpaired males, and capture and marking may result in disruption of pair bonds (Regehr and Rodway 2003). Black scoters likely form pair bonds during winter and early spring (Bordage and Savard 2011); therefore, the extensive within-winter movements in this species may play an important role in gene flow (Loring et al. 2014). Sonsthagen et al. (2019) observed greater genetic differentiation in black scoters than in other scoter species and suggested differentiation could result from strong site fidelity during winter; however, this does not appear to be the case in the Atlantic population.

Black scoters were distributed widely during winter and covered nearly the entire known wintering range of the Atlantic population, which extends farther south than most Atlantic Coast sea ducks (Bordage and Savard 2011, Silverman et al. 2013, Lamb et al. 2020*b*). Although black scoters occupy the Great Lakes and Gulf of Mexico in low densities during winter, none of our marked birds used these areas, suggesting less than comprehensive sampling of the Atlantic population. These birds could have arrived at capture sites in the Gulf of St. Lawrence too late to be sampled; however, as captures occurred around week 4 of the 6-week pre-breeding staging period, it seems more likely these individuals either used a different staging area or were randomly absent from our sample because of their rarity. In addition, unlike previous aerial survey data suggesting densities of black scoters are greatest in the South Atlantic Bight (Silverman et al. 2013), we found the highest proportions of tracked individuals using southern New England and Long Island Sound as wintering areas. This may be due to the timing of surveys; mean arrival (10 Nov) and departure (6 Jan) dates for marked birds were earlier in southern New England sites than in other regions, suggesting a proportion of the black scoter population begins winter concentrated in southern New England before dispersing southward in mid-winter when we conducted surveys (Silverman et al. 2013; Ramírez-Garofalo 2020). Because habitat characteristics and movement patterns differ between southern and northern wintering sites (Plumpton et al. 2020), such dispersal may allow individuals to access more favorable habitat conditions or escape competition as resource availability decreases during winter (Iverson et al. 2004).

### Pre-Breeding Migration

Individual tracking revealed uniformity in migration timing and routes of black scoters in eastern North America. This was most apparent during pre-breeding migration, when individuals from dispersed wintering sites along the Atlantic seaboard followed the same coastal migration route before turning inland toward breeding sites. Almost all tracked black scoters (99%) used the Gulf of St. Lawrence during the 6-week pre-breeding migration and staging period, which included migration from winter to staging sites (~9 days), staging (~15 days), and migration from staging to breeding or molting sites (~16 days). While previous observations have identified the Bay of Fundy as a key pre-breeding staging site for black scoters (Ross 1983, Bond et al. 2007), our results additionally highlight intensive use by black scoters of the Gulf of St. Lawrence, particularly Chaleur Bay, during this period. The Gulf of St. Lawrence is also an important pre-breeding staging area for surf (*Melanitta perspicillata*) and white-winged scoters (*Melanitta fusca*), making it one of the most important staging areas for scoters in eastern North America (Bordage and Savard 2011, Lepage et al. 2020). James Bay and Hudson Bay were also important intermediate stopover sites for ducks migrating to breeding sites west of Hudson Bay.

The uniformity in use of staging sites during pre-breeding migration among tracked individuals may have been influenced by capture locations, which occurred primarily in the Gulf of St. Lawrence. But the evidence that tracked black scoters used wintering sites throughout the known eastern range of the species suggests sampling was relatively comprehensive of the species' non-breeding range. Moreover, white-winged scoters tracked from a similarly narrow range of wintering sites in southern New England and the St. Lawrence River showed much greater variation in migratory strategies, with ≥4 distinct migratory routes involving several different staging areas (Meattey et al. 2018, Lepage et al. 2020, White and Veit 2020). Similarly, surf scoters tracked from wintering sites along the Pacific Coast also used multiple migration routes to and from inland breeding areas (De La Cruz et al. 2009). This suggests the concentration of the eastern black scoter population during migration may be relatively unique even among closely related sympatric sea duck species. Habitat modification (e.g., offshore wind energy development; Loring et al. 2014) or localized mortality events (e.g., oil spills, disease) at key migratory staging sites could potentially affect a larger segment of the population than similar events at winter sites. Nevertheless, eastern black scoter populations show greater genetic differentiation than closely related species such as surf and white-winged scoters, suggesting that breeding populations remain segregated despite the use of shared migration routes (Sonsthagen et al. 2019).

### Breeding

Individual tracking data considerably expand the known breeding range of North American black scoters. Of 52 individuals tracked in our study, only 16 used sites east of Hudson Bay in the presumed core breeding area of the regional population (Bordage and Savard 2011). The remainder of the tracked population bred across a broad swath of the Barrenlands (i.e., tundra areas to the west of Hudson

Bay in Nunavut and the Northwest Territories), an area identified as black scoter breeding habitat (Perry et al. 2006) but not considered part of the core breeding range (Bowman et al. 2021). This information is important to fill gaps in understanding of breeding ecology and demography of North American black scoters, and results from this study have already been used in the development of targeted efforts to survey breeding scoters in the Barrenlands (Reed et al. 2017). Compared to females, males spent less time in breeding areas, which is typical in sea ducks (Savard et al. 2007). Segregation by age or sex in post-breeding migration timing and habitat use (inland or coastal) could expose birds to different environmental and ecological pressures (Iverson et al. 2004). Few tracked males migrated to western breeding sites; however, males and females attend breeding sites in equal numbers, meaning that this imbalance likely resulted from disproportionately greater effects of capture and tagging on male breeding probability (Lamb et al. 2020*a*).

