



# Dispersal, movements and site fidelity of post-fledging King Eiders *Somateria spectabilis* and their attendant females

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Post-fledging dispersal and site fidelity are poorly understood, particularly for sea ducks that spend the majority of their annual cycle at sea. This is the first description of movements and their timing for first-year (juvenile) and second-year (subadult) King Eiders *Somateria spectabilis* in relation to their attendant females. We fitted satellite transmitters that operated for 2 years to 63 hatch-year birds and 17 attendant females at breeding areas in northern Alaska in 2006–2009. Our goals were to describe the spatio-temporal distribution of pre-breeding individuals and adult females that had been successful breeders. We also examined fidelity to wing moulting and wintering areas as well as natal philopatry. Juveniles did not appear to follow attendant adults, although they did winter in the same three general wintering areas, suggesting that genetic inheritance and social factors may have roles in the initial migration from the breeding area. Additionally, juveniles were more variable in the timing and duration of migration, moved longer distances during the winter, and were less faithful to moulting and wintering areas than adults, indicating that individual exploration and acquired navigational memory played a role in subsequent migrations. Most (75%) subadult females returned to natal areas, probably prospecting for future nesting sites, whereas subadult males were widely dispersed at sea. Timing and duration of moult migration and wing moult of adult females that were presumed to be successful breeders differed from those of unsuccessful breeders due to the extended time that the former spent on the breeding grounds. Temporal and spatial segregation of post-fledging King Eiders from adults has direct management implications in terms of resource development and population dynamics.

**Keywords:** juvenile, migration, satellite telemetry, sea duck, subadult, successful breeders, wing moult.

Knowledge of juvenile movement patterns, in addition to those of the adult life-stages, is critical for understanding population dynamics (Coulson 1984, Cooch & Cooke 1991), including dispersal and behavioural plasticity, interpreting genetic structure (Regehr 2003, Pearce & Petersen 2009), and in developing conservation strategies at the population level (Phillips *et al.* 2005, Trebilco *et al.* 2008, Shillinger *et al.* 2012). Juveniles departing on their first autumn migration either

rely on an inherited genetic component, with migration control being primarily based on an endogenous clock-and-compass system, or accompany adults on migration and learning the migratory route from experienced individuals (Newton 2010). Subsequent migrations may rely on learned landscape features and acquired navigational experience (Åkesson *et al.* 2001, Benhamou *et al.* 2003, Nevitt 2008), resulting in the core pattern being inherited either genetically or culturally with individual experience modifying the route. Juvenile inexperience in navigation, combined with intra-specific food competition, may influence

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distribution and other aspects of niche width for different life stages resulting in spatial segregation (Weimerskirch *et al.* 2006, Votier *et al.* 2008, 2011, Marques *et al.* 2009, Jorge *et al.* 2011). For example, in Black-footed Albatrosses *Phoebastria nigripes* there is total spatial segregation between age classes, suggesting ontogenetic niche separation (Gutowsky *et al.* 2014).

Very little is known about juvenile migration in seabirds, including sea ducks, as for methodological reasons migration studies generally focus on adults (Guilford *et al.* 2011, Péron & Grémillet 2013). A few recent studies have included juveniles but these studies have all focused on petrels or albatrosses (Trebilco *et al.* 2008, Alderman *et al.* 2010, Riotte-Lambert & Weimerskirch 2013, Gutowsky *et al.* 2014, Thiers *et al.* 2014, Weimerskirch *et al.* 2014), both of which are pelagic seabirds that have very different life histories to sea ducks (Mergini). It appears that juvenile seabirds progressively learn migration routes (Scopoli's Shearwater *Calonectris diomedea*; Péron & Grémillet 2013) and foraging behaviours (Wandering Albatrosses *Diomedea exulans*; Riotte-Lambert & Weimerskirch 2013), and it is possible that sea ducks behave similarly.

Ring recoveries and short-range radio-transmitters have been used to track some juvenile sea duck movements post-fledging (Regehr 2003) but these methods have limited use for species living in remote areas with little hunting pressure and low potential for ring recoveries. Recent improvements in satellite transmitter technology have greatly improved understanding of the spatio-temporal distribution of adult sea ducks (e.g. Mosbech *et al.* 2006, Petersen *et al.* 2006, 2012, Phillips *et al.* 2006, Chubbs *et al.* 2008, Oppel *et al.* 2008, Bustnes *et al.* 2010). However, there are few published studies on the movements of juvenile sea ducks (Harlequin Ducks *Histrionicus histrionicus*, 15 radiotagged juveniles; Regehr *et al.* 2001, Regehr 2003, and Common Mergansers *Mergus merganser*, eight juveniles marked with satellite transmitters; Pearce & Petersen 2009), and only one also tracked attendant females (Pearce & Petersen 2009). This is likely to be due to high rates of juvenile mortality combined with the difficulty of capturing individuals old enough to withstand transmitter implantation prior to dispersal from the breeding grounds. However, juvenile, subadult and adults birds are likely to vary in the routes, timing and behaviour of migration as the

younger age-classes learn the fine-scale details of migration routes, staging and wintering areas (Péron & Grémillet 2013).

