

Spatiotemporal distribution and migratory patterns of Spectacled Eiders



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Abbreviations and Acronyms

BOEM	Bureau of Ocean Energy Management
BS	Western Beaufort Sea
CRD	Colville River Delta, Alaska
CS	Eastern Chukchi Sea
ESS	East Siberian Sea
GME	Geospatial Modeling Environment; Beyer 2012
LC	CLS Argos Location Class
LSCV	Least Squares Cross Validation
NBS	Northern Bering Sea
NS	Norton Sound
OCS	Outer Continental Shelf
PB	Peard Bay, Alaska
USGS	U.S. Geological Survey
WBS	Western Bering Strait
YKD	Yukon–Kuskokwim Delta

1.0. EXECUTIVE SUMMARY

Spectacled Eiders (*Somateria fischeri*) are sea ducks that spend 9 to 12 months of the year in marine habitats of the East Siberian, Chukchi, Beaufort, and Bering seas where sea ice and benthic prey are important ecological components (Petersen et al. 1998, Petersen et al. 2000, Lovvorn et al. 2009). In the summer months, Spectacled Eiders are divided into three breeding populations in coastal areas of western and northern Alaska and northern Russia, respectively. Spectacled Eiders were listed as a threatened species under the U.S. Endangered Species Act in 1993 (U. S. Fish and Wildlife Service 1993) as a result of a dramatic decline (as much as 96% from 1952 to 1993) in the western Alaska breeding population (Stehn et al. 1993, Ely et al. 1994). The non-breeding distribution of Spectacled Eiders was unknown until advancement in satellite telemetry technology enabled tracking of individuals away from breeding areas (Petersen et al. 1995, 1999). Contemporary information regarding the spatiotemporal distribution of Spectacled Eiders is needed to expand upon existing knowledge and guide future research, management, and conservation decisions.

We designed a study to characterize the distribution and migratory patterns of Spectacled Eiders throughout the annual cycle. The objectives of our study were to: 1) delineate the current range of Spectacled Eiders and the location of seasonally used important areas, 2) estimate the timing of migration and duration of site occupancy throughout the annual cycle, 3) quantify site fidelity to important areas, and 4) quantify migratory connectivity among important areas.

We implanted a satellite transmitter with percutaneous antenna into the coelom of 129 Spectacled Eiders, including 92 adults (31 males, 61 females) and 37 juveniles (20 males, 17 females) in northern and western Alaska in 2008–2011. We received location data every 4–7 days from each Spectacled Eider, up to two years following implantation. We collected a total of 7,184 weekly locations between May 2008 and August 2012.

We identified seven spatially important areas, including: 1) the western Beaufort Sea within approximately 30 km of the coast of northern Alaska; 2) the eastern Chukchi Sea within approximately 70 km of the coast of northern Alaska; 3) the East Siberian Sea within 200 km of the coast of northern Russia; 4) the western Bering Strait within approximately 60 km of the coast of the eastern Chukotka Peninsula, Russia; 5) eastern and southern Norton Sound in the northeastern Bering Sea; 6) the Yukon-Kuskokwim Delta and adjacent marine areas within approximately 20 km of the coast of western Alaska; and 7) the northern Bering Sea within approximately 200 km of the southern coast of St. Lawrence Island.

Spectacled Eiders wintered exclusively in lead-dominated sea ice in the northern Bering Sea from late November through mid-February. Eiders used Norton Sound and the western Bering Strait during pre-breeding migration (mid-March through early May) and post-breeding migration (mid-July through mid-November). Pre-breeding, Spectacled Eiders also staged offshore in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and East Siberian Sea in early through mid-May. Important areas used during breeding included terrestrial sites in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, western Beaufort Sea, and East Siberian Sea areas. Eiders occupied the eastern Chukchi Sea and East Siberian Sea through late October, suggesting continued use during molt. Spectacled Eiders departed the Yukon-Kuskokwim Delta and western Beaufort Sea in late July through September, suggesting that these areas were not

molting areas. Juvenile Spectacled Eiders that fledged in northern Alaska showed similar post-breeding migratory patterns as adults, although juveniles were more widely distributed across the Bering Sea in early winter. Spectacled Eiders appeared to use direct over-water routes or follow coastlines between important areas.

Spectacled Eiders demonstrated complete interannual fidelity to the species' sole wintering area in the northern Bering Sea. Spectacled Eiders also showed strong interannual fidelity to important areas during pre- and post-breeding migration. Females demonstrated strong interannual fidelity to breeding areas. Males exhibited less fidelity to breeding areas; most spent subsequent breeding seasons in northern Russia after capture at breeding areas in Alaska.

Post-breeding, Spectacled Eiders departed northern Alaska and migrated through the eastern Chukchi Sea, East Siberian Sea, western Bering Strait, or directly to the northern Bering Sea. Spectacled Eiders that departed western Alaska migrated through the western Bering Strait, East Siberian Sea, Norton Sound, or directly to the northern Bering Sea. Males and females demonstrated different post-breeding migratory strategies. Males migrated greater distances to molt in the East Siberian Sea, whereas females migrated shorter distances to molt at sites closer to breeding areas. Post-breeding males that molted in the East Siberian Sea migrated through the western Bering Strait or directly to the northern Bering Sea.

Spectacled Eiders that returned to northern Alaska to breed migrated through the western Bering Strait, East Siberian Sea, and eastern Chukchi Sea, whereas Spectacled Eiders that returned to western Alaska migrated through the western Bering Strait or directly from the northern Bering Sea wintering area. Males migrated to northern Russia through the western Bering Strait or directly from the northern Bering Sea.

Spectacled Eiders exhibited strong migratory connectivity and site fidelity to the important areas identified in our study. These behavioral patterns created instances where a considerable proportion of a breeding population or the global population seasonally massed in distinct areas. If Spectacled Eiders maintain fidelity to areas undergoing habitat change, managers should expect concurrent change in the status of populations. If Spectacled Eiders respond to habitat change by dispersing to new areas or changing migratory patterns, managers should be prepared to redefine the spatiotemporal distribution of the species and reassess implications for management.

2.0. INTRODUCTION

Fundamental knowledge of the distribution of avian species in space and time is necessary to fully understand and investigate their ecology and life history. Spatiotemporal information is also critical to effectively monitor populations and important habitats, and plan management and conservation actions.

