

Annual cycle of White-winged Scoters (*Melanitta fusca*) in eastern North America: migratory phenology, population delineation, and connectivity

D.E. Meatley, S.R. McWilliams, P.W.C. Paton, C. Lepage, S.G. Gilliland, L. Savoy, G.H. Olsen, and J.E. Osenkowski

Abstract: Understanding full annual cycle movements of long-distance migrants is essential for delineating populations, assessing connectivity, evaluating crossover effects between life stages, and informing management strategies for vulnerable or declining species. We used implanted satellite transmitters to track up to 2 years of annual cycle movements of 52 adult female White-winged Scoters (*Melanitta fusca* (Linnaeus, 1758)) captured in the eastern United States and Canada. We used these data to document annual cycle phenology; delineate migration routes; identify primary areas used during winter, stopover, breeding, and molt; and assess the strength of migratory connectivity and spatial population structure. Most White-winged Scoters wintered along the Atlantic coast from Nova Scotia to southern New England, with some on Lake Ontario. White-winged Scoters followed four migration routes to breeding areas from Quebec to the Northwest Territories. Principal postbreeding molting areas were in James Bay and the St. Lawrence River estuary. Migration phenology was synchronous regardless of winter or breeding origin. Cluster analyses delineated two primary breeding areas: one molting area and one wintering area. White-winged Scoters demonstrated overall weak to moderate connectivity among life stages, with molting to wintering connectivity the strongest. Thus, White-winged Scoters that winter in eastern North America appear to constitute a single continuous population.

Key words: White-winged Scoter, *Melanitta fusca*, population delineation, migratory connectivity, annual cycle, satellite telemetry, phenology.

Résumé : La compréhension des déplacements sur un cycle annuel complet d'espèces qui migrent sur de longues distances est fondamentale pour délimiter les populations, évaluer la connectivité et les effets de chevauchement de différentes étapes du cycle biologique et élaborer de stratégies de gestion pour les espèces vulnérables ou en déclin. Nous avons utilisé des émetteurs satellitaires implantés pour suivre le cycle de déplacement annuel pendant jusqu'à deux ans de 52 macreuses à ailes blanches (*Melanitta fusca* (Linnaeus, 1758)) femelles adultes capturées dans l'est des États-Unis et du Canada. Nous avons utilisé ces données pour documenter la phénologie du cycle annuel, délimiter les routes de migration, cerner les principales aires d'hivernage, de séjour, de reproduction et de mue et évaluer la force de la connectivité migratoire et la structure spatiale de la population. La plupart des macreuses à ailes blanches hivernaient le long de la côte atlantique, de la Nouvelle-Écosse au sud de la Nouvelle-Angleterre, certaines passant plutôt l'hiver sur le lac Ontario. Les macreuses à ailes blanches suivaient quatre routes de migration vers des aires de reproduction allant du Québec aux Territoires-du-Nord-Ouest. Les principales aires de mue après la reproduction étaient dans la baie James et l'estuaire du fleuve Saint-Laurent. La phénologie de la migration était synchrone, quelles que soient les aires d'hivernage ou de reproduction d'origine. Des analyses typologiques ont délimité deux principales aires de reproduction, une aire de mue et une aire d'hivernage. Les macreuses à ailes blanches présentaient globalement une connectivité faible à modérée entre les étapes du cycle biologique, la connectivité entre la mue et l'hivernage étant la plus forte. Ainsi, les macreuses à ailes blanches qui hivernent dans l'est de l'Amérique du Nord semblent constituer une seule population continue. [Traduit par la Rédaction]

Mots-clés : macreuse à ailes blanches, *Melanitta fusca*, délimitation des populations, connectivité migratoire, cycle annuel, télémétrie satellitaire, phénologie.

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Introduction

Monitoring movement patterns of long-distance migratory animals over space and time provides insights into key aspects of their ecology (Trierweiler et al. 2014; Hallworth et al. 2015; Stanley et al. 2015). For example, estimating the interannual movements of female waterbirds reveals the extent of immigration and emigration from designated breeding areas (Madsen et al. 2014). Coordinated movements of individuals as they migrate between the same breeding and nonbreeding areas suggests strong migratory connectivity (Webster et al. 2002; Moore and Krementz 2017). Quantifying the spatial connectivity of a long-distance migrant throughout their annual cycle can identify key breeding, stop-over, molting, and wintering areas (Mehl et al. 2005; Bustnes et al. 2010; Barbaree et al. 2016), as well as delineate population structure. Strong connectivity is often the product of geographically or demographically separate subpopulations (Heath et al. 2006; Fraser et al. 2013). The strength of connectivity (i.e., the extent to which individuals from discrete breeding or nonbreeding areas remain in sympatry after migration) can also have critical implications for conservation strategies that consider the full annual cycle of a species.

Understanding migratory connectivity is especially vital for species of conservation concern, as environmental events and stressors during the nonbreeding season are well documented to affect population dynamics and productivity during the breeding season (Oosterhuis and van Dijk 2002; Gurney et al. 2014; Sedinger and Alisauskas 2014). Effective conservation and management rely on the identification of distinct population units from which accurate population size estimates and vital rates can be determined (Menu et al. 2002; Swoboda 2007). Similarly, the identification of discrete migratory flyways allows for more effective designation of management regions that may warrant varied harvest regulations (Krapu et al. 2011). A classic example of the importance of population delineation in waterfowl is “migratory” and “resident” populations of Canada Geese (*Branta canadensis* (Linnaeus, 1758)) in the Atlantic Flyway of the United States (Heusmann 1999; Sheaffer et al. 2007). Differential survival and harvest pressure led to steep declines in some migratory populations, while sedentary residents exploded to nuisance levels (Heusmann 1999), leading biologists and managers to develop targeted hunting seasons to reduce harvest of the migratory population.

Population structure in waterfowl species is typically female-mediated, as females from most species demonstrate strong natal and breeding site philopatry (Eadie and Savard 2015; Mallory 2015), whereas males are more likely to disperse depending on their paired status (Anderson et al. 1992). Most studies of waterfowl populations have focused on breeding areas when defining demographic or genetic structure within a population. However, Robertson and Cooke (1999) suggested that other annual cycle stages such as the wintering period are also important to consider. For example, pair formation in many species of waterfowl likely takes place on the wintering grounds (Robertson et al. 1998; Smith et al. 2000), so the proportion of males and females that exhibit site fidelity to certain wintering areas may be more important in determining population structure. Waterfowl are also unique among most migratory birds in that there is a postbreeding flightless remigial molt period in the annual cycle. Some individuals migrate thousands of kilometres to specific coastal or freshwater habitats to undergo a flightless molt for about 34–49 days (Savard et al. 2007; Dickson et al. 2012). These molt migrations add another level of complexity to the standard concept of migratory connectivity that typically only considers breeding and wintering areas as key life stages where individuals from discrete areas or subpopulations may mix or remain isolated.

For several species of North American sea ducks, long-term population declines have increased conservation concern and high-

lighted the need for focused understanding of annual cycle dynamics (Alisauskas et al. 2004; Zydulis et al. 2006; De La Cruz et al. 2014; Bowman et al. 2015). The causes of these declines remain uncertain in part because sea ducks range across the Arctic during summer and inhabit often remote, offshore marine environments during the nonbreeding period. As such, delineating the populations of North American sea ducks is a high priority of the Sea Duck Joint Venture (Sea Duck Joint Venture Management Board 2014), and understanding the migratory connectivity between breeding, molting, and wintering areas for these populations is crucial for species management and conservation (Mallory et al. 2006; Robert et al. 2008; De La Cruz et al. 2009). However, there remains a lack of detailed information about the population structure, migration strategies, and annual cycle movements of priority sea duck species including the White-winged Scoter (*Melanitta fusca* (Linnaeus, 1758)).