King Eiders *Somateria spectabilis* are large (approximately 1500–2000 g) sea ducks that breed in arctic tundra ecosystems but spend most of their lives in remote, mostly inaccessible marine habitats (Powell & Suydam 2012). After hatching, females move overland between tundra ponds with their broods and may form crèches in which females jointly care for the young (Powell & Suydam 2012). King Eiders do not breed until they are at least 3 years old (Mehl 2004), so young age groups spend up to 3 years at sea. However, virtually nothing is known of their spatio-temporal distribution during this period, how it relates to adult distribution or the mechanisms by which post-fledging individuals join the adult population. Adult King Eiders that breed in northern Alaska and northwestern Canada spend most of their annual cycle around the Beaufort, Chukchi and Bering Seas (Phillips *et al.* 2007, Oppel *et al.* 2008, Oppel & Powell 2009, Dickson 2012) and it is assumed that the pre-breeding population uses the same areas. These areas may be vulnerable habitats because of possible shifts in their benthic invertebrate prey base (Powell & Suydam 2012) associated with climate change (Richman & Lovvorn 2003, Lovvorn *et al.* 2005, Grebmeier *et al.* 2006). In addition, development of offshore oil and gas extraction is expected in the Beaufort and Chukchi Seas, where a spill could potentially impact the King Eider population (Bentzen & Powell 2012). Because King Eiders may remain as pre-breeders for 3–9 years (Alisauskas & Kellett 2014), information on their at-sea distribution is needed.

We used satellite telemetry to describe and compare spatial and temporal use of habitats of first-year (juvenile) and second-year (subadult) King Eiders and the females that were attending the juveniles on the coastal plain of northern Alaska prior to migration. Other migratory seabirds have been found to have reduced navigation ability, lower competitive abilities and fewer distinct habitat preferences in the juvenile age-classes (Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Gutowsky *et al.* 2014). Therefore, we predicted that juvenile and subadult King Eiders would exhibit (i) more exploratory behaviour, expressed as increased variability in the timing and duration of migration and moult,

(ii) lower fidelity to previously used wintering, moulting and summer areas, and (iii) a larger spatial distribution at all annual stages than adults. Because King Eiders do not breed until they are at least 3 years old, we predicted that juvenile and subadult habitat use and movements would differ from those of adults during the spring and summer periods, probably forgoing spring migration and remaining at sea throughout the summer. These data provide new insights on the dispersal and site fidelity of naïve age classes of long-lived sea ducks.

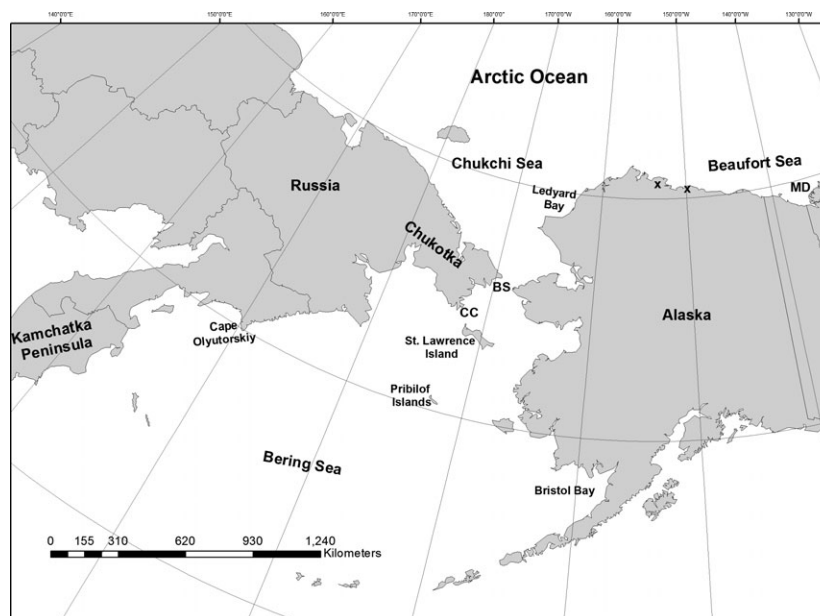
## METHODS

### Satellite telemetry

We captured 63 hatch-year King Eiders and 17 associated adult females at two locations in northern Alaska, the Kuparuk Oilfield (70°20'N, 149°45'W; 2006) and at an unnamed lake approximately 15 km south of Teshekpuk Lake (70°26'N, 152°34'W; 2007–2009; Fig. 1). The hatch-year birds were almost fully grown when trapped between 16 and 22 August, and were in family groups (Kuparuk) or crèches (near Teshekpuk Lake). It is not known whether the associated females were related to the hatch-year birds they

were captured with, but we assumed they were successful breeders in that year based on evidence that females leave the breeding area shortly after nest failure or brood loss (Phillips & Powell 2006, Mehl & Alisauskas 2007). We erected funnel traps along the shoreline or mist-net arrays in shallow ponds and used kayaks or waded to herd ducklings and adults into the traps or nets. Following standard surgical methods (Korschgen *et al.* 1996, Mulcahy & Esler 1999), we fitted each bird with an intra-abdominal satellite transmitter (approximately 38 g PTT, Microwave Telemetry, Inc., Columbia, MD, USA). We fitted each bird with a USGS ring and took standard measurements (e.g. wing chord, tarsus length and width, weight, body condition index) and sex was determined, when possible, via cloacal examination. All birds were released where captured within 2 h of surgery.

In 2006, we deployed transmitters programmed to broadcast signals for 6 h every 48 h (on/off duty cycle) from June to September, every 84 h from October to December, every 168 h from January to March, and every 84 h from April until the end of the battery life ( $n_{\text{juveniles}} = 4$ ), or every 84 h throughout the year ( $n_{\text{juveniles}} = 5$ ;  $n_{\text{adults}} = 5$ ). In 2007, 2008 and 2009, we deployed transmitters programmed to broadcast for 6 h