The non-breeding distribution of Spectacled Eiders (*Somateria fischeri*) was unknown until 1995 when advancement in satellite telemetry technology allowed transmitters to be implanted into the coelom of diving birds (Petersen et al. 1995, Petersen et al. 1999). Spectacled Eiders spend nine to 12 months of the year in marine areas of the East Siberian, Chukchi, Beaufort, and Bering seas, where sea ice and infaunal benthic prey are important ecological components (Figure 1; Petersen et al. 1998, 2000; Lovvorn et al. 2009, 2014). In winter (November through March), nearly the entire world population of Spectacled Eiders (approximately 375,000 individuals; Larned et al. 2012) occupies a single site south of St. Lawrence Island, Alaska in lead-dominated sea ice in the northern Bering Sea (Petersen et al. 1999). Winter endemism to the northern Bering Sea appears to be unique to Spectacled Eiders as other Arctic nesting sea duck species (e.g., Common Eiders (*Somateria mollissima*), King Eiders (*Somateria spectabilis*), and Long-tailed Ducks (*Clagula hyemalis*) use different wintering areas throughout the Bering Sea and more southern latitudes (Petersen and Flint 2002; Petersen et al. 2003, 2012; Phillips et al. 2006; Oppel et al. 2008).

In the summer months, the species is divided into three geographically isolated and genetically distinct breeding populations in coastal areas of western and northern Alaska and northern Russia. Breeding Spectacled Eiders form seasonally monogamous pair bonds in late winter through spring, and adults arrive at breeding areas as breeding pairs (Petersen et al. 2000). Approximately 4,000 breeding pairs occur in northern and western Alaska, respectively, and over 95% of the world population breeds in northern Russia (Julian Fischer, U. S. Fish and Wildlife Service pers. comm.). Spectacled Eiders reach breeding age during their second or third summer, and immature eiders appear to remain at sea until 2 or 3 years of age. Throughout the species' breeding distribution, adults initiate nests shortly after snow and ice melt provide access to breeding habitat. Males remain with females at nest sites through early incubation, after which pair bonds dissolve and males move to marine molting areas. Females remain at nest sites and incubate a 5–6 egg clutch for approximately 24 days. Spectacled Eider ducklings are precocial at hatching and adult females remain with broods until juveniles fledge, approximately 50 days after hatch. Adult females and juveniles move offshore after fledging. Unsuccessful breeding females depart breeding areas after loss of their nest or brood (Petersen et al. 2000).

Spectacled Eiders were listed as threatened under the U.S. Endangered Species Act in 1993 (U. S. Fish and Wildlife Service 1993) following significant declines (as much as 96% from 1952 to 1993) in the breeding population in western Alaska (Stehn et al. 1993, Ely et al. 1994). Critical habitat was designated within the western Alaska breeding area and at marine wintering and molting sites in the northern Bering and eastern Chukchi seas, respectively (U. S. Fish and Wildlife Service 2001). In addition to satellite telemetry and focused aerial surveys, federal designation prompted further investigation of the species' breeding ecology (e.g., Pearce et al. 1998, Flint and Grand 1999, Bart and Earnst 2005), population demographics (e.g., Flint et al. 2000a, 2006), and identification of threats, which included potential exposure to contaminants,

particularly expended lead shot (Franson et al. 1995, 1998; Flint et al. 1997; Grand et al. 1998; Wilson et al. 2004), and predators (Flint and Grand 1997, Grand and Flint 1997). Disturbance through subsistence harvest and research activity appear to have minimal impacts on population demographics (Petersen et al. 2000).

The non-breeding ecology of Spectacled Eiders has been studied to a lesser extent due to the species' offshore occurrence in remote areas only accessible by large aircraft or ships with icebreaking capability. Studies have principally focused on species ecology and related ecosystem processes in the northern Bering Sea wintering area, and include assessments of oceanographic conditions (Grebmeier et al. 2006a, b; Cooper et al. 2013), diet composition (Petersen et al. 1998; Lovvorn et al. 2003, 2014), the influence of environmental variables such as sea ice, prey abundance, and severe weather on breeding population size (Petersen and Douglas 2004), and winter habitat viability (Lovvorn et al. 2009). Aerial surveys in this area have also documented late-winter courtship behavior (Lovvorn et al. 2012) and potential predator-prey interactions between Spectacled Eiders and Pacific walrus (*Odobenus rosmarus divergens*; Lovvorn et al. 2010).

The spatiotemporal distribution of Spectacled Eiders during pre- and post-breeding migration has received far less research attention. Therefore aspects of the species' natural history have yet to be adequately described. Current understanding of the timing of pre-breeding migration and the location of spring staging areas is based on the observed timing and direction of arrival at breeding areas (Dau and Kistchinski 1977, McCaffery et al. 1999), as opposed to direct observations at-sea. Furthermore, prior satellite telemetry efforts failed to collect data during pre-breeding migration (Petersen et al. 1999) and few aerial surveys have been conducted during migratory periods (Larned et al. 1995). Spatiotemporal information is also needed to inform conservation and management decisions. Exploration and energy development in the Chukchi and Beaufort seas (Opper et al. 2009), increased vessel traffic in the Arctic, potential expansion of commercial fisheries, and uncertainty surrounding the short- and long-term implications of climate change (Grebmeier et al. 2010) are emerging conservation concerns for Spectacled Eiders during non-breeding months.

Therefore, we designed a study to characterize the distribution and migratory patterns of Spectacled Eiders throughout the annual cycle. The objectives of our study were to: 1) delineate the current range of the species and the location of seasonally used important areas, 2) estimate the timing of migration and the duration during which important areas were used, 3) quantify site fidelity to important areas, and 4) quantify migratory connectivity among important areas. We discuss our results in context with environmental variables as well as results from other Spectacled Eider and Beringian sea duck studies to offer possible explanation for observed patterns and to identify research needs.