White-winged Scoters are a long-lived sea duck species that has apparently experienced a long-term decline throughout the last half-century (Alisauskas et al. 2004). White-winged Scoters primarily winter along both the Atlantic and Pacific coasts of North America, with increasing populations overwintering on the Great Lakes, and breed throughout the interior boreal forest from Alaska (USA) to central Canada (Brown and Fredrickson 1997). White-winged Scoters are generally regarded as allopatric eastern and western populations, but studies have suggested some degree of sympatry during the breeding period (Swoboda 2007; Gurney et al. 2014). As in many sea duck species, breeding females show a high degree of natal and breeding area philopatry (Eadie and Savard 2015; Mallory 2015). Sea Duck Joint Venture (2015) documented individual male White-winged Scoters migrating to different breeding areas in consecutive years, which suggests that males may follow a different female each year. Several recent studies have focused on the western population of White-winged Scoters wintering along the Pacific Coast (Safine and Lindberg 2008; Dickson et al. 2012; Gurney et al. 2014; Uher-Koch et al. 2014), whereas much less is known about the movement ecology of the eastern population of White-winged Scoters that winter along the Atlantic Coast.

We deployed satellite transmitters in adult female White-winged Scoters from capture locations along the Atlantic Coast including a molting site and two wintering sites. Our primary objective was to identify the linkages between important breeding and nonbreeding areas to determine population delineation and assess migratory connectivity of White-winged Scoters wintering along the Atlantic coast of North America. This information will be useful for informing management and conservation efforts by highlighting important geographic areas and phenology, as well as providing a better understanding of the connectivity between key areas used throughout the annual cycle where birds may face varying degrees of environmental and anthropogenic stressors.

Materials and methods

Capture and marking

We used floating mist-net arrays (Brodeur et al. 2008) to capture White-winged Scoters in Cape Cod Bay, Massachusetts, USA (41.7°N, 70.3°W), and Long Island Sound, New York, USA (40.9°N, 72.8°W), from October to November 2015 and March 2016 (Fig. 1). We used two to four sets of mist nets (36 m long, 100 or 127 mm mesh) in nearshore (<1 km) areas previously identified as consistent feeding locations. We monitored nets with teams of two to four biologists in outboard boats from predawn to 3–6 h after sunrise. We also captured White-winged Scoters using a submerged gill net, adapted from Breault and Cheng (1990), in August 2016 at a known molting location in the St. Lawrence River estuary, Quebec (Canada; 48.7°N, 69.1°W; Fig. 1). All White-winged

Fig. 1. Three locations where female White-winged Scoters (*Melanitta fusca*) ($n = 52$) were captured in 2015 and 2016 in eastern North America, as well as place names used throughout the text.



Scoters were weighed (± 5 g) and banded (USGS size 7) soon after capture.

We selected 52 female White-winged Scoters that were aged either second-year (SY) or after-second-year (ASY) (Carney 1992; Mather and Esler 1999) to receive implanted satellite transmitters (Cape Cod Bay: $n = 22$; Long Island Sound: $n = 4$; Quebec: $n = 26$). Females of many sea duck species including White-winged Scoters exhibit a high degree of natal and breeding philopatry (Eadie and Savard 2015) and would thus be more likely to provide consistent breeding location data to achieve our objectives. We chose to implant only adult female White-winged Scoters with satellite transmitters because survival and likelihood of breeding is higher in adults compared with hatch-year birds (Brown and Brown 1981).

Veterinarians implanted White-winged Scoters with a 35–38 g coelomic implant platform terminal transmitter (PTT) with an external antenna manufactured either by Microwave Telemetry, Inc. (Microwave Telemetry, Inc., Columbia, Maryland, USA; $n = 31$) or by Telonics, Inc. (model IMPTAV-2635; Telonics, Inc., Mesa, Arizona, USA; $n = 21$). Veterinarians had prior sea duck surgery experience, and used sterile surgical procedures and techniques described by Korschgen et al. (1996) and Iverson et al. (2006) for all implants. Prior to implantation, all PTTs were wrapped in nylon mesh with a felt cuff added at the antenna base to provide additional anchor points to stabilize the PTT within the body cavity

and provide additional surface area for adhesion to the body wall (Iverson et al. 2006), and skin (felt cuff) at antenna exit site. After applying these external anchoring materials, we sterilized transmitters with ethylene oxide and allowed them to de-gas before implanting. We allowed birds to recover in modified pet carriers for 1–2 h after surgery and then released White-winged Scoters at or near their original capture location within 11 h of initial capture (mean = 7.5, range = 3.0–11.0). Surgical and release methods are described in greater detail in Meatley (2018). The project and methodology were approved by the University of Rhode Island Institutional Animal Care and Use Committee (IACUC #AN1516-002).

Location data

We used the Argos satellite-based location and collection system (Collecte Localisation Satellites 2017) to receive transmission signals and PTT diagnostic data from all deployed White-winged Scoters. We filtered data through the Douglas Argos Filter (DAF) (Douglas et al. 2012) to remove redundant data and unlikely point locations. Using the DAF, we employed a hybrid filter to retain the single location with the highest accuracy from each duty cycle to reduce redundant daily positional information in our analyses. Argos processing centers report calculated accuracy estimates for each of the four highest quality location classes (i.e., location classes 3, 2, 1, and 0 had estimated accuracies of <250 m, 250 to

Table 1. Criteria used for assigning individual White-winged Scoter (*Melanitta fusca*) locations to four stages of their annual cycle.

	Breeding	Molting	Wintering	Staging
Minimum length of stay	≥25 days ^a	≥48 days ^b	None	≥7 days ^c
Arrival date	May to June	July to September	October to January	NA
Departure date	July to August	August to October	April to May	NA

Note: NA, not available.
^aTakekawa et al. 2011.
^bDickson et al. 2012.
^cDe La Cruz et al. 2009.

<500 m, 500 to <1500 m, and >1500 m, respectively). We did not estimate accuracies for location classes A, B, or Z (invalid location) because these location classes were not used in our analyses and rarely occurred.

Individual location data, internal body temperature, and PTT operational information were transmitted from each unit based on pre-programmed duty cycles. This project was also a part of a study examining resource selection and winter habitat use in White-winged Scoters (Meatley 2018), therefore we programmed PTTs on more intensive duty cycles during the winter months to increase the frequency of transmissions during the nonbreeding period. We programmed transmitters with two different seasons of on-off duty cycles (i.e., Season 1 = 4 h on duty cycle and 72 h off duty cycle; Season 2 = 4 h on duty cycle and 96 h off duty cycle). White-winged Scoters captured in the fall of 2015 were programmed to transmit on the Season 1 duty cycle for 57 cycles, which extended from capture date to mid-April 2016. Thereafter, all PTTs switched to Season 2 until the end of battery life. We programmed all transmitters deployed in March 2016 to begin on the Season 2 duty cycle for 54 cycles (until mid-October 2016). Thereafter, PTTs switched to Season 1 for 57 cycles until the end of their first full wintering period (until mid-April 2017). These transmitters deployed in March 2016 then switched back to Season 2 until the battery died. Due to changes in capture timing, we programmed PTTs deployed in August 2016 to begin on the Season 2 duty cycle and then switch to Season 1 after the first winter period.