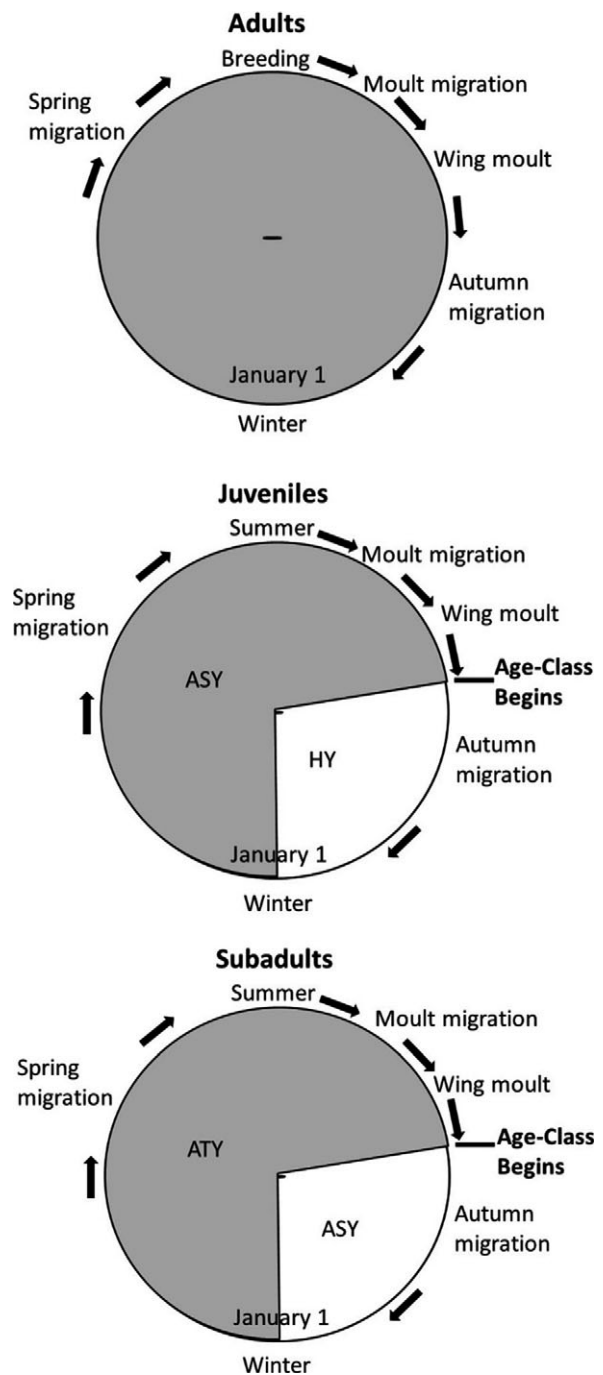


**Figure 1.** Map of northwestern North America and eastern Russia where King Eiders were tracked with satellite transmitters between 2006 and 2010. Capture locations are indicated by crosses. CC, Cape Chukotskiy; BS, Bering Strait; MD, Mackenzie River Delta.

every 120 h to maximize battery life ( $n_{\text{juveniles}} = 52$ ;  $n_{\text{adults}} = 11$ ). We deployed three additional transmitters in 2009 ( $n_{\text{juveniles}} = 2$ ;  $n_{\text{adults}} = 1$ ) that broadcast signals for 6 h every 48 h from June through mid-October, every 160 h from October through February, and every 48 h from February until the end of battery life. Transmitters were equipped with sensors to monitor internal body temperature of each individual, an indication of survival, as well as battery voltage. We used these parameters to identify mortality and transmitter failure, respectively. Transmitter data were received from Service Argos (CLS America, Inc., Largo, MD, USA); we filtered location data for accuracy using the Douglas Argos-filter V7.02 (Douglas 2006). We first eliminated low-quality locations (classes B and Z), then removed implausible locations based on location quality, and the distances, angle and rates of movement between subsequent locations (Douglas *et al.* 2012). More details regarding the capture, marking and satellite tracking of these King Eiders were reported by Oppel *et al.* (2008). All birds were handled under the Institutional Animal Care and Use Committee protocol 05-29 of the University of Alaska, Fairbanks.

### Definition of age and periods

The annual cycle of adult King Eiders can be characterized by the following periods: breeding, moult migration, wing moult, autumn migration, winter period and spring migration (Fig. 2; Oppel *et al.* 2008). For the purposes of this study, we define juveniles as local birds that fledge, leave the breeding ground and become subadults in the second summer after their first wing moult (Fig. 2). We define age classes in this way for three reasons: first, our study encompassed both the standard age classes of hatch-year (HY), after second year (ASY) and after third year (ATY) King Eiders, which do not breed; secondly, HY/ASY and ATY birds are likely to differ in behaviour; and thirdly, we describe periods and events that do not fit well into the artificial ageing system of beginning a new year on 1 January rather than the bird's first birthday. For the females captured as adults, we defined the period from departure from the breeding area on moult migration through departure from the subsequent breeding area as year 1 and the subsequent year as year 2. The moulting areas used in the first year after tagging by adults were



**Figure 2.** The annual cycle of adult, juvenile and subadult King Eiders as defined in this study in relation to the standard age classes of hatch year (HY), after second year (ASY) and after third year (ATY).

those occupied approximately 1 month after the transmitter was deployed, whereas juveniles did not moult until approximately 1 year later. Unless

otherwise noted, we used definitions of events and periods (seasons) developed by Oppel *et al.* (2008) (Table 1).

#### *Moult migration and wing moult*

Adults moult flight feathers after the breeding period and become flightless for > 20 days; thus, moulting locations and timing can be determined from satellite telemetry by delineating a period of very little movement (e.g. < 15 km; Phillips & Powell 2006, Guillemette *et al.* 2007). Juveniles presumably undergo moult migration and wing moult at approximately 1 year of age, and then again as subadults at approximately 2 years of age (Fig. 2; Table 1). If an individual did not undertake a moult migration, then summer ended with the onset of moult.