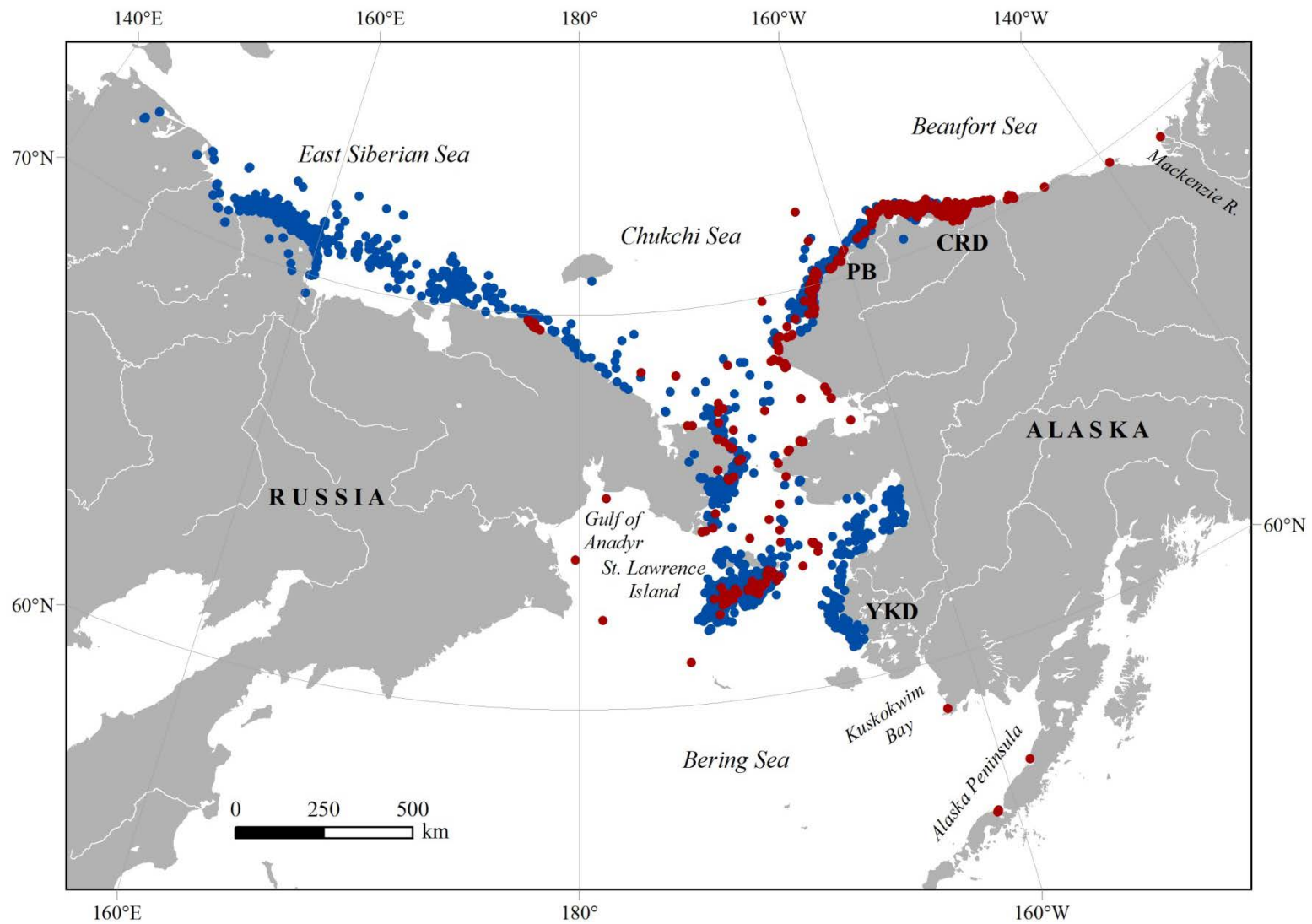


Figure 1. Satellite telemetry locations received from 89 adult (blue points, $n = 6,813$) and 27 juvenile (red points, $n = 371$) Spectacled Eiders between 30 May 2008 and 9 August 2012. We implanted satellite transmitters in Spectacled Eiders in the Yukon-Kuskokwim Delta (YKD) in 2008, at Peard Bay (PB) in 2009, and in the Colville River Delta (CRD) in 2009–2011.

3.0. METHODS

3.1. Study Sites

We surgically implanted satellite transmitters in adults and juveniles captured at coastal breeding areas in western (Yukon-Kuskokwim Delta; 61° 11' N, 165° 36' W) and northern Alaska (Peard Bay; 70° 46' N, 158° 22' W, and the Colville River Delta; 70° 26' N, 150° 41' W) (Figure 1). Spectacled Eider nesting habitat in the Yukon-Kuskokwim Delta is characterized by shallow wetlands and polygonal pond complexes within coastal areas of lowland and intermediate tundra, bisected by tidal sloughs and rivers (Petersen et al. 2000). During our study, vegetation communities within areas of nesting habitat were dominated by sedges (*Carex* spp.), and consistent with observations by Babcock and Ely (1994). Nesting habitat at Peard Bay and in the Colville River Delta is similar to that in the Yukon-Kuskokwim Delta, although dominant vegetation included dwarf willow (*Salix herbacea*), consistent with observations by Anderson et al. (1999) and Bart and Earnst (2005).

3.2. Transmitter Deployment

We obtained all necessary research and land use permits prior to initiating transmitter deployments. Our sampling protocols were reviewed and approved by Institutional Animal Care and Use Committees (IACUC) at the U.S. Geological Survey, Alaska Science Center (IACUC# 2008-04) and the University of Alaska Fairbanks (IACUC# 143488).

We used mist nets (*sensu* Dau 1976a) to capture adult Spectacled Eiders during spring arrival to breeding sites in May–July. We also used mist nets to capture full broods (adult females and associated juveniles) during late rearing in August in the Colville River Delta. We used bow traps (*sensu* Salyer 1962) and mist nets (*sensu* Bacon and Evrard 1990) to capture adult females on nests in May–July at all sites.

In 2008, we captured 46 adult (16 males, 30 females) Spectacled Eiders in the Yukon-Kuskokwim Delta. In 2009–2011, we captured 62 juvenile (35 male, 27 female) and 48 adult (16 male, 32 female) Spectacled Eiders at Peard Bay and in the Colville River Delta. In 2010, we captured four adults and 19 juveniles in four broods. In 2011, we captured 11 adults and 43 juveniles in 12 broods. Mean brood size was four juveniles ($n = 16$; range = 2–8 juveniles).

