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The American common eider *Somateria mollissima dresseri* is a sea duck of coastal mid-Atlantic North America, and breeding colonies in the southern part of its range have been in decline. To better understand threats faced by the subspecies, we used satellite telemetry to track 46 eiders through their annual cycle in four years from three regions in the southern part of the range, to identify key locations and migratory corridors. Female eiders exhibited highly variable movement phenology within and among colonies, but coastal Maine and Massachusetts were consistent, important moulting areas for males and females from all breeding colonies. Most birds wintered in coastal waters around Cape Cod and Nantucket Sound, meaning that threats in this region (industrial development, disease outbreak, harvest) could have deleterious effects on much of the population.

Keywords: common eider, migration, moulting, satellite telemetry, sea duck, wintering

Understanding annual movements of migratory wildlife is critical for sound management of populations, especially those that are at risk from anthropogenic activities (Petersen and Savard 2015, Hays et al. 2019). This knowledge allows us to identify locations where a species may experience threats (Amélineau et al. 2018, Mason et al. 2018), as well as where and when dispersed breeding individuals aggregate, which might be critical for determining exposure to contaminants and disease (Ballard et al. 2017). The common eider *Somateria mollissima* is a large, long-lived sea duck with a circumpolar breeding distribution (Goudie et al. 2000). Common eiders are colonial nesters with high philopatry to breeding colonies (Mallory 2015), and are gregarious at most stages of their annual cycle, notably in the winter and during postbreeding remigial moult (Merkel 2004a, Milton et al. 2006). These eiders have high cultural significance to sport hunters and indigenous peoples due to their long-held importance to

people for food and down, but in many parts of the range, abundance is in decline (Suydam et al. 2000, Merkel 2004b, Descamps et al. 2009, Gilliland et al. 2009, Ekroos et al. 2012, Milton et al. 2016), which is attributable to a suite of factors (overharvest, changing food supplies, habitat change and/or predator increases at colonies, disease, poor recruitment; see Goudie et al. 2000, Koneff et al. 2017, Allen et al. 2019).

The American common eider, *Somateria mollissima dresseri*, Sharpe, 1871, is the subspecies that breeds on coastal islands from Labrador, Canada to New York, USA (Goudie et al. 2000, Chaulk et al. 2005, Waltho and Coulson 2015). There are an estimated 240 000 individuals in the population (Canadian Wildlife Service Waterfowl Committee 2017), but more southern breeding numbers are in decline (Bowman et al. 2015), and *S. m. dresseri* is listed as an international priority species for the Sea Duck Joint Venture (2017). Banding efforts have suggested that colonies in Maine, Massachusetts and Nova Scotia were part of the same subpopulation through affinities to breeding and wintering areas (Reed and Erskine 1986, Krementz et al. 1996). However, banding efforts in some regions have declined in the last decade (Milton et al. 2016), and surveys suggest eiders

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are changing their nonbreeding locations (Milton unpubl.). Adult female survival in this subpopulation is variable. Female survival among breeding colonies in Nova Scotia is low, likely due to increased predation and habitat changes at colonies (Milton et al. 2016), while survival rates among Maine adult female eiders were notably higher (Allen et al. 2019). However, other threats to this subpopulation include windfarm and aquaculture development in key habitats (Žydelis et al. 2006, Langston 2013), oil spills in a coastal area of high shipping traffic (Sperduto et al. 2003, Thieltges et al. 2006), declining food resources (Sorte et al. 2016), contaminants (Meattey et al. 2014, Pratte et al. 2015), and outbreak of a novel disease (Ballard et al. 2017).

To better understand how common eiders in this subpopulation move and use different locations through the year, as well as the extent to which they may overlap in habitat use, we tracked American common eiders with satellite transmitters from several breeding colonies in the southern part of the *S. m. dresseri* range. Earlier banding data suggested that the Cape Cod region was an important wintering area for this subpopulation (Krementz et al. 1996), so we expected high spatial overlap in birds from different colonies in that area. We also predicted that birds from the northernmost colony would be the first to depart for autumn migration and the first to depart for their breeding grounds in the spring. Female eiders have sole responsibility for rearing young and failed or non-breeders may help rear eider crèches (Goudie et al. 2000), so we expected males to depart breeding areas and reach wintering areas earlier than females.

Methods

Study sites and deployments

Implantable satellite transmitters were deployed at five breeding colonies over four years in the southern part of the *Somateria mollissima dresseri* breeding distribution (Fig. 1). These included colonies near Boston in Massachusetts, USA (Calf Island, 42°33′N, 70°89′W, in 2013: n = 6 females, 5 males; 2014: 9 females, 10 males), colonies 30–100 km northeast of Portland, ME, USA (Flag Island, 43°75′N, 69°89′W, in 2010: 4 females; Metinic Island, 43°88′N, 69°13′W, in 2012: 4 females), and two colonies in Nova Scotia, Canada approximately 100 km northeast of Halifax near Sheet Harbour, NS (2014, East Bird Island, 9 females; West Brothers Island, 3 females, both in the Eastern Shore Islands Wildlife Management Area, 44°90′N, 62°25′W). Nova Scotia colonies were ~7 km apart and Maine colonies were ~65 km apart. Calf Island, the southernmost colony, was ~200 km from the sites in Maine and 750 km from the Nova Scotia sites.