#### *Autumn migration*

Juveniles do not moult in the first autumn after departure from the breeding grounds. Therefore, we defined migration from the breeding grounds to the first wintering area as juvenile autumn migration (Fig. 2; Table 1).

#### *Winter period*

If autumn migration was not evident, we defined the start of the winter period as the end of wing

moult (Table 1). After arriving in wintering regions, adults occasionally move > 50 km during the winter period, effectively wintering in several areas but remaining within the same broad wintering region. We assumed that juveniles and subadults would also move between wintering areas within the same broad regions.

#### *Spring migration and summer period*

We classified locations as spring migration if movement away from a wintering area was noted prior to 1 June each year. However, we classified locations as non-migratory if movement was not noted prior to 1 June (Table 1). We felt confident using 1 June to delineate spring migration because adult King Eiders arrive on tundra breeding grounds between 25 May and 24 June, with most arriving on 9 and 10 June (males and females, respectively). Furthermore, adults initiate nests throughout the month of June, with mean nest initiation occurring on 17 and 19 June (two sites; Bentzen *et al.* 2008), suggesting that most adult King Eiders are present in their summer area throughout June. In addition, 1 June was used by Phillips *et al.* (2006) to define the summer areas for adults that did not go onshore during the breeding period. We did not expect King Eiders younger than 3 years to spend the summer on land.

**Table 1.** Definitions of juvenile, subadult and adult female King Eider life history events and use areas used to classify satellite telemetry data from King Eiders marked in northern Alaska, 2006–2009.

	Definition
Juvenile autumn migration	Starting with > 120 km movement west followed by another west movement and ending when the wintering area was reached
Wintering area	An area defined from the first of a series of locations < 50 km apart and lasting until the onset of spring migration, or until 1 June as some juveniles did not leave their wintering areas. If an autumn migration was not evident, the start of the winter period was defined as the end of wing moult
Spring migration	Starting with the first unreversed displacement in a northerly direction at a rate of 50 km per day and lasting until the summer area is reached. Post-winter movements by juveniles were either classed as spring migration or as non-migratory (after 1 June).
Juvenile/subadult summer area	A series of locations < 50 km apart, or occurring between late May and early July and ending with the onset of wing moult migration
Adult breeding area	A series of locations beginning at the northernmost terrestrial location reached between late May and early July, if two subsequent locations were within 10 km of each other, occurring after the completion of spring migration and ending with the onset of moult migration
Wing moult migration	Beginning with > 120 km movement followed by another movement in the same general direction and ending with moult
Wing moult site	A series of locations < 15 km apart for > 20 days
Adult autumn migration	The period of migration beginning with movement > 500 km that was initiated before January
Subadult autumn migration	> 120 km movement followed by another movement in the same general direction after moulting has occurred

### Estimation of time periods, distances and ranges

We estimated the duration of every period as the difference in days between the first and last location of a period (defined above). For stationary periods (wing moult and winter), this included the 2 days of the first and last location and yielded a minimal estimate of period duration. For migratory periods (moult, autumn and spring migration), the days defining the onset and end of the respective period were excluded, and the period between those dates yielded a maximal estimate of the duration of migration. If no points occurred on migration, the onset of migration was assumed to be the last date of the previous period. We calculated the total distance moved for each period as the sum of distances between all successive locations within that period. The distances assume a straight-line travel between successive locations, are minimal estimates of distance travelled and include staging times within a migratory period. Duration and distance of migration were not estimated if the record of locations ended before the subsequent stationary period began, so sample sizes for initiation of migration do not necessarily match those for distance and duration. Staging areas were defined as an area where the bird stopped while on migration and remained for at least two duty cycles ( $> 7$  days) with no movement  $> 50$  km (Petersen & Flint 2002, Dickson 2012). We plotted locations using ARCGIS 10.0.

### Statistical analysis

We pooled migration data from the two trapping sites as they were close enough (approximately 130 km) that migratory behaviour should not differ. We compared distance and duration of migrating and wintering King Eiders with non-parametric Mann–Whitney  $U$ -tests between age classes using SAS (SAS Institute, Cary, NC, USA). We used  $\alpha = 0.05$  for all tests and report results as mean  $\pm 1$  sd.

### RESULTS

Of the 63 juveniles ( $n_{2006} = 9$ ,  $n_{2007} = 42$ ,  $n_{2008} = 6$ ,  $n_{2009} = 6$ ;  $n_{\text{females}} = 31$ ,  $n_{\text{males}} = 23$ ,  $n_{\text{unknown}} = 9$ ) equipped with satellite transmitters, three died within 3 weeks of surgery (5% of all birds marked) and were not included in the analysis, 15 birds

(24%) died before reaching their juvenile wintering area and nine (14%) died before the subadult spring. In four birds, transmitter signals were lost for unknown reasons; the remaining 32 transmitter batteries lost power while the birds were still alive. On average, transmitter life was 511 days and allowed tracking of approximately 40% of the juvenile and subadult birds for a complete annual migration cycle. Data were obtained for more than 2 years for 10 birds.

Of the 17 ( $n_{2006} = 5$ ,  $n_{2007} = 7$ ,  $n_{2008} = 4$ ,  $n_{2009} = 1$ ) attendant females equipped with satellite transmitters, two transmitters failed prior to the birds reaching the wintering area and an additional transmitter failed before spring migration. One bird died prior to the first spring migration, two during the second moult migration and a fourth died on the breeding grounds 2 years after tagging. Transmitters lasted an average of 504 days, allowing tracking of approximately 70% of attendant females for a complete annual migration cycle. Nine adult females provided data for more than 2 years.