We implanted a satellite transmitter with percutaneous antenna into the coelom of 129 individuals, including 92 adults (31 males, 61 females) and 37 juveniles (20 males, 17 females) (Table 1). We selectively implanted transmitters in all juveniles weighing ≥ 950 g to minimize transmitter load. Transmitter load was not a selective factor in our sample of adults as all weighed > 1000 g. In 2010, we implanted transmitters in four adults and 13 juveniles from four broods. In 2011, we implanted transmitters in 10 adults and 24 juveniles from 12 broods. Juveniles in three broods did not meet the 950-g threshold; therefore we implanted a transmitter only in the attending adult female. We implanted a transmitter in at least one juvenile and the attending adult female from 11 of 16 captured broods. In two broods, we implanted a transmitter in only the juveniles. On average, we implanted a transmitter in three juveniles from each eligible brood ($n = 13$; range = 1–5 juveniles).

Veterinarians used standard surgical methods (Korschgen et al. 1984, 1996; Olson et al. 1992; Mulcahy and Esler 1999) to implant each satellite transmitter (44-g Model PTT 100, Microwave Telemetry Inc., Columbia, MD, USA). Individuals were induced and maintained under general anesthesia during surgery using either vaporized isoflurane (Isoflo[®], Abbott Laboratories, North Chicago, IL, USA) or intravenous propofol (Abbott Laboratories, North Chicago, IL, USA). During surgery, we collected subcutaneous or abdominal adipose tissue. After surgery, we collected blood and feather tissues. We also recorded body measurements, and banded each bird with a single stainless steel band (size 7A).

After anesthetic recovery, we held each individual in a kennel until they were deemed stable for release. We released Spectacled Eiders at nest sites (incubating females), near the site of capture (broods), or near the surgery site. In order to minimize nest abandonment, we released incubating females on nests under brief anesthesia induced by propofol (0.8 to 1.0 mL) administered into the jugular vein (Machin and Caulkett 2000). We monitored anesthetized females from a distance until they were alert to ensure that anesthetized females and their nests were not depredated. We applied molecular techniques (following Griffiths et al. 1998) to individual blood samples to determine the sex of each juvenile.

Table 1. Number of satellite transmitters implanted in Spectacled Eiders in the Yukon-Kuskokwim Delta, Colville River Delta, and at Peard Bay, Alaska; 2008–2011.

Year	Site	Total	Age	Sex
2008	Yukon-Kuskokwim Delta	45	45 adults	15 males 30 females
2009	Peard Bay	7	7 adults	4 males 3 females
	Colville River Delta	14	14 adults	9 males 5 females
2010	Colville River Delta	29	16 adults	3 males 13 females
			13 juveniles	9 males 4 females
2011	Colville River Delta	34	10 adults	10 females
			24 juveniles	11 males 13 females
TOTALS		129	92 adults	31 males 61 females
			37 juveniles	20 males 17 females

3.3. Data Analysis

A satellite transmitter is a platform transmitter terminal that produces data transmissions at specified intervals termed a ‘duty cycle’. A duty cycle includes a period during which the transmitter is ‘on’ and transmitting data, and a period during which the transmitter is ‘off’. During each ‘on’ period, location and body temperature data are received through the CLS Argos system (www.argos-system.org). The quality and quantity of data received depends on several factors including satellite coverage, antenna positioning, and the behavior of marked individuals. For example, less data may be received from a Spectacled Eider that is actively diving during the ‘on’ period of a duty cycle, or data quality (i.e., location error) will be poor if too few transmissions are received during a satellite overpass. CLS Argos uses location classes (LC) to categorize the inferred quality of each location. LC 3 is the highest quality class and is assigned to a location with an estimated location error of < 250 m, LC 2 (250–500 m), LC 1 (500–1500 m), LC 0 (> 1500 m), LC A (no accuracy estimation), LC B (no accuracy estimation), and LC Z (invalid location).

We used satellite transmitters programmed to send location data during an on:off duty cycle of either 5:96 hours, 5:106 hours, 5:116 hours, or 6:160 hours to collect location data from each eider every 4–7 days, up to two years following implantation. We adjusted the duty cycle between deployment efforts to extend battery life. We initially processed the raw data to exclude poor quality locations (i.e., LC B and Z) and data from dead individuals (body temperature < 30° C). We also censored locations received within 14-days of implantation to minimize behavioral bias potentially induced by a period of recovery following release (Mulcahy and Esler 1999, Esler et al. 2000). We then used the Douglas Argos-filter (Douglas et al. 2012) to: 1) remove improbable locations based on distance between locations and Argos location class, and 2) select the single most likely location from each duty cycle to avoid spatial autocorrelation bias in our analysis. Finally, we projected and visually validated the plausibility of selected locations in ArcMap 10 (ArcGIS, ESRI, Redlands, California) before further analysis.

We classified each location in our final dataset as geographically ‘stationary’ or ‘transient’. Among King Eiders with implanted satellite transmitters, sequential locations were considered to represent random, within area, movement if they occurred within 50–150 km of each other and did not demonstrate directional movement (Oppel et al. 2008). Therefore, we used a threshold of 100 km between subsequent locations for classification. A location was ‘stationary’ if it was either: 1) < 100 km from the previous location, 2) > 100 km from the previous location, yet < 100 km from the subsequent location, or 3) > 100 km from the subsequent location but without apparent directional movement within the sequence. A location was ‘transient’ if it was > 100 km from both previous and subsequent locations, and the sequence exhibited directional movement. We could not determine the nature of a location if it was > 100 km from the previous location and not followed by a subsequent location within two transmission cycles. Because we received locations every 4–7 days, ‘stationary’ locations suggested sustained use (> 1 week) of an area, whereas ‘transient’ locations suggested short-term (< 1 week) use.

3.3.1. Important Areas

Kernel density estimation is a method used to estimate the spatial probability of animal occurrence from a set of georeferenced observations. Kernel density estimates can be visualized in a geographic information system using isopleths that delineate the probability of occurrence at a specified level. Among peer-reviewed publications, the 95% kernel isopleth is the standard used to represent animal home ranges, or the broad area within which the probability of animal occurrence is 95% (Laver and Kelly 2008). We assumed that areas delineated by regional 95% Gaussian kernel density isopleths within the geographic extent of our data were important to Spectacled Eiders.

We used a 3-step procedure to indiscriminately partition and subsample our data to delineate important areas. First, we used Geospatial Modeling Environment (GME, Beyer 2012) to calculate the Gaussian kernel density of all 'stationary' locations, using least squares cross validation (LSCV) to estimate kernel bandwidth. We calculated the 95% isopleth of the range wide kernel density to identify regions where locations occurred in greater density. We then used the boundary of resulting isopleths to select regional subsets of location data. Second, we calculated the Gaussian kernel density (GME using LSCV) of locations within each regional subset, and used the 95% isopleth of each resulting kernel density to select locations within regional subsets. Third, we calculated the Gaussian kernel density (GME using LSCV) of selected locations within regional subsets, and used a 95% isopleth to delineate the boundaries of important areas within each region. We partitioned locations occurring east and west of Point Barrow, Alaska to derive boundaries for important areas in the western Beaufort and eastern Chukchi seas, respectively.