Eiders were captured using various techniques. In Nova Scotia, female eiders were captured on their nest (artificial nesting structure) using a fishing net placed over the incubating bird. Weather conditions were relatively calm and warm (≤ 10 km h⁻¹, ≤ 9.4°C), so eggs were left inside the structures. Captured females were put in a small plastic dog kennel and transported to the base camp, where veterinarians were waiting to anaesthetize the birds with isofluorane and implant
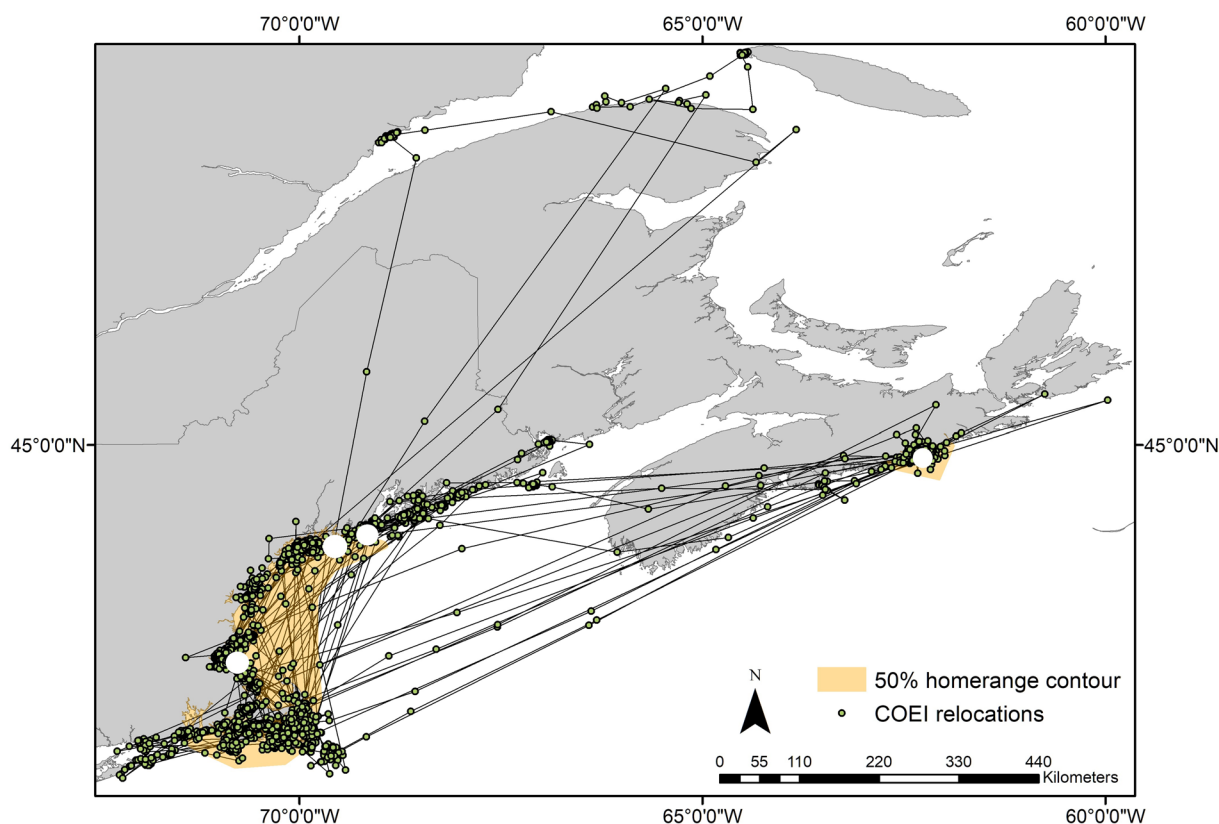

Figure 1. Movements and utilization distributions (50% orange) of American common eiders from colonies in Nova Scotia, Maine and Massachusetts. Individual dots are estimated daily positions based on state–space modelling. Large white dots are the locations of the breeding colonies.

a transmitter. Experienced wildlife veterinarians used surgical procedures that have been well-established for sea ducks (Fitzgerald et al. 2001, Mallory et al. 2006). Transmitters were from Microwave Telemetry Inc. or Telonics Inc., weighed 35–49 g representing 2.2–4.0% of female body mass, and had a duty cycle set at 8 h on, 40 h off. Surgeries took 28–83 min, and females recovered in a plastic storage container until they were alert and their visual health metrics appeared good. Total time in captivity (including post-operation recovery) was 2.2–6.2 h. After surgery, some females were returned to their nest site, while others were released on the water away from the base camp. All eiders returned to their nesting island within two days. We did not monitor nesting success, but several of the females appear to have completed incubation, departed their nest site with and attended broods based on visual inspection of tracking data.