### Autumn/moult migration and wing moult

After tagging, juveniles remained on the breeding grounds or staged in the nearby Beaufort Sea for about 4 weeks ( $28 \pm 2$  days,  $n = 52$ ) in contrast to attendant females, which departed about 1 week earlier ( $20 \pm 2$  days,  $n = 17$ ;  $U = 362$ ,  $P = 0.001$ ). Although 30% of juveniles moved to the sea at the same time as an associated female and departure dates overlapped (Table 2), no juvenile and adult departed on migration together. Attendant females moved relatively quickly to moulting areas (Table 2) and most (88%) did not stage en route. In contrast, juveniles moved approximately 1000 km shorter distances, and because they did not undertake a moult the year they were tagged, reached their wintering area on average 3 weeks earlier than attendant females, which moved first to a moulting area and then to a wintering area (Table 2). Subadults departed on autumn migration about 1 month later and 1–2 months earlier than adults (Table 2).

For the second year after capture, 52% of juveniles migrated from their summer area to a moulting area, initiating moult migration in mid-July (Table 2). The remainder moulted in the vicinity of their summer area. Unlike adults, juveniles moulted primarily along the Chukotka

**Table 2.** Start dates (means and ranges), duration (mean  $\pm$  1 sd) and distances (mean  $\pm$  1 sd) for phases of the annual cycle for three age-classes of King Eider tracked with satellite telemetry from breeding areas in northern Alaska, 2006–2009.

Phase	Age-class			
	Juvenile	Subadult	Adult <sup>a</sup>	Adult <sup>b</sup>
<b>Moult migration</b>				
Mean start date	13 Jul (12)	31 Jul (8)	14 Sept (17)	3 Aug (12)
Start date range	1–31 Jul	19 Jul–24 Aug	1–21 Sept	9 Jul–7 Sep
Duration (days)	15 $\pm$ 14	21 $\pm$ 14	19 $\pm$ 8	35 $\pm$ 17
Distance (km)	585 $\pm$ 286	1525 $\pm$ 368	1533 $\pm$ 566	2025 $\pm$ 740
<b>Wing moult</b>				
Mean start date	25 Jul (23)	6 Aug (6)	28 Sept (17)	30 Aug (10)
Start date range	13 Jun–28 Aug	23 Jul–16 Aug	13 Sep–14 Oct	17 Aug–29 Sep
Duration (days)	64 $\pm$ 19	21 $\pm$ 14	19 $\pm$ 8	62 $\pm$ 18
<b>Autumn migration</b>				
Mean start date	24 Sep (52)	31 Oct (16)	8 Dec (6)	21 Dec (3)
Start date range	2 Sep–24 Oct	17 Sep–1 Dec	10 Nov–3 Jan	2 Dec–16 Jan
Duration (days)	54 $\pm$ 35	30 $\pm$ 24	24 $\pm$ 20	27 $\pm$ 23
Distance (km)	1794 $\pm$ 756	1023 $\pm$ 563	1310 $\pm$ 788	1052 $\pm$ 143
<b>Winter</b>				
Mean start date	12 Nov (42)	18 Nov (20)	5 Dec (15)	2 Dec (9)
Start date range	21 Sep–31 Dec	23 Sep–6 Jan	5 Nov–21 Jan	19 Oct–21 Jan
Duration (days)	194 $\pm$ 37	150 $\pm$ 11	165 $\pm$ 95	123 $\pm$ 49
<b>Spring migration</b>				
Mean start date	28 May (15)	28 Apr (13)	14 Apr (13)	8 Apr (7)
Start date range	24 Apr–26 Jun	27 Mar–29 May	1 Apr–19 May	18 Mar–30 Apr
Duration (days)	16 $\pm$ 14	48 $\pm$ 21	59 $\pm$ 17	67 $\pm$ 35
Distance (km)	898 $\pm$ 639	2495 $\pm$ 849	2719 $\pm$ 1168	3364 $\pm$ 1789
<b>Summer</b>				
Mean start date	7 Jun (26)	12 Jun (11)	17 Jun (12)	19 Jun (7)
Start date range	10 May–5 Jul	6 May–13 Jul	12 Jun–23 Jun	10 Jun–30 Jun
Duration (days)	37 $\pm$ 17	39 $\pm$ 10	30 $\pm$ 22	42 $\pm$ 11

Adults are females: <sup>a</sup>tagged with juveniles in year 1 and presumed to have been successful breeders, and <sup>b</sup>adult females in year 2 after tagging. Distances are estimates of straight-line travel along great circle routes. Sample sizes (in parentheses) depend on the number of birds initiating a particular phase and may not sum to the total number of tagged birds. Distances travelled are only reported for the first year after tagging for adult females to prevent pseudoreplication.

Peninsula. Subadults also initiated moult migration in July, and migrated further than juveniles to their moulting areas ( $U = 65$ ,  $P = 0.001$ ,  $n_{\text{juveniles}} = 12$ ,  $n_{\text{subadults}} = 8$ ; Table 2). Subadults moulted in the Bering Sea near southwestern

Alaska, around St Lawrence Island, and along the northern Chukotka Peninsula, and half were faithful to their juvenile moulting site (Table 3). The three that switched moult sites moved 280–1030 km between years. Unfortunately, no

**Table 3.** Site fidelity and natal philopatry of subadults and successfully breeding (in year 1) adult female King Eiders, tracked with satellite telemetry from breeding grounds in northern Alaska, 2006–2009. Fidelity is the proportion of individuals returning to sites (overlap in the minimum convex polygon) or regions used in the previous year or, for the natal area, 2 years previously.

	Subadult	Adult female (year 2)	Adult female (year 3)
Wintering area	9/14 (64%)	9/9 (100%)	No data
Wintering region	14/20 (70%)	9/9 (100%)	No data
Natal area <sup>a</sup>	6/8 (75%)	n/a	n/a
Breeding area	n/a	12/12 (100%)	7/7 (100%)
Wing moulting area	3/6 (50%)	8/10 (80%)	3/3 (100%)

<sup>a</sup>Area where individuals were tagged as ducklings.

transmitters lasted through the initiation of the autumn migration following the subadult wing moult, preventing an estimation of duration of their wing moult.