The kernel density of location data is estimated within grid cells and the size of each cell can influence the shape of kernel isopleths. Therefore, propensity for animal movement, frequency of data collection, and location error need to be considered to size grid cells appropriately for the species and dataset (Laver and Kelly 2008). The frequency at which data were collected during our study precluded detection of migratory movement. Therefore we chose to analyze the kernel density of 'stationary' locations within grid cells sized to reflect inherent error in Argos location data alone. Douglas et al. (2012) compared Argos location data to global positioning system (GPS) location data to estimate Argos error relative to true locations (GPS data), and we used respective root mean square error values presented by Douglas et al. for unfiltered (LC 3, 2, and 1) and filtered (LC 0 and A) locations to calculate the weighted average of estimated circumferential error within our dataset. Throughout analysis, we estimated kernel density within grid cells measuring 4,621 m².

3.3.2. Timing of Migration and Site Occupancy

Since we could not determine the precise date of migratory events due to the weekly frequency of data collection, we determined the range of potential arrival and departure dates for each individual at each area and then used the median date as our estimate of arrival or departure. Potential arrival dates included the day of the location before the first ‘stationary’ location in an area, through the date of the first ‘stationary’ location. Potential departure dates included the date of the last ‘stationary’ location through the day of the next location received. We did not calculate median arrival and/or departure date if subsequent locations were separated by > 14 days. When possible, we used the duration between median arrival and departure dates to estimate the duration of sustained use of an area. We used the same approach to estimate arrival, departure, and residency duration of individuals on land during the breeding season. We used Natural Earth 10-m resolution vector map data (naturalearthdata.com) to select locations that occurred on land. We summarized the mean, standard deviation, and range of seasonal arrival and departure dates, and residency duration within each year for each sex and age class that provided data from each important area or on land during the breeding season. For each important area, we inferred representative annual cycle phases (i.e., pre-breeding, breeding, post-breeding, and wintering) according to the timing of use as described by Petersen et al. (2000). We could not determine the behavior of marked individuals during pre- and post-breeding phases, but we assumed that they included staging and molt, respectively.

3.3.3. Site Fidelity

We used ‘stationary’ locations to assess interannual fidelity at each important area. For each individual that occupied an important area and provided data in the subsequent year, we recorded that individual’s presence or absence in the subsequent year. Among Spectacled Eiders that provided sufficient data to record fidelity in a third consecutive year, we treated each potential return as an independent occurrence. We calculated the proportion of Spectacled Eiders present in a subsequent year to estimate interannual site fidelity for each sex and age at each important area.

At important areas used during pre- and post-breeding migration, we also calculated fidelity of use among these migratory phases. For each individual that occupied an important area during pre- and post-breeding migration and provided location data during the subsequent pre- and post-breeding migration period, we recorded that eider’s presence or absence in that area in the subsequent period. We treated each potential return as an independent occurrence.

3.3.4. Migratory Connectivity

We used ‘stationary’ locations to quantify migratory connectivity during pre-breeding (i.e., wintering to breeding sites) and post-breeding (i.e., breeding to wintering sites) migration. For all Spectacled Eiders that occurred in an important area and subsequently migrated, we counted the number that arrived at destination important areas. Among Spectacled Eiders that occurred in the same area on different migratory occasions, we treated each occurrence/departure as an independent observation. Within each migratory season (i.e., pre- and post-breeding), we calculated the proportion of Spectacled Eiders migrating to all destinations from each important area for each sex and age.

4.0. RESULTS

4.1. Data Collection

Our final dataset consisted of 7,184 locations received from 116 Spectacled Eiders (59 adult females, 30 adult males, 12 juvenile females, 15 juvenile males) between 30 May 2008 and 9 August 2012 (Figure 1). We did not include data from 13 Spectacled Eiders (3 adults, 10 juveniles) that died or ceased transmission within 14 days of release. Most of our data were of the more accurate Argos location classes; 3,855 (53.7%) were LC 3 locations, 1,805 (25.1%) were LC 2, and 773 (10.8%) were LC 1. Fewer locations were of the less accurate Argos location classes; 428 (6.0%) were LC A and 323 (4.5%) were LC 0. We classified 6,950 (96.7%) locations as geographically ‘stationary’ and 192 (2.7%) ‘transient’. We could not classify the nature (stationary vs. transient) of 42 (< 0.6%) locations.

On average, we collected 62 ± 51 locations from each individual, spanning a period of 318 ± 256 days. Juveniles ($n = 27$) provided fewer locations per individual ($\bar{x} = 14 \pm 14$) over a shorter period ($\bar{x} = 77 \pm 127$ days) than adults ($n = 89$, $\bar{x} = 76 \pm 49$ locations, $\bar{x} = 391 \pm 240$ days). Most adults outlived the battery life of their transmitters, whereas most juveniles died before transmissions ceased. Of 89 adults, 24 (27%) died before transmissions ceased, 48 (53.9%) outlived their transmitter, and 17 (19.1%) carried transmitters that inexplicably deactivated. Of 27 juveniles, 18 (66.7%) died before transmissions ceased, one (3.7%) outlived its transmitter, and eight (29.6%) carried transmitters that inexplicably deactivated. We could not determine the cause of mortality or transmitter failure within our sample.

4.2. Important Areas

We identified seven spatially important areas where locations occurred in greater density as defined by 95% Gaussian kernel density isopleths (Figure 2). Important areas included: 1) the western Beaufort Sea within approximately 30 km of the coast of northern Alaska and the coast between Point Barrow and the Sagavanirktok River Delta, 2) the eastern Chukchi Sea within approximately 70 km of the coast of northern Alaska and the coast between southern Ledyard Bay and Point Barrow, 3) the East Siberian Sea within 200 km of the coast of northern Russia and the coast between the Indigirka River Delta and Cape Billings, 4) the western Bering Strait within approximately 60 km of the coast of the Chukotka Peninsula, Russia and the coasts between Mechigmenskiy Bay and the Utavcem River, 5) eastern and southern Norton Sound in the northeastern Bering Sea within approximately 60 km of Shaktoolik Bay and the Yukon River Delta, Alaska, respectively, 6) the Yukon-Kuskokwim Delta and adjacent marine areas within approximately 20 km of the coast of western Alaska between Scammon Bay and Nelson Island, and 7) the northern Bering Sea within approximately 200 km of the southern coast of St. Lawrence Island, Alaska and coastal areas near Southeast Cape, St. Lawrence Island. Of 7,184 total locations, 6,686 (93.1%) occurred within the boundaries of important areas.