We managed and analyzed all telemetry data, as well as produced all maps, using ArcGIS version 10.4.1 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA). We performed all statistical analyses using the statistical software R version 3.3.1 (R Core Team 2016).

Annual cycle phenology and migration strategies

We used the highest quality location collected during each duty cycle to calculate the timing of movements and identify key geographic areas throughout each stage of the annual cycle. To account for location error associated with satellite-derived locations, we assigned breeding, wintering, and molting areas to each bird by calculating a centroid from all of that individual's locations which were recorded during that time period. We used temporal life-stage criteria adapted from the Sea Duck Joint Venture (2015) to assign locations to each life stage (Table 1). Due to the varying accuracy estimates of each location and the time gaps between consecutive locations during the "breeding" period, we did not attempt to quantify nesting success of birds that migrated to suspected breeding areas. During the wintering period, two birds began the winter in one area before migrating large distances to a new wintering area. In these instances, we classified the individual's wintering area as the area in which it spent the majority of the wintering period. More detailed and robust descriptions of intrawinter movements and home-range size are described in Meatley (2018). To minimize potential bias in habitat use and movement behavior associated with capture and surgery trauma, we excluded the first 14 days of data collected after release (Esler 2000; Sexson et al. 2014). For the same reason, we only included birds that transmitted >60 days after release in our anal-

yses. We summarize movement data collected from 27 October 2015 to 6 December 2017.

We used data collected over a 1-year period for each individual to calculate their breeding, wintering, and molting centroids. This approach standardized for mortality and PTT longevity and avoided biasing the analysis towards individuals that had PTTs transmit for longer time periods. As the potential exists for movement patterns and behavior of birds to be affected by transmitter implantation during the period following capture and deployment (Barron et al. 2010; White et al. 2013), we preferentially used data for an individual in the second year that they were tracked when possible. When calculating movement phenology and inter-annual site fidelity, we used multiple years of data when available.

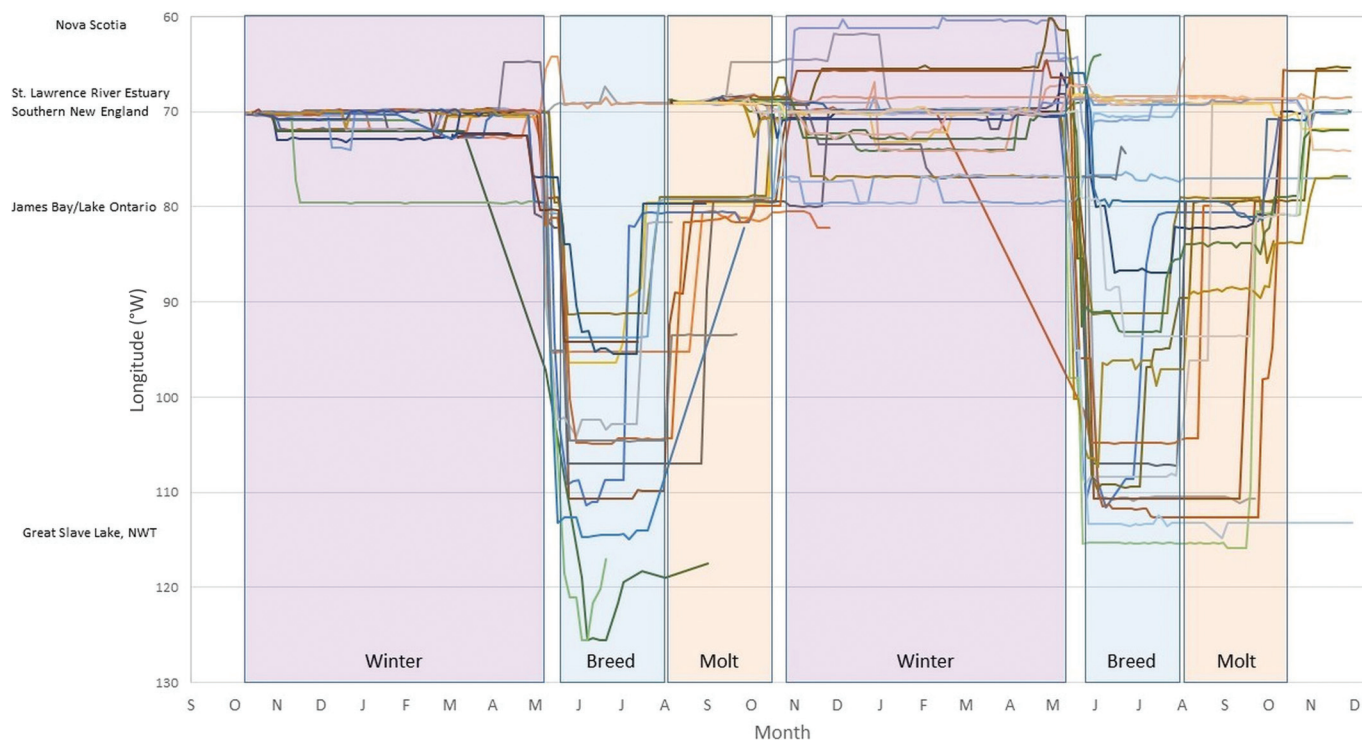
We calculated the arrival dates to areas within each life stage as the median date between the last location outside that area and the first location within it. Likewise, we calculated departure dates as the median date between the last location within and the first location outside of a particular area. We estimated total length of stay within an area during each life stage as the difference between the departure date and the arrival date at each location plus 1 day. We added an additional day to account for biases associated with the length of time transmitters were off during their duty cycles, thus the approach accounted for the possibility that a bird was present in an area on both the arrival date and the departure date (De La Cruz et al. 2009).

Following De La Cruz et al. (2009), we calculated total duration of spring migration as the difference between the winter departure date and the date of arrival at the breeding location plus one additional day. Similarly, we estimated duration of fall migration as the difference between the departure date from the molting grounds and the arrival date at the wintering area plus 1 day. We defined spring and fall migration routes based on the first recorded location at least 200 km from the wintering area or fall staging area, at which point we considered migration to have been initiated. To estimate migration routes and total distances travelled by migrating White-winged Scoters, we measured straight-line geodesic distances between consecutive locations during migration periods. We report the overall length of stay at a location and total migration duration and distance as mean ± SE (range), whereas we report only the median (range) arrival and departure dates. We used one-way ANOVA to test for statistical significance of migration phenology based on wintering location and migration route, as well as to assess differences in migratory duration and distance among different migration strategies. We used Tukey's honest significant difference (HSD) test for multiple comparisons when ANOVA indicated significance. We considered results significant at $P < 0.05$. Analyses were replicated using non-parametric Kruskal-Wallis tests and our results and interpretations were unaffected.

Population delineation and migratory connectivity

To assess for spatial population structuring on either breeding, molting, or wintering grounds, we performed cluster analyses on all centroid locations within the breeding, molting, and wintering areas using the OPTICS function in R package dbscan (Hahsler 2016; but see Ankerst et al. 1999). This method uses an ordering

Fig. 2. Migration chronology for female White-winged Scoters (*Melanitta fusca*) ($n = 52$) wintering in eastern North America. All 52 White-winged Scoters captured are depicted, including those that did not provide data long enough to be included in summary or statistical analyses. Life-stage blocks are based on median arrival and departure dates to and from each life stage.



algorithm similar to a density-based spatial clustering algorithm (i.e., DBSCAN function) to calculate the number of clusters that best represents the breeding, molting, or wintering area centroids for all individuals combined. The algorithm allowed for the possibility that some centroids would not be assigned to a cluster (Hahsler 2016). The algorithm inputs included an epsilon neighborhood that effectively set a distance threshold for identifying clusters. We determined an appropriate value for the epsilon neighborhood by identifying the “knee” in a plot of calculated k -nearest neighbor distances of our point matrices. We set the minimum number of centroids allowed for identifying a cluster to five, as tests with fewer centroids identified multiple small clusters that we did not consider ecologically meaningful.