Among adult female black scoters that attended breeding sites, apparent breeding success was relatively consistent among years, suggesting individual differences in quality and experience outweigh carry-over effects of breeding. Breeding site attendance and breeding success were less during the year following transmitter attachment relative to subsequent years (Lamb et al. 2020*a*); however, aside from these effects, we did not see evidence of intermittent breeding among tracked females. Very few apparently successful breeders failed or skipped breeding in a subsequent year, unsuccessful breeders had less apparent success during the subsequent breeding season, and non-breeders skipped breeding in the subsequent season more often than either successful or unsuccessful breeders. Females may be able to buffer the energetic consequences of breeding and avoid long-term effects by adjusting non-breeding habitat use and timing (Briedis et al. 2018). Our data also show that some successful (12%) and unsuccessful (20%) breeders transitioned to non-breeding during the following year. Given that sea ducks are long-lived and may have reduced breeding propensity compared to other waterfowl (Flint 2015), occasionally foregoing breeding could be part of a long-term strategy that would allow individuals to maximize lifetime reproductive success (Shaw and Levin 2013, Shoji et al. 2015). Direct observations of marked females at breeding sites across multiple years could help to clarify the relationship between apparent and actual breeding success and long-term interannual patterns in breeding site attendance and duration. But low nest densities and inaccessibility of breeding areas in these regions pose significant challenges to direct observations of breeding success in this species (Takekawa et al. 2011). Additionally, limited breeding success at observed nests may make it difficult to achieve sufficient sample sizes for mark-recapture survival analysis (Schamber et al. 2010).

### Post-Breeding Migration

Compared to pre-breeding migration, the shorter, overland post-breeding migration route was similarly uniform among individuals, with 89% of black scoters passing through James Bay during post-breeding staging. Because timing and duration of post-breeding staging varied by sex and breeding status, individuals were less concentrated during post-breeding than pre-breeding. Males arrived at molt and post-breeding staging sites earlier and occupied sites longer than did females, which is as expected given that many males did not visit breeding areas and those that did left breeding sites earlier than females. Earlier movements of males continued throughout post-breeding migration, with males arriving earlier at winter sites. These patterns align with earlier arrival of male black scoters at Pacific (Mitchell 1952) and Atlantic (Palmer 1976) wintering sites. The direct post-breeding overland movement of black scoters from James Bay to coastal New England contrast with those of surf and white-winged scoters, which tend to migrate through the Gulf of St. Lawrence (Bordage and Savard 2011, Lepage et al. 2020) before reaching the New England coast.

Some individuals segregated by breeding status, particularly during molt and post-breeding staging. Coastal Atlantic molt sites were used almost exclusively by individuals that did not attend breeding sites; sites in Western Hudson Bay were occupied primarily by presumed breeders. Correspondingly, molt occurred earliest at Atlantic Coast sites and latest at Western Hudson Bay. Timing of molt was intermediate and variable in James Bay, which was used by breeders and non-breeders. Understanding distribution patterns during molt is important given the flight feather molt is a period of extreme mobility restriction and vulnerability for sea ducks (Viain et al. 2014, Savard and Petersen 2015). Individuals in our study moved 5.7 km/day during molt, compared to 8–20 km/day during other periods of non-breeding residency (winter, pre-breeding and post-breeding staging). These results are similar to observations of molting surf scoters along the Labrador coast, which moved an average of 5.4 km/day based on coarse temporal tracking and 7.8 km/day based on hourly tracking (O'Connor 2008). This level of movement makes sea ducks particularly dependent on fine-scale productivity at molt sites (Fox et al. 2014, Lamb et al. 2020*b*), meaning localized changes in habitat quality in molting areas, disturbances such as shipping activity (Kaiser et al. 2006), and introduced bivalve prey species (Kottsieper et al. 2019), could disproportionately affect individual fitness and distribution. Our results further suggest such localized effects may influence different segments of the breeding population depending on the timing and location of the effect.

### Migratory Connectivity and Site Fidelity

Given the extensive intra- and inter-annual movement of individuals during non-breeding periods, it is perhaps unsurprising migratory connectivity between breeding and wintering areas was weak in space and time. This low level of migratory connectivity suggests the observed separation of individuals into distinct and consistent breeding areas did not carry over into segregation in non-breeding habitats. Because pair bonds form before arrival at breeding sites, distinct sub-populations within the Atlantic population of black scoter are unlikely to exist unless breeding populations remain segregated spatially or temporally during the non-breeding season. White-winged scoters captured in the same Atlantic Coast staging and wintering areas used in this study showed similarly low connectivity values (Meattey et al. 2018), despite greater individual variation in migration routes and less within-season movement (Meattey et al. 2018, Lepage et al. 2020). Despite the lack of direct connectivity between wintering and breeding areas, we did observe greater connectivity between wintering and pre-breeding staging sites and between breeding and molt sites, suggesting individuals departing from shared habitat areas may concentrate during migration before dispersing to distinct wintering or breeding areas where they are more dispersed.