Most locations that did not occur in an important area were merely peripheral to the 95% kernel density locations in a particular region. Locations between important areas may have also been received during migratory movement, although the temporal frequency at which we collected data precluded identification of movement and migratory routes. During post-fledging dispersal, three juvenile Spectacled Eiders provided locations from areas distant from important areas. A juvenile female departed its natal site in the western Beaufort Sea in mid-October and moved east to the Mackenzie River Delta before turning west and rejoining other transmitting Spectacled Eiders. A juvenile male departed the eastern Chukchi Sea in mid-October and used pelagic areas in the Gulf of Anadyr through late November before dying. A second juvenile female departed the western Bering Strait in late October and stopped in southern Kuskokwim Bay, Alaska before moving to coastal sites on the Alaska Peninsula where this individual remained until its death in early December. Within our sample, no other Spectacled Eiders used the Mackenzie River Delta, Gulf of Anadyr, Kuskokwim Bay, or the Alaska Peninsula, respectively (Figure 1).

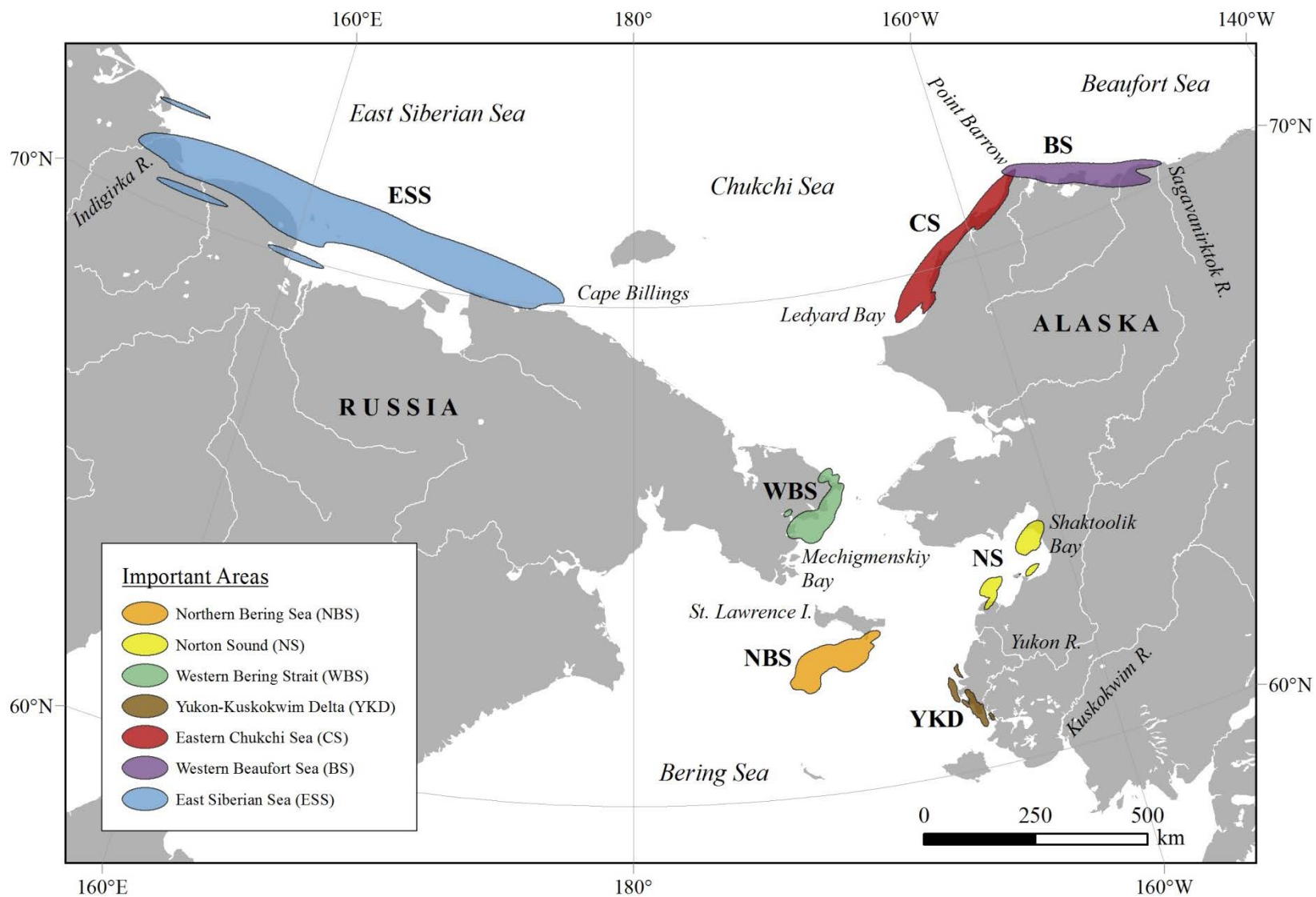


Figure 2. Important areas (95% Gaussian kernel density isopleths) used by Spectacled Eiders with satellite transmitters that provided data in 2008–2012. Important areas included marine and coastal habitats.

4.3. Timing of Migration and Site Occupancy

4.3.1. Annual Cycle Overview

Among all important areas, Spectacled Eiders used the northern Bering Sea exclusively to winter from late November through mid-February. Spectacled Eiders used Norton Sound and the western Bering Strait during pre-breeding migration (mid-March through early May) and post-breeding migration (mid-July through mid-November), but not breeding. Pre-breeding migration in the western Bering Strait began approximately one month earlier than in Norton Sound, while both areas were used during approximately the same period through post-breeding migration. Breeding sites included terrestrial areas of the Yukon-Kuskokwim Delta, eastern Chukchi Sea, western Beaufort Sea, and East Siberian Sea important areas. Eiders began staging offshore of the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and East Siberian Sea in early through mid-May, while staging was not apparent in the western Beaufort Sea where Spectacled Eiders arrived in late May through early June. Eiders occupied the eastern Chukchi Sea and East Siberian Sea through late October, suggesting continued use during the molting period. Spectacled Eiders departed the Yukon-Kuskokwim Delta and western Beaufort Sea in late July through early August and late-August through September, respectively, suggesting limited use of the Yukon-Kuskokwim Delta and western Beaufort Sea during molt (Table 2, Figure 3).