We conducted the Mantel test (r_M) using the R package *ade4* (Dray and Dufour 2007) to quantify migratory connectivity between different life stages. This model does not require an a priori designation of distinct population units and thus serves as a null model that only considers distances among individuals during two different life stages. The null hypothesis of random mixing among individuals would thus produce an expected correlation coefficient (r_M) of zero (Ambrosini et al. 2009). We constructed distance matrices of centroid locations for the breeding, molting, and wintering periods for birds who provided data between successive life stages (i.e., a bird would not be included if a molting area was known, but it did not survive to the subsequent winter). We then computed r_M of connectivity between (i) wintering and breeding periods, (ii) breeding and molting periods, and (iii) molting and wintering periods. We determined statistical significance at $P < 0.05$ after 9999 random permutations. We duplicated these analyses including only White-winged Scoters captured in Quebec to assess whether capture location influenced our conclusions regarding migratory connectivity and population delineation.

To further test whether White-winged Scoters in the eastern United States behave as multiple distinct subunits or as a single continuous population, we used linear regression to model the

effect of breeding longitude on arrival date to the wintering grounds. We also tested the relationship between spring departure date from the wintering grounds and ultimate breeding longitude, given the hypothesis that birds breeding farthest west from their wintering area would arrive on their wintering area later and depart earlier in the spring than birds that did not migrate as far between breeding and wintering areas.

Results

We initially deployed satellite transmitters in 52 female White-winged Scoters. Seven individuals were excluded from the analysis due to mortality or radio failure within 60 days of deployment. An additional 10 birds died prior to their first breeding season after deployment and were not included in any analyses after their first wintering period. We were able to document spring migration routes and breeding areas for 27 individuals. We documented molting areas for 23 individuals and fall migration routes for 17. Five individuals provided data long enough to document breeding locations and migration routes in their second year after deployment.

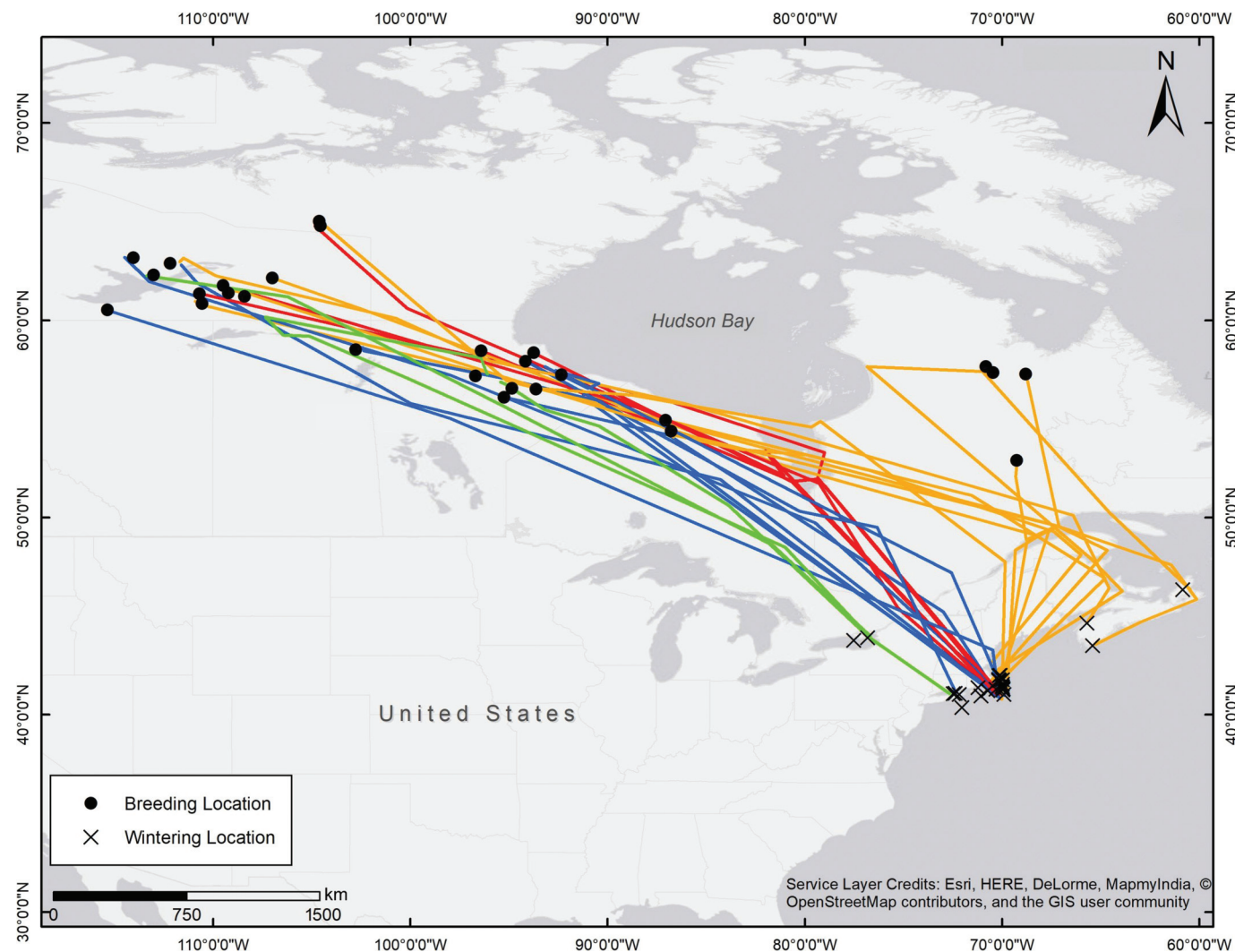
Annual cycle phenology and migration strategies

We collected movement data of female White-winged Scoters across a 2-year time period, allowing for the identification of key geographic areas used throughout the annual cycle and of the phenological patterns underlying each life stage. Annual cycle phenology and longitudinal location data for all birds deployed in this study are presented in Fig. 2. We describe below in more detail the spatial and temporal movements of female White-winged Scoters within the wintering, breeding, and molting stages of the annual cycle.

Wintering

All female White-winged Scoters captured near Cape Cod or Long Island generally remained in southern New England (USA)

Fig. 3. Estimated spring migration routes ($n = 27$) between wintering and breeding areas for female White-winged Scoters (*Melanitta fusca*) captured in eastern North America. Lines represent connections of consecutive locations along migration, but do not necessarily represent actual migration paths. Colors symbolize identified migration routes: blue = direct overland; orange = coastal route; green = Great Lakes route; red = James Bay route.



throughout the winter, except one bird that migrated west to Lake Ontario (Canada; 43.6°N, 77.8°W), approximately 3 weeks after deployment. In contrast, birds captured during the molting period in the St. Lawrence River estuary wintered throughout a broader geographic range. Fifteen of 24 (62%) White-winged Scoters captured in Quebec that survived through fall migration wintered throughout southern New England to south of Long Island, with one bird later relocating to Lake Ontario for the remainder of the winter. Three (12%) White-winged Scoters wintered along the coast of Nova Scotia (Canada; 45.0°N, 63.8°W), four (15%) individuals spent most of the winter on Lake Ontario, and one (4%) wintered along the mid-coast of Maine (USA; 44.1°N, 69.0°W; Fig. 3). We found no difference in spring departure date ($F_{[2,24]} = 2.10$, $P = 0.14$), breeding ground arrival date ($F_{[2,24]} = 0.29$, $P = 0.75$), and migration duration ($F_{[2,24]} = 0.57$, $P = 0.57$) of birds among different wintering locations. Total length of stay in the wintering areas was 189 ± 6 days (110–225 days). Total spring migration distance was shorter for birds wintering on Lake Ontario than those wintering in southern New England ($P = 0.02$). However, the low sample size of birds wintering in areas outside of southern New England likely precludes robust analysis.