Capture and handling procedures for eiders marked in Maine were generally similar to those used in Nova Scotia. Eiders were anesthetized with either isoflurane or propofol and followed similar surgical procedures described above for Nova Scotia eiders. Transmitters were manufactured by Microwave Telemetry Inc. or Northstar Science and Technology, weighed 26–38 g, representing 1.8–2.6% of female body mass. Microwave Telemetry transmitters were programmed with a multi-season duty cycle of 6 h on, 120 h off for 39 duty cycles (season 1) and 8 h on, 48 h off for the remainder of the transmitter battery life (season 2). Northstar transmitters were programmed with varying duty cycles consisting of 4 h on, 68 h off; 4 h on, 44 h off; and 6 h on, 66 h off. Surgery ranged from 34 to 65 min and total time in captivity was 1.4–5.0 h. All females were returned to their nest following the recovery time period.

Eiders marked with satellite transmitters in Massachusetts included both male and females. Surgical and handling procedures were similar to methods described above. Males were captured along the perimeter of the nesting colony in floating mist nets, while females were captured either by mist net or on nest, similar to methods utilized in Nova Scotia and Maine. Transmitters were manufactured by Telonics Inc., weighed 39–42 g, and were 1.8–2.7% of the bird's body mass. Transmitters were programmed with a 2 h on, 72 h off duty cycle. The total time in captivity ranged from 4 h to 12 h and males were released on the water near base camp while females were released back at their nests.

Data analyses

Data were omitted from three individuals (two males and one female from Calf Island) who were tracked for < 2 weeks, and one individual (female, Calf Island) which sent only 16 locations over a 75 d period. From the remaining 46 tags, we obtained n = 11 917 Argos locations of location classes 3 (31%), 2 (20%), 1 (12%), 0 (5%), A (13%) and B (19%). An average of 259 ± 241 SD (all means hereafter reported with standard deviation SD) locations were obtained for each bird, with an average tracking duration of 312 ± 124 d (range 41–678). There was no significant difference in tracking duration among sites (ANOVA; $F_{2,43} = 1.193$, p = 0.313) but females (334 ± 118 d) tended to be tracked longer than males (256 ± 125 d; $F_{1,44} = 3.926$, p = 0.054).

The timing of migration onset is likely to be affected by the breeding status of nesting hens, thus we classified each individual as 'failed' or apparently 'successful' breeders. This was based on: 1) observations of nest sites on subsequent visits (only for a few nests in Maine and Boston Harbor); and 2) movements of birds with respect to expected hatch dates. For the latter, we based this on raw Argos location data with location classes 3, 2 and 1 (error typically less than 2000 m; Boyd and Brightsmith 2013) and typical hatch dates for each region: 25 May (Boston Harbor), 01 June (Flag Is, ME) and 10 June (Metinic Is, ME, and Eastern Shore, NS). Incubating females do not typically leave the nest site, so we assumed 'failed' nests if an individual was > 2 km from a nest during ≥ 2 d prior to the expected hatch date. Post-hatch, females attend their crèches up to 60–65 d, and may move away from nesting islands (Goudie et al. 2000). Therefore, we assumed 'failed' chick-rearing if females moved > 30 km from a nest site during the first 45 d post-hatch. The 45-d mark was used because crèche attendance can be highly variable among individuals and the exact hatch date was unknown (Goudie et al. 2000). Together, this classified 36% (12/33) of females as failed: Eastern Shore 5/12, Maine 3/8 and Boston Harbor 4/13. Males were not classified as 'failed' or 'successful', though all tagged individuals stayed within 10 km of the colony during the first week of incubation.

Initial investigation of tracking data suggested that some birds were non-migratory and year-round residents of their nesting locations. A histogram of maximum distance traveled revealed a tri-modal distribution with clusters between 0–50, 100–300 and 700–900 km. We classified birds as 'resident' if they moved less than 50 km from their tagging site.

State–space modeling and home ranges

Argos locations were run through a Bayesian state space model (package bsam; Jonsen et al. 2013) to improve location estimates and evenness of the sampling interval (Jodice et al. 2015). We used all Argos location classes as 'observed' data to derive 'estimated' daily locations and behavior-state using the hierarchical model, and then the model was run with a Markov chain Monte Carlo method, with the first 80 000 samples discarded as a burn-in, followed by 100 000 iterations from which 2000 samples were retained after thinning by every 50th record. We used a modeled time step of 24 h to generate a daily location and behavior state. This 1-day time step was selected to model a temporal scale that is more relevant to the interpretation of migratory movements, while still acknowledging the inherent limitations of long (40 h) 'off' periods for these duty-cycled tags (Therrien et al. 2015). The model provided daily locations but some tags occasionally experienced longer 'off' periods of weeks to months when no locations were obtained. During these periods it is unrealistic to assume an even accuracy in location or behavior-state estimates, therefore we filtered the modeled locations to include only those that occurred within 1 d of any Argos location, hence eliminating data with high uncertainty during 'off' periods (Jodice et al. 2015).