Table 2. Migratory timing and represented annual cycle phase(s) of all Spectacled Eiders that provided satellite telemetry data from each important area. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) for all years (2008–2012). Sample sizes (*n*) are provided in parentheses.

Important Area	Annual Cycle Phase(s)	Arrival	Departure
Northern Bering Sea	Wintering	15 Oct \pm 10 days 28 Sep, 6 Nov (102)	14 Apr \pm 22 days 11 Feb, 11 Jun (58)
		Pre-breeding Migration	28 Apr \pm 2 days 25 Apr, 29 Apr (4)
Norton Sound	Post-breeding Migration	6 Aug \pm 23 days 17 Jun, 18 Sep (48)	7 Oct \pm 25 days 29 Jun, 1 Nov (44)
		Pre-breeding Migration	7 Apr \pm 21 days 17 Feb, 17 June (36)
Western Bering Strait	Post-breeding Migration Post-fledging Dispersal	15 Aug \pm 54 days 5 Jun, 12 Nov (23)	1 Oct \pm 46 days 13 Jun, 30 Nov (24)
		Pre-breeding Migration Breeding Post-breeding Migration	10 May \pm 8 days 22 Apr, 21 May (21)
Yukon-Kuskokwim Delta	Pre-breeding Migration Breeding Post-breeding Migration Post-fledging Dispersal	18 May \pm 15 days 2 May, 2 Jun (14)	4 Oct \pm 22 days 11 Sep, 26 Oct (41)
		Pre-breeding Migration Breeding Post-breeding Migration Post-fledging Dispersal	6 Jun \pm 7 days 20 May, 17 Jun (11)
Eastern Chukchi Sea	Pre-breeding Migration Breeding Post-breeding Migration Post-fledging Dispersal	8 May \pm 10 days 21 Apr, 5 Jun (21)	4 Oct \pm 17 days 11 Jul, 20 Oct (22)
		Pre-breeding Migration Breeding Post-breeding Migration	8 May \pm 10 days 21 Apr, 5 Jun (21)
Western Beaufort Sea	Pre-breeding Migration Breeding Post-breeding Migration Post-fledging Dispersal	8 May \pm 10 days 21 Apr, 5 Jun (21)	4 Oct \pm 17 days 11 Jul, 20 Oct (22)
		Pre-breeding Migration Breeding Post-breeding Migration	8 May \pm 10 days 21 Apr, 5 Jun (21)
East Siberian Sea	Pre-breeding Migration Breeding Post-breeding Migration	8 May \pm 10 days 21 Apr, 5 Jun (21)	4 Oct \pm 17 days 11 Jul, 20 Oct (22)
		Pre-breeding Migration Breeding Post-breeding Migration	8 May \pm 10 days 21 Apr, 5 Jun (21)

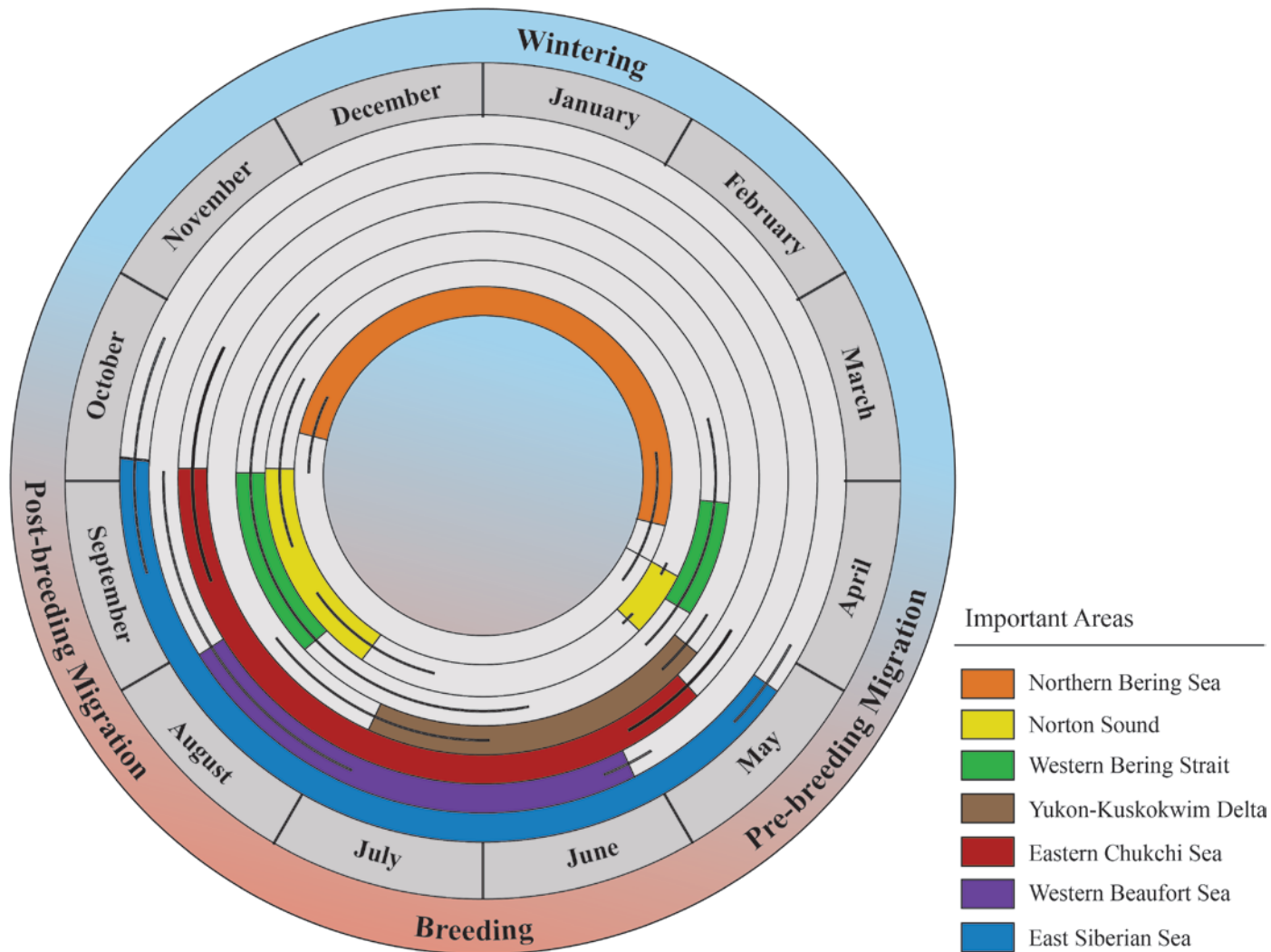


Figure 3. Migratory timing of Spectacled Eiders with satellite transmitters that provided data at important areas in 2008–2012. We present the mean date \pm standard deviation (days) of arrival and departure at each important area for all individuals (see Table 2). Color filled bars represent periods during which at least one individual exhibited sustained occupancy of the respective important area.