Spring migration

White-winged Scoters from all capture locations generally initiated spring migration by either heading northeast along the Canadian Maritime coast (i.e., Nova Scotia and New Brunswick (Canada; $n = 11$) or northwest overland ($n = 16$; Fig. 3). Within the group that undertook the northwest overland route, we identified three distinct spring migration routes to suspected breeding areas including an overland route stopping over at James Bay (Canada; $n = 5$), a direct overland route from the wintering areas to inland breeding locations ($n = 8$), and an overland route stopping over in the Great Lakes ($n = 3$). Those that migrated along the coastal route through the Canadian Maritime provinces crossed over the St. Lawrence River estuary before continuing on to eventual breeding areas. We recorded two individual White-winged Scoters using different migration routes between years. Both birds migrated from southern New England using the overland route through James Bay (52.8°N, 80.3°W) during their first spring migration; one switched to the coastal route through the St. Lawrence River estuary during its second year and the other took a direct inland route apparently bypassing James Bay during its second year. However, this bird had a large gap in transmissions (~3 weeks) be-

tween its last location in the wintering area and its first inland location, so a stopover in James Bay could have occurred without being detected.

Across birds from all wintering areas, the median date of spring migration initiation was 15 May (27 April – 27 May, $n = 28$). We found no differences in spring departure date based on migration route. Across all birds, spring migration lasted 24 ± 2 days (8–43 days). Migration along the coastal route (29 ± 3 days, 14–41 days) took significantly longer than the direct overland route (18 ± 3 days, 8–28 days; $P = 0.03$). Total spring migration distance averaged 3034 ± 157 km (1480–4090 km) across birds from all wintering locations. There was no difference in total migration distance among migration routes ($F_{[3,23]} = 1.33$, $P = 0.29$) and no correlation between migration duration and total migration distance ($R^2 = 0.004$, $F_{[1,25]} = 0.09$, $P = 0.76$). We also found no correlation between spring departure date and total migration distance ($R^2 = 0.00005$, $F_{[1,25]} = 0.001$, $P = 0.97$). Median arrival date at suspected breeding locations was 8 June (25 May – 27 June). There was no difference in arrival date among migration routes ($F_{[3,23]} = 1.37$, $P = 0.28$).

Staging areas included James Bay ($n = 8$), St. Lawrence River estuary ($n = 7$), Prince Edward Island (Canada; 46.3°N , 63.3°W ; $n = 2$), Lake Ontario ($n = 1$), and the Gulf of St. Lawrence (48.2°N , 62.0°W ; $n = 1$), as well as inland freshwater locations in eastern Ontario ($n = 2$) and central Manitoba (Canada; $n = 1$). Length of stay at spring staging locations was 18 ± 1.5 days (8–33 days).

Breeding

For White-winged Scoters that migrated to potential breeding areas ($n = 24$), individuals spent 57 ± 5 days (25–101 days) at breeding areas before departing to molting areas (Fig. 2). The median departure date from the breeding area was 8 August (23 June – 9 September). Five birds transmitted long enough to document migration to breeding locations in consecutive years. In all cases, birds returned to the same location in the second year, suggesting strong breeding site fidelity for female White-winged Scoters.

Suspected breeding sites for individuals ranged in longitude from 68°W to 115°W ; northeastern Quebec to the southwest of Ungava Bay (Canada; 59.8°N , 67.8°W), the Hudson Bay lowlands of northern Manitoba, northwestern Manitoba, northeastern Saskatchewan (Canada), Nunavut (Canada), and areas of the Northwest Territories (Canada) surrounding Great Slave Lake (Canada; 62.5°N , 111.3°W ; Fig. 3). One bird migrated during early June as far west as the southeastern portion of the Yukon Territories (Canada), but only remained for ~5 days, suggesting that this individual did not initiate nesting.

Breeders vs. nonbreeders

Eight of the 35 birds (23%) alive during summer did not migrate to the breeding grounds during the first breeding season after deployment. Of these eight birds, only one provided data long enough to determine breeding status in the subsequent year. This bird migrated to the breeding grounds during their potential second breeding season. We found that nonbreeding White-winged Scoters departed the wintering area a mean of 6 days later than suspected breeders, but this difference was nonsignificant ($F_{[1,29]} = 1.29$, $P = 0.27$) and was likely influenced by a single outlier that did not depart her wintering area until late June. Nonbreeding birds migrated directly from the wintering grounds to suspected molting or staging areas (e.g., James Bay, the St. Lawrence River estuary, and mid-coast Maine) where they stayed until returning to their wintering areas.

Remigial molt

Molting areas appeared to be directly related to breeding status. Most birds that migrated to suspected breeding areas, and transmitted long enough to record subsequent molting areas, spent the molt period in James Bay (57%; $n = 13$; Fig. 4). One bird appeared to molt in Nunavut along the western shore of Hudson Bay, two

molted along the southwest shore of Hudson Bay, two molted among the Belcher Islands (Canada; 56.2°N , 79.4°W) in southeastern Hudson Bay, and three molted in the St. Lawrence River estuary. One bird that apparently nested near Great Slave Lake, Northwest Territories, appeared to migrate only 50 km west to molt on a small inland pond. Nonbreeding females primarily molted in the St. Lawrence River estuary (75%; $n = 6$), apart from two birds that molted in James Bay and mid-coast Maine, respectively. Two breeding females transmitted long enough to document consecutive molting sites, and both returned to the same location within James Bay in both years. For birds migrating from suspected breeding areas ($n = 21$), median arrival date on the molting grounds was 12 August (18 July – 14 September; Fig. 2). All birds that molted away from the breeding grounds remained at or near their molting area until fall migration was initiated.