Behaviour-state was modeled based on speed and turning angle at each estimated location, which in other species is typically used to distinguish between 'transitory' movements and 'Area restricted search', the latter which may indicate locations of 'searching' or 'foraging' (Therrien et al. 2015). By running the model over the annual cycle of common eider tracks and

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with daily estimated locations, we used the behaviour-state to classify locations as 'stationary' (akin to 'searching' state) or 'migratory' (akin to 'transitory' state). We conducted visual inspections of tracks and defined spring migration (departure) as the date when a bird made a directional movement of ≥ 1 d and ≥ 50 km from the wintering area towards the breeding grounds. Stopovers were defined by the state–space model (i.e. a switch from migratory to stationary), and spring migration ceased once the model indicated that the bird stopped moving near the breeding grounds. This process was repeated for defining the departure date and duration of autumn migration, with the caveat that multiple movements could occur to a moulting area or wintering grounds. Collectively this procedure appeared to capture directional movements and stopovers well; for example, we had no cases where birds moved back and forth from a breeding area in what would be considered the normal period for birds to remain on breeding colonies based on other studies. Maximum migratory distance (km) was the sum of distances from migratory days between breeding grounds and wintering grounds.

We defined the home ranges (total, winter, moulting) using the 50% contour of the utilization distribution calculated from common eider relocations. To estimate the smoothing parameter (h) we used the ad hoc method (href) in the R package adehabitatHR (Calenge 2006). The h values ranged from 0.23 to 0.82, and after we visually inspected resultant plots and maps, we determined that this approach was suitable for our descriptive purposes. We calculated the proportion of home range overlap between American and Canadian birds during both the moulting and winter periods, using the kerneloverlap function in the adehabitatHR package (Calenge 2006).

Statistical analyses

We visualized data distributions and tested how well data approximated normality using Kolmogorov–Smirnov tests. If data were suitable we applied parametric analysis of variance (ANOVA) followed by Tukey HSD post hoc tests, or t-tests, but if distributions were quite non-normal we used Kruskal–Wallis tests. In some cases we describe patterns but did not apply statistical tests to the data.

Results

State–space model

From 11 917 observed Argos locations obtained from 46 individuals, the state–space model estimated 14 364 daily

locations. We filtered these data to omit estimated locations which occurred > 1 d apart from an observed location, retained 10 846 estimated locations. This filtering retained a mean of 76% ± 15 SD of locations per individual bird (range 39–98%). The behaviour-switching model identified 95.4% of locations as 'stationary', 3.9% as 'migratory', and < 1% as uncertain state. Based on visual inspection of tracks, we classified all uncertain locations as migratory.

Migration distances

Twelve of the 46 birds (26%) that we tracked traveled a maximum distance of less than 50 km from the nest, and so they were considered 'residents'; however, this included some individuals that were not tracked throughout the full annual cycle, so migration could have been missed if tags failed prior to or early in migratory movements (tag failure, tag effects, but most likely harvest as eiders are hunted in eastern North America; Koneff et al. 2017). Therefore, we looked at migratory distances only for birds tracked longer than 01 November in their year of capture (37 of 46 tagged birds; Table 1). Both males and females from the southernmost colonies in Massachusetts showed higher rates of residency (22 and 36%, respectively) than females from Maine (0%) or Nova Scotia (10%). There was no difference in the proportion of female eiders that were migratory after successful breeding (64%) compared to resident after successful breeding (62%; Fisher Exact test, p = 1.0). Excluding resident birds, maximum migratory distances were not significantly different between males and females from Massachusetts ($F_{1,12} = 0.011$, p = 0.92; Table 1). There were significant differences in maximum migration distances among sites ($F_{2,27} = 22.04$, p < 0.001; Table 1) with longer migrations from Nova Scotia colonies compared with both USA sites (Tukey's HSD comparisons: p < 0.001), but no difference between birds from Massachusetts and Maine (p = 0.76). Massachusetts birds also showed the greatest variance in maximum migratory distances (Table 1) possibly owing to capture of birds adjacent to nesting colonies which may have included immature birds or non-breeders. Birds from Maine and Nova Scotia showed limited variance in maximum migratory distances (Table 1, except for one non-migratory bird in Nova Scotia) suggesting consistency in general migratory behavior from these sites.

Movement timing and behavior of migrating eiders

For female eiders that provided data on migration from breeding to wintering areas (n = 23), the average individual left the breeding grounds at the end of August, spent 83 ± 54 d

Table 1. Summary statistics of migratory movements for common eiders tracked beyond 01 November in their tagging year. % resident are those individuals which traveled < 50 km from their nesting site. First 'n' column represents numbers of all birds tracked; second 'n' column is number of individuals that were migratory.

Region	Sex	n	% resident	Maximum distance traveled (km) for migratory birds			
				n	mean	SD	range
Massachusetts	F	11	36%	7	309	301	111–970
Massachusetts	M	9	22%	7	325	263	86–866
Maine	F	7	0%	7	254	68	112–312
Nova Scotia	F	10	10%	9	804	53	727–885

moving between the breeding grounds and the wintering area (which included a 64 ± 26 d stop to moult), arrived at the wintering grounds in late November, spent 116 ± 43 d in the vicinity of Cape Cod and Nantucket Sound, then departed at the end of March for a 6 ± 5 d spring migration north with no stops to return to the breeding grounds in early April (Fig. 2, Table 2). Males from one region generally exhibited a similar pattern, although they departed the breeding grounds earlier (Fig. 2). Some Nova Scotia eiders travelled ~300 km offshore between wintering and breeding locations, and some flew overland between breeding and moulting sites (Fig. 1). However, we found some minor differences in timing and patterns of movement by birds breeding in different regions (Fig. 2).