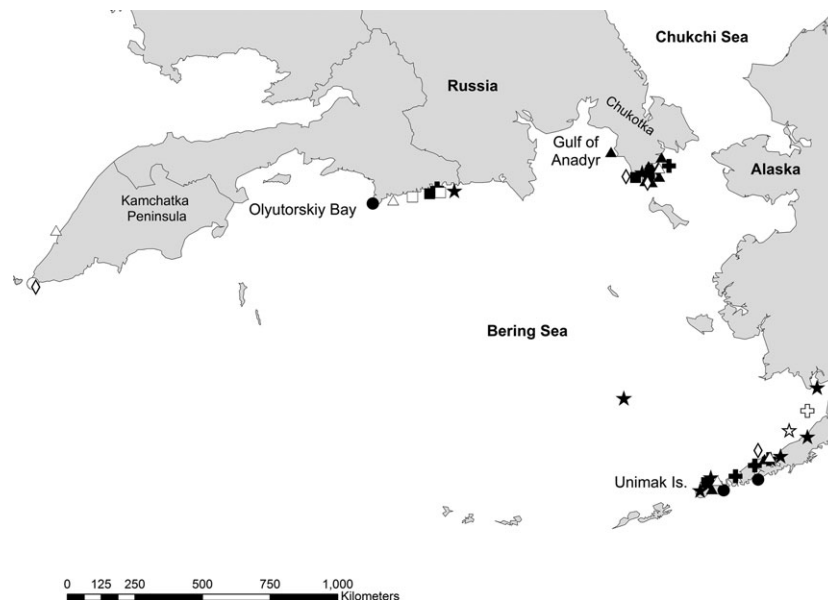
There was greater variation in the timing and duration of moult for adult females the second year after tagging (Table 2). Females moulted around the Bering Sea coast and were faithful to the previous year moulting site with two exceptions (Table 3). The centroids of site-faithful females were an average of 12 km ( $\pm 11$ ,  $n = 8$ ) apart between years. Females were site-faithful through the third year (Table 3).

### Winter period

Adults and juveniles tagged together on the breeding grounds did not necessarily winter in the same regions (Fig. 3). Juveniles wintered primarily in near-shore (< 100 km) areas in the northern Bering Sea; 5% wintered further south around the Kamchatka Peninsula, Russia. In general, juveniles remained on their wintering grounds longer than subadults or adult females, primarily because they arrived earlier (Table 2). The average total distance individuals moved during the juvenile winter was  $651 \pm 394$  km ( $n = 42$ ).

The subadult winter period was of shorter duration than for juveniles ( $U = 179$ ,  $P < 0.01$ ,  $n_{\text{juveniles}} = 42$ ,  $n_{\text{subadults}} = 20$ ; Table 2). Subadults wintered mostly in southwestern Alaska (57%) and Chukotka (38%), with a few in Kamchatka (5%); one individual wintered around the Pribilof Islands (southwestern Alaska region). Subadults showed some fidelity to their juvenile wintering area within each wintering region but, unlike adults, did not have complete fidelity to the previous winter region (Table 3). Individuals switched between the Chukotka region and the Alaska Peninsula region (five moved south, one moved north) but not the Kamchatka region. Although some juveniles (15 of 23) and subadults (six of 14) remained relatively sedentary during winter, they often used two or more areas ( $\leq 300$  km distant), but always within the same region. The average total distance individuals moved during the subadult winter was  $712 \pm 431$  km.

For adult females, arrival in the wintering areas and duration of winter was similar between the first and second winter after tagging and to subadults ( $U < 160$ ,  $P > 0.05$ ; Table 2). They wintered in the Kamchatka (40%), southwestern Alaska (33%) and Chukotka (27%) regions, and none switched regions between years (Table 3). A proportion of these females wintered in the same



**Figure 3.** Wintering areas for juvenile and associated adult King Eiders trapped together (crèches and family groups) on the breeding grounds and marked with satellite transmitters in northern Alaska between 2006 and 2010. Centroids of winter locations of individual birds are represented by the same symbol for all individuals within a family group or crèche. Adult locations are indicated by unfilled symbols, and juvenile locations by filled symbols.



areas in which they moulted in the first winter (60%) and second winter (66.7%). As with the subadults, females moved around within their wintering region; the total distance adults moved during the first winter was  $784 \pm 597$  km.

### Spring migration

For juveniles undergoing their first spring migration, 15 migrated north and 13 remained on their wintering areas through the summer. Conversely, of the subadults undertaking their second spring migration, only one remained on the wintering grounds and the other 13 migrated north. Spring migration of subadults was considerably longer in duration ( $U = 185$ ,  $P < 0.001$ ,  $n_{\text{juveniles}} = 15$ ,  $n_{\text{subadults}} = 13$ ) and distance ( $U = 186$ ,  $P < 0.001$ ) and was initiated approximately 1 month earlier than for juveniles (Table 2). Like the subadults, adult females generally departed on spring migration in April and May; duration and distances travelled were slightly longer, but not significantly so ( $U = 194$ ,  $P = 0.06$ ; Table 2).