Fall migration

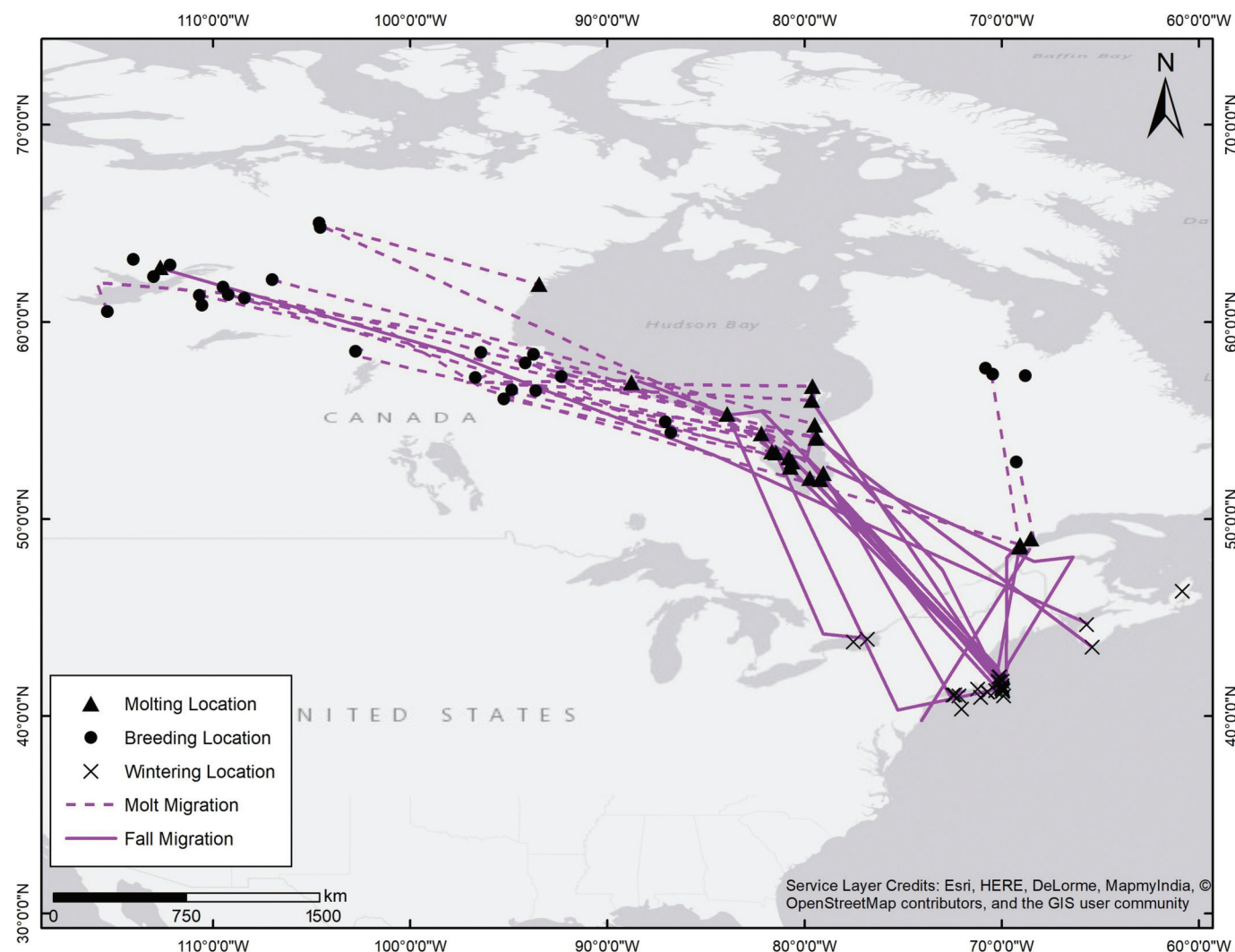
Most birds ($n = 12$) that molted in James Bay undertook a direct overland flight to southern New England, except one individual that flew along a coastal route through the St. Lawrence River estuary and Canadian Maritimes. Birds that molted in the St. Lawrence River estuary ($n = 13$) either took a direct overland route to southern New England, a coastal route to Nova Scotia, or an overland route to Lake Ontario. Total migration duration across all birds ($n = 28$) was 6 ± 3 days (2–79 days). Most White-winged Scoters migrated directly to their wintering areas without using stopover locations. One individual that migrated from James Bay stopped in Chaleur Bay (Canada; 47.9°N , 65.5°W) for 2 weeks before continuing to southern New England. One female White-winged Scoter that molted near her breeding area in the Northwest Territories took 15 days to complete fall migration after a 1-week stopover on a freshwater pond in northern Manitoba. One individual staged on Lake Champlain (USA; 44.4°N , 73.3°W) on the border of Vermont (USA) and New York for roughly 2.5 months before ultimately wintering on Lake Ontario, which represented the longest duration migration that we documented. Median arrival date to the wintering area was 1 November (27 September – 10 February; Fig. 2). There was no difference in fall departure date from different molting areas ($F_{[3,24]} = 1.29$, $P = 0.28$). We also found no difference in arrival date to the wintering areas ($F_{[3,24]} = 0.39$, $P = 0.76$) or total fall migration duration based on molting area ($F_{[3,24]} = 0.35$, $P = 0.79$).

Population delineation and migratory connectivity

We identified two disjoint clusters of 8 and 10 breeding centroids, respectively, with 9 breeding centroids not assigned to any cluster. The two identified breeding clusters were located southwest of Hudson Bay and immediately surrounding Great Slave Lake in the Northwest Territories (Fig. 5). Analysis on molting area centroids revealed one single cluster encompassing all of James Bay. Five additional molting areas inland within the breeding grounds, as well as Hudson Bay and the St. Lawrence River estuary, were unclassified. Cluster analysis on wintering areas identified a single cluster encompassing all locations within southern New England. Additional wintering areas in the Great Lakes ($n = 2$), Long Island Sound ($n = 4$), and Canadian Maritimes ($n = 3$) were not assigned to any cluster (Fig. 5). Cluster analysis including only White-winged Scoters captured during the molting period in Quebec identified one breeding cluster southwest of Hudson Bay, one molting area in James Bay, and one wintering area in southern New England.

We found weak, nonsignificant migratory connectivity between wintering and breeding areas ($r_M = 0.13$, $P = 0.15$) among the 27 females where both locations were known within the same year. Connectivity between breeding and molting areas exhibited a weak, though slightly more positive correlation, although this relationship was not statistically significant ($r_M = 0.24$, $P = 0.08$, $n = 21$). Connectivity between molting areas and wintering areas ex-

Fig. 4. Estimated molt migration routes ($n = 21$) between breeding and molting areas and fall migration routes ($n = 17$) between molting or staging and wintering areas of female White-winged Scoters (*Melanitta fusca*) captured in eastern North America. Lines represent connections of consecutive locations along migration, but do not necessarily represent actual migration paths.



hibited the most positive correlation among life stages, exhibiting moderate but nonsignificant connectivity ($r_M = 0.46$, $P = 0.07$, $n = 20$). Migratory connectivity between life stages exhibited a similar pattern when only birds captured in Quebec were included in the analysis.

We found no relationship between either breeding longitude and wintering arrival date ($R^2 = 0.06$, $F_{1,19} = 1.24$, $P = 0.28$) or spring departure date and breeding longitude ($R^2 = 0.04$, $F_{1,25} = 1.09$, $P = 0.31$), suggesting no difference in migration phenology for White-winged Scoters in the eastern United States irrespective of their breeding and wintering areas.