Departure dates from breeding areas differed (Table 2; $F_{3,26} = 6.1$, $p = 0.0027$), with Maine females departing later than eiders in Massachusetts, and Nova Scotia females departing later than Massachusetts males (both $p < 0.05$). Seven female eiders from Massachusetts spent 75 ± 10 d at the main staging/moulting site post-breeding, six Massachusetts male eiders spent 100 ± 50 d at a moulting site, three Maine females spent 47 ± 48 d at a site post-breeding (although four birds apparently moulted near breeding colonies, and then flew directly to the wintering grounds), and seven Nova Scotia females spent 60 ± 17 d at a moulting site. Because the range of time spent in the main moulting site post-breeding varied markedly (range 10–152 d) among birds from each region, there was no significant difference among the groups (Kruskal–Wallis $KW = 5.7$, $p = 0.3$). If time spent at moulting sites is included, the duration of the post-breeding migration to arrive at the wintering site differed among groups (Table 2; $F_{3,26} = 3.5$, $p = 0.028$), although the only significant difference was that Massachusetts male eiders had a longer post-breeding migration than Maine female eiders ($p < 0.05$). There was no significant difference among groups in the number of stops eiders made between leaving the breeding grounds and arriving at the wintering grounds (overall mean 1.7 ± 1.5; $KW = 4.3$, $p = 0.23$). For female eiders, their first period of movement

departing the breeding area (9.2 ± 5.7 d, $n = 16$) was typically of longer duration than any subsequent moves before reaching the wintering grounds (5.4 ± 3.0 d, $n = 38$; $t_{18} = 2.5$, $p = 0.02$; note that seven of 25 [28%] eiders flew directly from the breeding grounds to the wintering grounds in one move). From departure of the breeding grounds to arrival at the wintering grounds, the mean duration of periods of movement by female eiders (6.6 ± 4.3 d, $n = 54$) was significantly shorter than the mean duration of stops (12.1 ± 8.9 d, $n = 37$, which excludes the long moult period; $t_{47} = 5.6$, $p = 0.0009$).

Eiders from Massachusetts, Maine and Nova Scotia varied markedly in the date of arrival at their wintering grounds (Table 2, group means 21 Oct to 8 Dec) and consequently arrival dates did not differ significantly among regions ($F_{3,26} = 1.7$, $p = 0.18$). Eiders (males and females) spent similar periods of time at the wintering grounds (mean 118 ± 40 d, $n = 21$; $KW = 0.39$, $p = 0.94$), and eiders from all groups departed for spring migration around the same time (Table 2; $KW = 5.4$, $p = 0.14$), although sample sizes were small for some groups.

Using maximum distance travelled from the breeding site, females that migrated farther had similar breeding ground departure dates, duration of post-breeding migration, arrival date at the wintering ground, duration of wintering stopover, departure date from the wintering grounds to the breeding grounds, and duration of spring migration as females that migrated much shorter distances (Pearson correlations; all $r_{14-24} \leq 0.32$, all $p \geq 0.12$).

Key locations

Following the breeding season, most female eiders from Nova Scotia moved to the coast of Maine to join local breeding birds, in a large moulting region stretching from Bar Harbor ME to Boston, MA (Fig. 1). During moulting, 38% of the home ranges of birds from American breeding colonies overlapped with those of eiders from Canadian colonies, while 29% of Canadian birds' home ranges overlapped with those of American birds (Fig. 1). Overall, from the three breeding colony regions, most female (76%) and male (69%) eiders moved to a core wintering area that stretched from Boston, MA east through the Cape Cod/Nantucket Sound region, and south to coastal Rhode Island (Fig. 3). In fact, all (100%) of the American eiders' winter home range overlapped with that of Canadian eiders, but 16% of the Canadian birds' home range overlapped with that of American eiders. Some American common eiders remained near nesting colonies in the Boston Harbor, MA and Portland (Casco Bay), ME, while one Canadian eider remained near Sheet Harbour, NS (thereby creating a much larger home range for eiders from Canadian breeding colonies).

Discussion

Our tracking of American common eiders in eastern North America provided new insights into movements of this subspecies, but largely confirmed previous research which suggests that common eiders are highly variable in migratory behavior among subspecies and even among individuals.
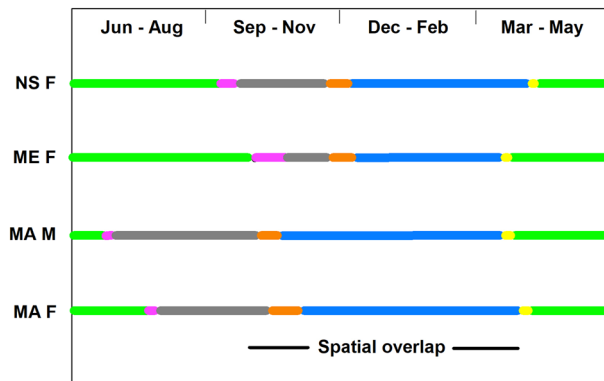

Figure 2. Schematic of components of the annual cycle of American common eiders from three sites in eastern North America: NS F – Nova Scotia (Canada) females; ME F – Maine (USA) females; MA M – Massachusetts (USA) males; MA F – Massachusetts (USA) females. Colours correspond as follows: green – breeding season; pink – post breeding migration for moult; gray – moulting/staging; orange – autumn migration to wintering site; blue – wintering season; yellow – spring migration.