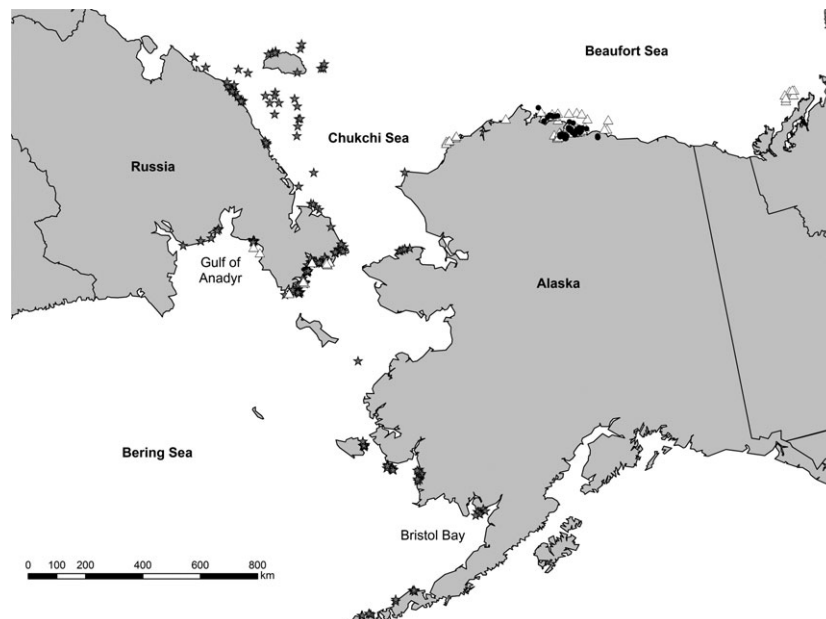
### Summer period

Juveniles spent their first summer at sea (Fig. 4). In contrast, six (75%) subadult females spent at

least part of their summer in terrestrial locations 1–15 km distant from where they were initially trapped as ducklings (Table 3), spending a minimum of 1–38 days (mean duration  $27 \pm 6$  days) on land and moving an average of  $9 \pm 7$  km between duty cycles. Of the two females that remained at sea, one summered in the Beaufort Sea approximately 27 km from the trap site and one remained offshore near the Chukotka Peninsula. Subadult males spent the summer entirely at sea, moving along the coastlines of northern Alaska ( $n = 1$ ), Chukotka ( $n = 1$ ) and the MacKenzie River Delta, Canada ( $n = 1$ ). All 12 adult females with active transmitters returned to the breeding grounds the first summer after being tagged (year 2; Fig. 4; Table 3) spending a minimum of between 5 and 71 days (mean duration  $30 \pm 22$  days) on land (Table 2). All seven adult females with active transmitters returned to the breeding grounds the second summer after being tagged (year 3; Fig. 4; Table 3) spending a minimum of between 30 and 57 days (mean duration  $42 \pm 11$  days) on land.

### DISCUSSION

As we predicted, juveniles were more variable in the timing and duration of migration and were



**Figure 4.** All summer locations of juvenile (stars,  $n = 22$ ), subadult (triangles,  $n = 10$ ) and adult female (points,  $n = 12$ ) King Eiders from individuals marked with satellite transmitters in northern Alaska between 2006 and 2010.

less faithful to moulting and wintering areas, suggesting that individual exploration and acquired navigational memory played a role in subsequent migrations. This pattern of exploration and learning has been observed in some seabirds (Votier *et al.* 2008, Péron & Grémillet 2013) although not all (Guilford *et al.* 2011). The mechanisms by which juveniles join wintering populations remain unknown for both waterfowl and seabirds (Robertson & Cooke 1999, Péron & Grémillet 2013).

For King Eiders, the most variable period of the annual cycle among the different age groups was post-summer migration (autumn or moult migration depending on age class): migration strategies of juveniles, subadults, adult females that successfully reared young during the breeding period, and unsuccessful adult females (Oppel *et al.* 2008) all differed. Juveniles left their natal areas fairly synchronously. However, unlike waterfowl that have long-term pair bonds, juveniles did not migrate in association with their attendant females, as would be expected if migration was learned from experienced individuals (Newton 2010). Moult and moult migration were synchronous among individuals, suggesting a strong selection pressure on the timing of wing moult, as was found previously for adults (Oppel *et al.* 2008). However, subadults were not all faithful to their juvenile moulting areas, and moved much longer distances between years (280–1030 km) than adults (maximum distance between moult locations 70 km; Phillips & Powell 2006), suggesting that subadults were exploring their environment and perhaps cueing in to environmental and social factors in their second year.

Implantation of satellite transmitters with percutaneous antennae may impact both survival and the timing of migration, but because there is no information from juvenile sea ducks without transmitters, the effects are difficult to assess. Although dive performance was impacted for up to 3.5 months after surgery for six adult captive-reared Common Eiders *Somateria mollissima* (Latty *et al.* 2010), transmitters did not affect timing of migration in wild Canada Geese *Branta canadensis* or survival of Common Eiders (adults; Petersen 2009). Because of uncertainty regarding transmitter effects, most studies involving implanted transmitters censor data for 2 weeks after implant (see Esler *et al.* 2000). It is possible that some of the differences in timing of autumn migration between

juveniles and subadults were due to the longer recovery, but they are more likely to be due to differences in the annual cycle where subadults do not have a distinct summer area and often remain close to the wintering area.

In winter, adult King Eiders use three discrete regions in the Bering Sea in roughly equal proportions (Oppel *et al.* 2008, Dickson 2012, this study). Juveniles wintered in these same wintering regions, suggesting that genetic inheritance may play a role in the initial migration from the breeding area; however, juveniles may also choose wintering areas by settling where they encounter conspecifics. Adults that did not breed in a given year would already be present on wintering areas when juveniles arrived. Unfortunately, we cannot distinguish whether juveniles choose wintering areas because of environmental factors or social cohesion (Robertson & Cooke 1999). The wintering regions vary in habitat quality; the northern Bering Sea is characterized by a rich benthic fauna resulting from cold, nutrient-rich waters moving north from the continental shelf-break, while the two continental shelf regions (southwestern Alaska and the Kamchatka Peninsula) are less nutrient-rich and have a lower benthic biomass (Dunton *et al.* 2005, Grebmeier *et al.* 2006). Young King Eiders may winter in the more northern region because they do not have the body reserves to continue to more southerly locations, trading off the more benign environmental conditions at lower latitudes against the costs of migration and instead choose to remain farther north in potentially poorer quality habitat (Brodersen *et al.* 2008).