Site fidelity was considerably less during migration and wintering than during breeding. Males and females displayed interannual fidelity to broad non-breeding regions at the scale of 200–300 km; however, individuals moved extensively among regions and among and within years. Black scoters in our study displayed weak fidelity to non-breeding sites relative to other species of sea ducks, which typically return to the same molting and wintering sites and show limited within-season movement (Robertson and Cooke 1999, Beuth et al. 2017, Meattey et al. 2018). Within-season movements, which varied among individuals in timing and direction, are likely responses to variation in prey availability and fluidity of conditions in the marine environment (De La Cruz et al. 2014). Localized prey depletion resulting from intensive use of non-breeding areas by sea ducks increased movement distances in Pacific surf scoters (Kirk et al. 2008) and Atlantic common eiders (*Somateria mollissima*; Guillemette et al. 1996). Visiting multiple sites within a season may also provide an opportunity to sample conditions at distinct habitat areas and likely reflect a combination of previous experience, individual variation, and current conditions (Oppel et al. 2009). Overall, tracked black scoters appeared to respond readily to changing conditions in non-breeding areas on intra- and inter-annual scales, although the ability to change sites may vary between sexes and is likely to have energetic implications. In contrast, inter-annual fidelity to breeding sites was evident in each sex, and females showed considerably greater breeding site fidelity than males. This pattern is consistent with female-biased philopatry in waterfowl (Rohwer and Anderson 1988). Given the long-distance migrations required to access breeding sites, breeding female sea ducks cannot sample conditions before arrival in a given breeding season; thus, relying on experience from previous seasons may be the most effective means of ensuring the chosen location meets the habitat conditions required for successful breeding. It is not surprising breeding site fidelity for male sea ducks is weak; males may switch partners among years, and many are likely unpaired and spend little time at any single location during the breeding period.

Our results suggest migratory patterns may vary widely even among closely related sympatric sea duck species. In contrast to the Atlantic-wintering white-winged scoter population, which is concentrated during winter and dispersed during migration (Meattey et al. 2018), the largely sympatric Atlantic black scoter population is substantially more dispersed in winter and more concentrated during migration, particularly during pre-breeding staging. Scoter species, including white-winged, surf scoters, and black scoters, are frequently grouped together in habitat analyses (Smith et al. 2019), potentially limiting assessment of these differential patterns. Even within the black scoter population, individual differences in site use and timing of migration could result in differential exposure to external stressors, with potential population-level effects. Because successful breeders are more likely than unsuccessful breeders or non-breeders to breed successfully in subsequent seasons, changes to habitat quality in molting areas favored by later-arriving breeders may have greater demographic effects than similar factors in coastal sites used by non-breeders. Thus, environmental or anthropogenic changes affecting shared habitat areas could have differential population-level effects depending on their timing and location.

## MANAGEMENT IMPLICATIONS

Our results suggest different survey methodologies may be needed to effectively detect population trends in different sea duck species. Previous sea duck surveys in eastern North America have occurred during winter, when black scoters are dispersed throughout the Atlantic Coast and individuals move extensively among sites, potentially introducing greater variability than in other sea duck species. Because there is strong spatial segregation of males from females and young-of-year during molt, monitoring these sites could provide an opportunity to gather information on interannual variation in numbers of black scoters. Numbers of individuals and timing of occupancy at post-breeding sites are likely to vary from year to year depending on breeding conditions, which could affect the number and length of time females remain at nest sites and how many recently fledged young arrive at staging areas. The considerable interannual movement of individuals among sites throughout the molting period and the difficulty of identifying molting scoters to species based on plumage, introduce additional complications. Although our study shows that the eastern black scoter population is highly concentrated during pre-breeding migration, the brief occupancy period and individual variation in timing at pre-breeding staging sites would restrict the survey window. We observed the most consistent site use during the breeding season; thus, monitoring of key breeding areas identified using telemetry data may provide a more stable index of population trends than either winter or migration counts. Targeting surveys to occur shortly after peak arrival at breeding sites—mid-June in our study—would maximize opportunities to detect breeding males because they generally spent about 3 weeks at breeding sites and departed in late June.

Our results further elucidate the importance of James and Hudson bays, which support large portions of the Atlantic black scoter population during molt. The telemetry data reveal these areas are used throughout most of the ice-free season, with large portions of Atlantic black scoters relying on these areas for about a third of the year (Table 2). Use of James and Hudson bay habitats by black scoters is particularly intense during post-breeding migration by post-molting males and post-breeding females. Marine prey resources from James and Hudson bays may be important for successful breeding because the bays are the last sites where birds may acquire nutrient reserves before moving inland to their breeding sites, and fueling the remainder of post-breeding migration.

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## DATA AVAILABILITY STATEMENT

Data and code used in this project are available in the Zenodo Digital Repository https://doi.org/10.5281/zenodo.5172297 (Lamb et al. 2021).

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