Table 2. Metrics of movement behavior (mean (SD), range) for common eiders breeding in different locations. Departure and arrival values are ordinal dates.

| Region | Sex | n | Post-breeding movement | | | Winter | | Pre-breeding movement | | | Breeding |
			Departure	Stops	Duration (d)	Arrival	Duration (d)	Departure	Stops	Duration	Arrival
Massachusetts	F	8	203 (40) 163–291	2.1 (1.4) 0–4	107 (51) 7–168	309 (51) 200–377	107 (46) 54–136	91 (11) 83–98	0**	6** 4–8	96** 90–102
Successful		5	221 (41) 192–291	2 (1.6) 0–4	82 (45) 7–124	303 (65) 200–377	134* 131–136	90* 83–98	0**	6** 4–8	96** 90–102
Fail		3	172 (14) 163–188	2.3 (1.5) 1–4	147 (32) 110–168	319 (19) 298–334	54	24			
Massachusetts	M	6	174 (72) 135–321	1.7 (1.4) 0–4	146 (68) 13–203	294 (57) 182–338	127 (16)* 113–144	78 (14)* 64–93	0*	4 (1)* 3–5	82 (14)* 62–96
Maine	F	7	276 (46) 174–309	1 (1) 0–2	50 (37) 10–122	326 (25) 296–359	119 (61)*** 16–196	78 (39)*** 10–128	0***	7 (7)*** 3–21	85 (41)*** 13–132
Successful		4	295 (14) 280–309	0.5 (1) 0–2	41 (25) 10–67	336 (28) 296–359	95 (74) 16–162	64 (47)* 10–94	0*	9 (10) 3–21	73 (52)* 13–109
Fail		3	251 (67) 174–295	1 (1) 0–2	62 (53) 23–122	313 (15) 296–325	143 (46) 112–196	92 (32) 66–128	0	5 (1) 4–6	97 (32) 71–132
Nova Scotia	F	9	252 (39) 205–293	2.0 (1.6) 0–4	89 (58) 10–173	342 (32) 302–382	118 (33) 70–159	96 (5) 87–103	0.2 (0.4)**** 0–1	5 (2)**** 3–9	102 (10)**** 91–116
Successful		6	256 (40) 205–293	1.7 (1.9) 0–4	77 (64) 10–173	340 (30) 303–378	122 (29) 88–159	98 (4) 92–103	0.5** 1–1	4** 3–5	106** 97–116
Fail		3	233 (33) 210–271	2.7 (1.1) 2–4	113 (45) 83–165	346 (40) 302–382	109 (45) 70–159	91 (5) 87–97	0	6 (3) 4–9	99 (8) 91–106

* n = 3, ** n = 2, *** n = 6, **** n = 5.

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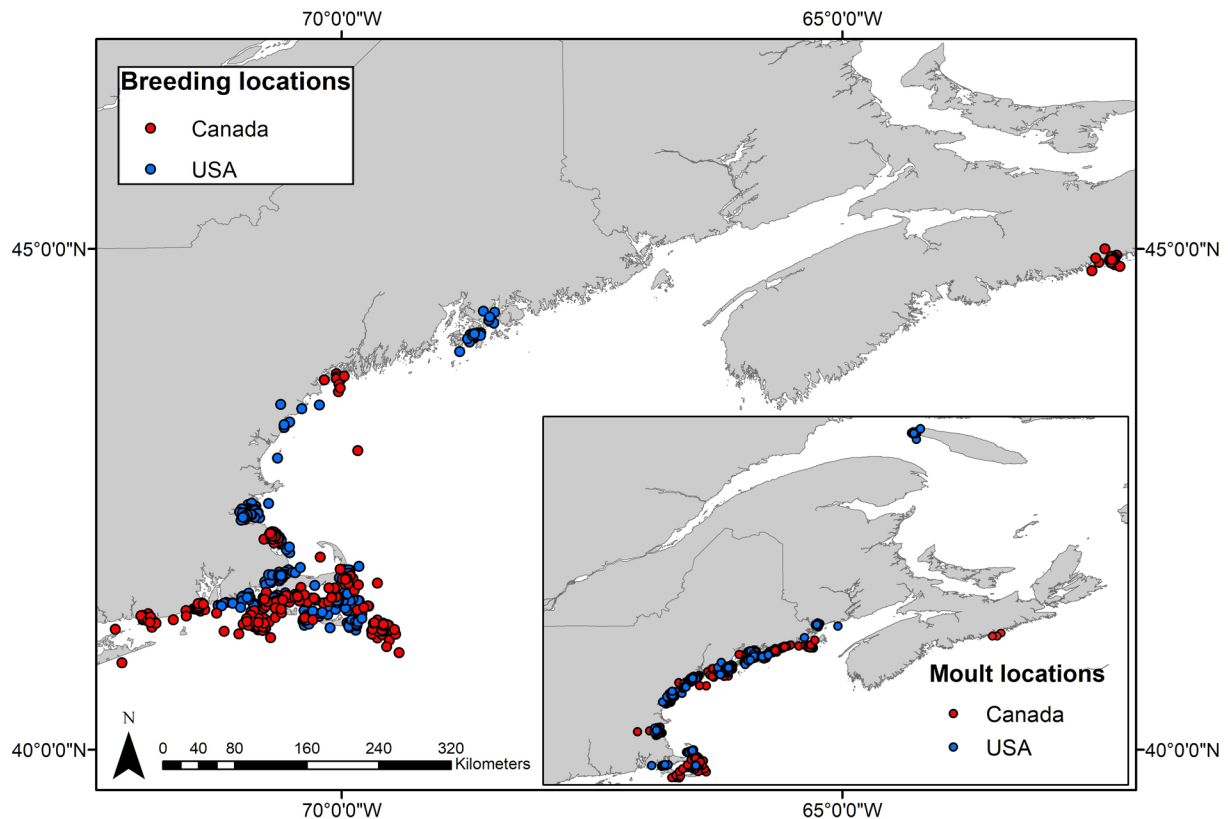
Figure 3. Winter distribution of American common eiders that bred in Canada (red dots) or the USA (blue dots), showing that the majority of birds winter around Cape Cod/Nantucket Sound, but some birds remain resident near all breeding colonies.