Little is known about the heritability of migration/wintering strategies in sea ducks. One study suggested that wintering in different regions did not impact breeding condition, arrival date on the breeding grounds or breeding success of female King Eiders nesting in Alaska (Oppel & Powell 2009). Unfortunately, we have no information on body condition on the wintering or spring staging areas, which could mitigate any effects of wintering region. The maintenance of three different wintering strategies in the Alaskan population indicates that there is either no consistent long-term benefit for a given strategy or no heritability of wintering region choice resulting in persistence of different strategies despite the presence of a selection gradient (van Noordwijk *et al.* 2006, Oppel & Powell 2009).

Although adult King Eiders do not move among the three wintering regions within or between winters, they use large areas within these regions and may move long distances during this time (Oppel *et al.* 2009); we found that juveniles and subadults moved similar distances to adults during the winter. Adult King Eiders are more plastic in terms of distances travelled, and areas used for wintering and moulting, than the other species of eiders that breed in Alaska (Common, Spectacled *Somateria fischeri* and Steller's *Polysticta stelleri* Eiders; Petersen *et al.* 1999, Petersen 2009, Oppel *et al.* 2009, P. Martin, US Fish and Wildlife Service, Fairbanks, pers. comm.). The naïve age-classes of King Eiders appear to have even more flexibility in areas used during winter and moult than adults. Movements of individual adults within wintering areas vary widely and do not appear to be strongly correlated with sea ice concentration, region or body size, and occur under a wide variety of conditions (Oppel *et al.* 2009). These movements may represent prospecting for alternative sites, which may enhance an individual's survival if a particular wintering site becomes unsuitable, such as due to changes in food availability (Vaitkus & Bubinas 2001, Lovvorn *et al.* 2013). Unfortunately, we know little about intra- or interspecific competition or depletion of food resources in these regions. In addition, age-related changes of phenotype (e.g. variability in timing of arrival to the breeding grounds and body condition) have been documented in seabirds (Ezard *et al.* 2007), suggesting that wintering strategy may change during the lifetime of long-lived species such as King Eiders. Switching wintering regions by subadult King Eiders may indicate exploration of options prior to selecting a consistent wintering area as an adult. In fact, adult fidelity to wintering sites may not be established for a number of years: one of the juveniles in this study was killed in southwestern Alaska in May 2012 as a 5-year-old bird. This individual spent her first two winters in the northern Bering Sea region before her transmitter failed. Given the timing and location where she was shot, she probably wintered in southwestern Alaska during her fifth winter; we do not know where she wintered the previous 2 years.

As predicted, spring migration was much shorter for migratory juveniles than for subadults and adults, and tended to be initiated later, probably because they did not have a specific summer destination. Similarly, the summer period for

juvenile King Eiders was variable and hard to define. Some individuals remained on the wintering areas throughout their juvenile summer, subsequent wing moult and subadult winter. Others migrated north, generally without remaining in any one area for long. The spring migration patterns of subadults resembled those of adults much more closely; like adults, 90% of individuals migrated > 2000 km. However, adult King Eiders arrive on the breeding grounds within a 28-day range, a month earlier than subadults, probably due to the lack of selective pressure on timing of arrival for non-breeding birds.

The fidelity of subadult females to their natal area suggests they will nest in this area as adults. These birds (75% of subadult females) returned to within 15 km of where we captured them as HY birds, and were probably investigating breeding sites for future reproduction. Fidelity to general breeding areas as well as to local nest-sites has been documented previously for adult female King Eiders (Kellett 1999, Phillips & Powell 2006). However, the only previous documentation of natal fidelity, based on the recapture of 25 breeding-age adults from 1196 ducklings ringed within their natal colony in northern Canada, suggested it was very low (Mehl 2004). The disparity between studies can be explained by several factors: breeding may be delayed for more than 6 years in a significant portion of the population, low juvenile and subadult survival, differences in temporal and spatial scale, and techniques (band returns vs. satellite telemetry). High fidelity to the natal area has implications for population structure and dynamics and for conservation.

The use of the Bering, Chukchi and Beaufort Seas by juvenile and subadult King Eiders from Alaska was variable, and they did not migrate with or necessarily winter in the same regions as the attendant females. However, some patterns emerged; as predicted, juvenile movements differed from those of adults during their first spring and summer periods. This age group either remained stationary on the wintering area through their ASY summer or moved north. In contrast, subadult movements were more similar to those of adults; females returned to marine and terrestrial areas near their natal areas during summer, while males summered in a wide variety of at-sea locations. Due to the limitations of information derived from satellite telemetry, we could not infer that subadult females were breeding, but it is

likely that they were prospecting for future reproduction. Subadults did not appear faithful to their juvenile wintering region and only 50% were faithful to their juvenile wing moulting site, suggesting that this is a period of exploration. Until newer technologies become available, logistical constraints will continue to limit studies of movements of juvenile sea duck species that use remote, inaccessible marine habitats. Despite its limitations, this study provides the first information on movements and site fidelity of young age classes of a long-lived sea duck. Although more information is needed on the potential impacts of changes in benthic food resources and sea ice cover related to climate change, this study maps the timing and use of marine areas by post-fledging King Eiders around the Bering, Chukchi and Beaufort Seas, providing important information for the management of resource development.

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