Discussion

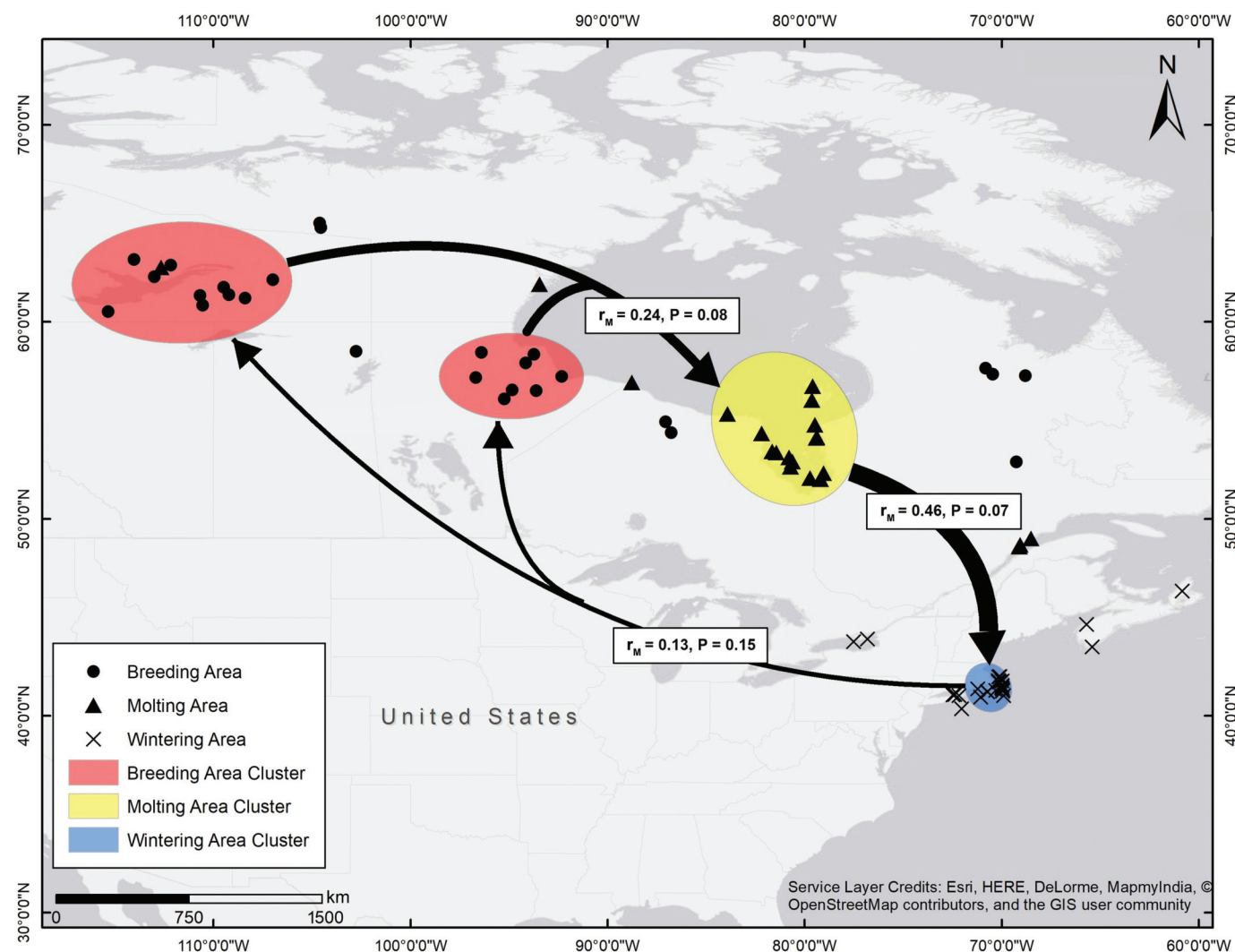
This study provides comprehensive documentation of annual cycle phenology, migration patterns, and population delineation of female White-winged Scoters in eastern North America. This information provides a rationale for managing eastern White-winged Scoters as a single, continuous population and highlights key geographic areas throughout their range that warrant consideration for conservation efforts.

Annual cycle phenology and migration strategies

White-winged Scoters in this study were initially captured either during the wintering period or during remigial molt prior to

fall migration, allowing us to assess seasonal distribution and migration chronology for birds starting in distinctly different life stages. We corroborated past survey data (Silverman et al. 2013; Baldassarre 2014; Veit et al. 2016), and telemetry studies (Meatley 2018; C. Lepage, unpublished data) that highlighted the importance of southern New England as a wintering area for White-winged Scoters, since most individuals captured on their molting grounds subsequently wintered in this region. Results from the USA Atlantic Coast Wintering Sea Duck Survey estimated that 94% of eastern White-winged Scoters winter between Cape Cod Bay and Long Island Sound (Silverman et al. 2012, 2013). Satellite-tagged female White-winged Scoters in our study spent approximately 52% (189 days) of their annual cycle at their wintering areas. This is within the same range as White-winged Scoters of both sexes tagged during the molting period in the St. Lawrence River estuary (173 ± 31 days, $n = 37$; C. Lepage, unpublished data), but longer than estimates for Black Scoters (*Melanitta americana* (Swainson, 1832)) (Loring et al. 2014) and Common Eiders (*Somateria mollissima* (Linnaeus, 1758)) (Beuth et al. 2017) wintering in southern New England, which spent a mean of 147 and 135 days, respectively. Surf Scoters (*Melanitta perspicillata* (Linnaeus, 1758)) wintering along the mid-Atlantic coast of the United States spent a mean of 133 days on the wintering grounds (Meatley et al. 2015),

Fig. 5. Annual cycle migratory connectivity of female White-winged Scoters (*Melanitta fusca*) ($n = 27$) that migrated between breeding, molting, and wintering areas. Colored areas represent clusters of life-stage areas identified by cluster analysis. Connectivity correlations account for migration between locations not assigned to clusters. Line width symbolizes comparative strength of connectivity. Lines indicate direction of migration, but do not represent actual migration routes.



while King Eiders (*Somateria spectabilis* (Linnaeus, 1758)) in Alaska spent a mean of 160 days wintering on the Bering Sea (Oppel et al. 2008).

Spring migration chronology in eastern White-winged Scoters was consistent with past observations of sea duck migration, as most birds in our study departed their wintering area by the third week of May. Timing was similar to Black Scoter departure dates from southern New England (range: 4 March – 24 May; Loring et al. 2014) but later than Common Eiders (range: 18 March – 20 April; Beuth et al. 2017). Surf Scoters wintering in four different locations along the Pacific Coast also initiated spring migration between mid-April and late-May (De La Cruz et al. 2009). Timing of migration and arrival to breeding locations showed little variation based on wintering location or migration route and exhibited no relationship with overall migration distance or duration, suggesting that White-winged Scoters breeding throughout the entire documented range exhibit relatively synchronous migration. Petersen (2009) similarly found no correlation between dates of migration initiation and migration distance in Common Eiders migrating from coastal Russia and Alaska. In contrast, Surf Scoters on the Pacific Coast appeared to migrate earlier from southern wintering areas than from northern areas (De La Cruz et al. 2009).

Recent satellite telemetry studies have highlighted individual variation in migration routes and timing. Surf Scoters on the Pacific Coast used three separate migration routes from coastal wintering areas to breeding locations in the Northwest Territories (De La Cruz et al. 2009). Similarly, Petersen (2009) documented Common Eiders wintering in the western Beaufort Sea using three distinct migration strategies to breeding areas. We documented four primary spring migration routes based on two criteria: the initial direction of travel from the wintering area and the differences in spring staging or stopover sites along each route. Most birds staged on larger coastal water bodies, with few birds stopping over on smaller inland freshwater areas. This stopover strategy of using coastal stopover sites is similar to Surf Scoters on the Pacific coast and Alaska (De La Cruz et al. 2009; Lok et al. 2011). However, we note that the reduced transmission frequency for most birds during migration could have missed short inland stopovers, particularly for individuals that undertook direct overland routes from wintering areas to breeding areas. The total duration of spring migration did not differ among individuals during this study based on wintering locations or migration routes. Similarly, Mosbech et al. (2006) found little difference in migration duration among breeding populations of Northern Common Eider (*Somateria*

mollissima borealis (C.L. Brehm, 1824)) in Greenland and Arctic Canada that used different migratory routes. In contrast, Common Eiders in Alaska using different migration strategies demonstrated some variation in migration duration, which Petersen (2009) attributed to differences in migration distance and length of stay at stopover locations.