Indeed, some common eiders move several thousand kilometers during spring or autumn migration, whereas others move < 5 km, sometimes never leaving the coastal area near their nest site (Petersen and Flint 2002, Mosbech et al. 2006, Petersen 2009, Petersen and Savard 2015, Hanssen et al. 2016, Beuth et al. 2017). The migratory distances moved by *Somaterial mollissima dresseri* are among the shortest for migratory eiders within the *Somateria mollissima* complex, although there are largely resident populations in Iceland and the United Kingdom that exhibit little migration tendency (Goudie et al. 2000, Waltho and Coulson 2015). Nonetheless, we observed high variation among individuals and colonies in migration timing and strategies. Like Beuth et al. (2017), we showed that some eiders migrate far offshore, others travel overland during autumn moult migration, some leave the breeding grounds directly for the wintering grounds, and others head to moulting areas and make multiple stops on a slow southward movement to the wintering area. We also confirmed the importance of the Cape Cod/Nantucket Sound area for this subspecies in the winter, echoing earlier work by Beuth et al. (2017) which demonstrated that this region, and an area slightly farther south in Rhode Island, are important winter sites. The Cape Cod/Nantucket Sound marine region supports one of the highest wintering densities for a variety of sea ducks anywhere in eastern North America (Lamb et al. 2019).

Petersen (2009) noted that Pacific common eiders *Somateria mollissima v-nigrum* had three spring migration strategies, which varied in where and how long they staged during migration. We did not observe this; in fact,

our data were more consistent with previous studies from other eider breeding populations around the North Atlantic Ocean (Mosbech et al. 2006, Beuth et al. 2017), which showed that female common eiders had a relatively longer, slower autumn migration in comparison to a short spring migration. Indeed, even birds migrating from Svalbard to Iceland or coastal Norway tended to have a shorter spring migration (Hanssen et al. 2016). However, we did see an analogous, multiple migration strategy in American eiders during autumn migration, whereby some left the breeding area to arrive at a moulting or fall stopover area along coastal Maine, others flew directly from their breeding grounds to the wintering grounds, and some birds remained resident year-round near breeding areas. Moreover, another common feature across studies (Mosbech et al. 2006, Petersen 2009, Savard et al. 2011, Hanssen et al. 2016, Beuth et al. 2017, this study) is the high variation around dates of departure and arrival at breeding or wintering grounds for common eiders from the same colony. Most of these studies saw a range of at least one month between early and late arrivals, often two months or more (Petersen and Savard 2015). Collectively, our data suggest that the *S. m. dresseri* subspecies has high reliance and spatial overlap in the same wintering area, but that there was much variation in movement phenology and patterns among individuals (particularly females). Thus, movements were not well co-ordinated from different breeding sites, with spatial and temporal overlap only during part of the year and for part of the breeding population, resulting in moderate migratory connectivity (Webster et al. 2002) for this short-distance migrant.

American common eiders that flew farther between wintering and breeding sites showed no differences in any of the metrics of migration chronology, and in particular all departed for spring migration around the same time. This is consistent with results from Petersen (2009) on the Pacific subspecies, with Hanssen et al.'s (2016) results for eiders breeding in Svalbard, as well as the pattern for white-winged scoters *Melanitta fusca* that winter along New England (Meattey et al. 2018). In contrast, Mosbech et al. (2006) found that common eiders with the longest migration departed later than those with a shorter migration, but their study agreed with ours in that common eiders wintering in Greenland or Arctic Canada had similar migration duration to their breeding colony irrespective of the route they travelled. For many eider subpopulations, environmental conditions at the breeding site following winter (e.g. break up of sea ice cover in feeding areas, melt of snow cover at nest sites) likely places a greater constraint on spring migration timing than conditions following breeding for the timing of moult and fall migration (see also Petersen and Savard 2015).

We found that coastal Maine and Massachusetts were the principle moulting areas for the American common eider subpopulation that we studied. Most birds from breeding colonies in these areas made a short move after nesting and then remained nearby, like other studies which showed that common eider females moulted within 100 km of their breeding area (Mosbech et al. 2006, Savard et al. 2011). In contrast, most of the Nova Scotia eiders left Canada by late August/early September and flew to coastal areas of Maine, presumably to moult, before continuing south to the Nantucket Sound region for the winter. Male eiders departed breeding grounds for nearby moulting areas earlier than females, consistent with many other studies (Petersen and Savard 2015).

Our telemetry data suggest that American common eiders spent 32% of the annual cycle in the wintering grounds. This was identical to the pattern exhibited by northern common eiders *S. m. borealis* from Ungava Bay (32%; Savard et al. 2011), but less than American common eiders wintering in Rhode Island (39%; Beuth et al. 2017), Pacific common eiders *S. m. v-nigra* in Alaska (40%; Petersen et al. 2012) or northern common eiders *S. m. borealis* breeding in Svalbard and wintering in Iceland or the United Kingdom (48%; Hanssen et al. 2016). Oppel et al. (2008) found that king

eiders *Somateria spectabilis* remained 44% of the year on their wintering grounds. Among other sea ducks wintering in this part of the Atlantic coast, Meattey et al. (2018) showed that female white-winged scoters spent 52% of their year in this general wintering area, Loring et al. (2014) observed black scoters *Melanitta americana* staying for 40% of the year, and Meattey et al. (2015) found that surf scoters *Melanitta perspicillata* remained for 36% of the year. Other studies on common eiders have shown that, depending on the breeding population, eiders can vary considerably in how they allocate time to components of their annual cycle (Table 3). Nonetheless, while there is likely interannual variation in the duration of the stay on the wintering grounds driven by environmental conditions, our research and earlier studies show that many sea ducks spend at least one third of their year along the mid-Atlantic coast, highlighting the importance of this region as key marine habitat for this waterfowl group.

Conservation implications

Beuth et al. (2017) showed that American common eiders exhibit high wintering site fidelity, especially to coastal, shallow, nearshore habitats; our transmitters did not last long enough to establish this well for the birds from our colonies, but we assume that this occurs with our eiders as well. Beuth et al. (2017) also highlighted the potential conflict between industrial activities on the ocean and wintering eiders, and the fact that the Wellfleet Bay Virus has killed many eiders in this region over the past decades (Allison et al. 2015). We strongly share these concerns given the movement patterns of the eiders we studied, and that Wellfleet Bay Virus has been detected in breeding eiders in Nova Scotia (Ballard et al. 2017). However, we also point out that American common eiders feed heavily on a variety of marine invertebrates but especially blue mussels *Mytilus edulis* (Goudie et al. 2000, Houle et al. 2017). These were once common and abundant along this entire coastal region but are now exhibiting significant declines in abundance and reductions in their southern range (Sorte et al. 2016), in part attributable to much greater human harvest of mussels, but also concurrent with long-term warming of the Gulf of Maine (Pershing et al. 2015). If this pattern continues and intertidal or nearshore benthic communities (i.e. prey

Table 3. Comparisons of annual movement phenology for common eiders breeding in different regions around the North Atlantic Ocean.

Movement feature	Rhode Island 1	This study	Canada – West Greenland 2	Canada – West Greenland 3	Svalbard 4
Maximum sample size	24	37	87	15	47
Maximum wintering ground latitude (°N)	41.1	40.8	49	63	64.7
Maximum breeding ground latitude (°N)	48.2	44.9	64	59	79
Winter duration (d)	141	116		116	176
Spring departure	4 Apr	28 Mar	11 May	9 May	22 Apr
Spring migration duration (d)	16	6	24		3
Breeding ground arrival	19 Apr	4 Apr	4 Jun		25 Apr
Breeding ground duration (d)	168	149	136		183
Fall departure	21 Oct	31 Aug (11 Nov)	18 Oct	4 Nov	24 Oct
Fall migration duration (d)	47	9 + 10		30	4
Moult duration (d)		64		53	
Wintering grounds arrival	15 Nov	22 Nov		4 Dec	28 Oct

1 – Beuth et al. 2017; 2 – Mosbech et al. 2006; 3 – Savard et al. 2011; 4 – Hanssen et al. 2016.

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for eiders) continue to shift structure (Sorte et al. 2016), the suitability of these coastal areas to support large numbers of wintering eiders may be reduced. Consequently, we could expect to see declines in population size or shifts in distribution, irrespective of the oft-mentioned anthropogenic risks (oil spills, aquaculture, windfarms, hunting; Goudie et al. 2000) to this species.

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