Breeding areas identified in this study represent much of the known breeding range for White-winged Scoters in eastern North America (Brown and Fredrickson 1997; Sea Duck Joint Venture 2015), with probable breeding birds ranging as far west as Great Slave Lake in the Northwest Territories. Two White-winged Scoters were found as far west as Great Bear Lake in the Northwest Territories and the southeastern portion of the Yukon Territories, although they did not remain long enough to be classified as nesting in this region. Four White-winged Scoters migrated to suspected breeding areas in northern Quebec, much farther east than the known breeding range for the species. The Sea Duck Joint Venture (2015) also documented two White-winged Scoters breeding in Quebec farther west in the coastal lowlands of northeastern James Bay, which support the largest known breeding concentration of White-winged Scoters in Quebec (Benoit et al. 1994, 1996).

Eastern White-winged Scoters breeding in the Northwest Territories and as far east as northern Saskatchewan likely overlap with breeding White-winged Scoters from Pacific and Alaskan wintering areas. For example, White-winged Scoters breeding at Redberry Lake in northern Saskatchewan represent wintering populations from both the Atlantic (25%) and the Pacific (75%) coasts based on stable isotope analysis (Swoboda 2007). Despite this overlap, satellite telemetry studies have yet to document White-winged Scoters wintering on opposite coasts in different years. This pattern of east–west segregation is likely the result of historic population isolation during the last glaciation (Talbot et al. 2015) and is likely maintained due to pair formation during the nonbreeding period. Similar disjunct distributions have been documented in other bird species in North America such as Cooper's Hawk (*Accipiter cooperii* (Bonaparte, 1828)) (Sonsthagen et al. 2012) and Sharp-shinned Hawk (*Accipiter striatus* Vieillot, 1807) (Hull and Girman 2005), with eventual population overlap being attributed to westward expansion following glacial retreat (Hull and Girman 2005).

We identified two principal molting areas for eastern White-winged Scoters in James Bay and the St. Lawrence River estuary. Most birds that migrated to suspected breeding areas apparently molted within James Bay or Hudson Bay based on the timing and length of their stopovers. All White-winged Scoters that molted away from the breeding area migrated to molting areas in a seasonally appropriate direction (i.e., along fall migration routes) rather than undergoing a true molt migration in a different direction from the expected fall migration route as has been observed in some species of ducks and geese (Yarris et al. 1994). Timing of arrival on molting grounds typically varies by age, sex, and reproductive status (Savard and Petersen 2015), with males, subadults, and nonbreeding females undertaking remigial molt before breeding females (Petersen 1980, 1981; Savard et al. 2007; Dickson et al. 2012). Although our study consisted of only adult females, arrival dates to their molting areas were approximately 3 weeks later than arrival dates of males reported in Sea Duck Joint Venture (2015). We did not investigate differences in migration chronology between nonbreeding and breeding females in our study, as nonbreeding White-winged Scoters migrated directly to their eventual molting areas after the wintering period, thus we were unable to determine the approximate date that molt was initiated.

Molting areas for many sea ducks often also serve as fall staging locations (Petersen et al. 2006; Savard et al. 2011; Savard and Petersen 2015). White-winged Scoters in our study remained at or near their molting areas throughout the fall until migrating relatively quickly to their wintering area. Similar to most White-

winged Scoters in our study, Harlequin Ducks (*Histrionicus histrionicus* (Linnaeus, 1758)) in eastern North America migrated directly to their wintering areas without using stopover locations in between (Robert et al. 2008). In contrast, Common Eider have a protracted fall migration that can last several weeks and include several stopover locations along the route (Savard et al. 2011). King Eiders in Alaska typically take 3–105 days during fall migration to reach wintering areas, with 60% of birds taking longer than 3 weeks to complete migration after using several stopovers for up to 6 weeks (Oppel et al. 2008). The phenology of fall migration for female White-winged Scoters originating from different molting areas showed little to no variability, suggesting that annual harvest along migration does not disproportionately target any segment of the population.

Population delineation and migratory connectivity

Population delineation and migratory connectivity for species of waterfowl have usually relied on band recovery data (Madsen et al. 2014; Guillemain et al. 2017), genetic markers (Fleskes et al. 2010; Liu et al. 2012), stable isotopes (Mehl et al. 2005; Swoboda 2007; Caizergues et al. 2016), or some combination thereof (Pearce et al. 2008, 2014). Assessing stable isotopes or genetic markers, such as nuclear or mitochondrial DNA, can reliably identify overlap in population units and estimate gene flow between discrete breeding locations (Mehl et al. 2005; Sonsthagen et al. 2009). However, information from tracking individuals provides insights into whether such population delineation has resulted in coordinated movements across the annual cycle and thus strong connectivity (Webster et al. 2002; Moore and Krementz 2017), and can identify key breeding, stopover, molting, and wintering areas used (Mehl et al. 2005; Bustnes et al. 2010; Barbaree et al. 2016).

We identified two primary breeding regions for White-winged Scoters in the Northwest Territories and the lowlands southwest of Hudson Bay. These two areas corresponded with areas of high White-winged Scoter density identified by the Waterfowl Breeding Population and Habitat Survey conducted by the U.S. Fish and Wildlife Service (Bowman et al. 2015), though this survey does not distinguish between the three scoter species. As population structure in sea ducks is heavily female-mediated due to strong natal and breeding area philopatry (Eadie and Savard 2015; Mallory 2015), one would expect any spatial population structure to be evident within the breeding areas, though most pair formation occurs during the nonbreeding season (Robertson et al. 1998; Smith et al. 2000) and should ensure genetic mixing (Anderson et al. 1992). We estimated weak connectivity between breeding locations and other life stages, and thus little evidence of population delineation among eastern White-winged Scoters, although we recognize that these calculations are based on tracking relatively few females ($n = 27$) captured at wintering and molting areas. White-winged Scoters captured at the molting site in the St. Lawrence River estuary subsequently occurred across the same east–west extent as those captured in southern New England. However, some White-winged Scoters captured in the St. Lawrence migrated to breeding areas in areas of northern Quebec that the birds captured in southern New England did not. Our conclusions regarding population delineation and migratory connectivity were supported when only White-winged Scoters captured in Quebec were included in the analyses, which provides some validation that birds captured on the St. Lawrence molting grounds provide an adequate representation of the eastern population of White-winged Scoters. Future capture efforts of eastern White-winged Scoters should consider this area, as winter conditions and seasonally variable White-winged Scoter distributions make capture efforts during the winter more unpredictable.

Studies of migratory connectivity typically describe movements of individuals between breeding and nonbreeding areas (Webster et al. 2002). However, studies of connectivity in waterfowl species must also consider the postbreeding flightless remigial molt pe-

riod as an additional critical life stage where population structure and mixing may differ from either breeding or wintering periods. In our study, the strength of migratory connectivity was dependent on which life stages were being compared. Though all were nonsignificant, connectivity was weakest between winter and breeding sites and strongest between molting and wintering sites. This highlights the importance of accounting for the entire annual cycle when assessing migratory connectivity and population delineation in waterfowl.

This study has important implications for conservation and management of eastern White-winged Scoters and provides new insights into their life history. We identified probable breeding locations in Nunavut, northern Ontario, and Quebec that fall outside of published breeding range maps and could warrant further refinement of range maps of the species and expansion of breeding area surveys. Additionally, this study documented the importance of James Bay and the St. Lawrence River estuary as prominent molting and staging areas for this population, corroborating findings also reported by the *Sea Duck Joint Venture* (2015). As in many other bird species, these staging and molting areas often act as geographic bottlenecks where large numbers of birds congregate for extended periods of time and thus present unique implications for conservation and management (Leu and Thompson 2002; Lok et al. 2011; Fox et al. 2014; Barbaree et al. 2016). Conservation efforts should consider the value that these molting areas provide to White-winged Scoters.

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