4.3.2. Western Beaufort Sea

Adult and juvenile Spectacled Eiders marked in the Colville River Delta used the western Beaufort Sea important area during breeding or post-fledging dispersal, respectively. Adult females arrived in the western Beaufort Sea during the first two weeks of June and moved on land within a week of arrival. We detected greater variation in arrival date in 2011 than in 2010, although sample sizes were limited by the number of returning individuals. We did not receive sufficient data to estimate the timing of arrival among juvenile males and females, nor adult males. Adult females departed the western Beaufort Sea in mid to late August, although we found considerable variability in the departure date of females within each year ranging from 4 July to 27 September. Adult females remained in the western Beaufort Sea area for 34–65 days. Adult females remained on land through early July to late September for a total of 35–53 days. Adult males departed the western Beaufort Sea in early July. Juvenile males and females that fledged in the western Beaufort Sea area remained on land through mid-September, and departed the western Beaufort Sea in September in 2010, and October in 2011 (Table 3).

Table 3. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the western Beaufort Sea important area. Locations on land represent a subset of all locations occurring within the western Beaufort Sea area within each year. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2009	Post-breeding Migration	Adult Males	–	1 Jul \pm 6 days 27 Jun, 12 Jul (6)	–
		Adult Females	–	14 Aug \pm 19 days 2 Aug, 18 Sep (5)	–
	On Land (Breeding)	Adult Male	–	5 Jul (1)	–
		Adult Females	–	1 Aug \pm 6 days 23 Jul, 7 Aug (15)	–
	Post-breeding Migration	Adult Male	–	11 Jul (1)	–
2010	Pre-breeding Migration Breeding Post-breeding Migration	Adult Females	9 Jun \pm 1 day 8 Jun, 9 Jun (4)	13 Aug \pm 19 days 20 Jul, 15 Sep (15)	52 days 42, 56 days (3)
	Post-fledging Dispersal	Juvenile Males	–	30 Sep \pm 4 days 22 Sep, 5 Oct (8)	–
		Juvenile Females	–	19 Sep, 30 Sep (2)	–
	On Land (Breeding)	Adult Male	–	26 Jun (1)	–
		Adult Females	10 Jun \pm 2 days 8 Jun, 13 Jun (4)	25 Jul \pm 12 days 14 Jul, 30 Aug (13)	40 \pm 4 days 35, 45 days (4)
		Juvenile Males	–	10 Sep \pm 3 days 7 Sep, 15 Sep (5)	–

Table 3 continued

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2011	Pre-breeding Migration	Adult Females	4 Jun \pm 9 days	26 Aug \pm 30 days	49 \pm 15 days
	Breeding		20 May, 17 Jun	4 Jul, 27 Sep	34, 65 days
	Post-breeding Migration		(6)	(10)	(4)
	Post-fledging Dispersal	Juvenile Males	–	6 Oct \pm 13 days 17 Sep, 25 Oct	–
		Juvenile Females	–	7 Oct \pm 20 days 21 Sep, 12 Nov	–
					(6)
2011	On Land (Breeding)	Adult Females	6 June \pm 6 days 31 May, 17 Jun	16 Aug \pm 32 days 4 Jul, 27 Sep	41 \pm 14 days 26, 53 days
			(6)	(8)	(4)
		Juvenile Males		17 Sep \pm 4 days 12 Sep, 22 Sep	
				(6)	
		Juvenile Females		12 Sep \pm 7 days 5 Sep, 21 Sep	
				(6)	
2012	On Land (Breeding)	Adult Female	10 June (1)	–	–

4.3.3. Eastern Chukchi Sea

Spectacled Eiders marked at Peard Bay in the eastern Chukchi Sea area and the Colville River Delta in the western Beaufort Sea area used the eastern Chukchi Sea during pre-breeding migration, breeding, post-breeding migration, and/or post-fledging dispersal. Two adult males that used the eastern Chukchi Sea during pre-breeding migration arrived on 5 and 16 May and departed on 30 May and 15 June, remaining for 26 and 31 days, respectively. Adult females that used the eastern Chukchi Sea during pre-breeding migration to the western Beaufort Sea arrived in May and stayed for 6–37 days, before continuing migration in June. Adults moved on land in the eastern Chukchi Sea area to breed in June and remained on land for 7–44 days (Table 4).

Adult males that used the eastern Chukchi Sea during post-breeding migration arrived in early July and departed in early September, although we found substantial variability in departure date ranging from 4 July to 5 October. Consequently, we found considerable variability in the duration of sustained occupancy among adult males during post-breeding migration, ranging from 30–97 days. Adult females that used the eastern Chukchi Sea during post-breeding migration arrived in August and departed in October. Among females, we found considerable variability in the timing of arrival during post-breeding migration, which occurred as early as 15 July and as late as 28 September. Consequently, we also found considerable variability in the duration of sustained occupancy among adult females during post-breeding migration, which ranged from 16–84 days. Two Spectacled Eiders, one adult male and one adult female, arrived in the eastern Chukchi Sea on 9 May and 10 June respectively, and remained through breeding and molt. The male departed on 23 September (remained for 138 days), while the female departed on 13 October (remained for 126 days). Juveniles that fledged in the western Beaufort Sea arrived in the eastern Chukchi Sea in early October and stayed for 13–29 days before departing by late October (Table 4).

Table 4. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the eastern Chukchi Sea important area. Locations on land represent a subset of all locations occurring within the eastern Chukchi Sea area within each year. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2009	Post-breeding Migration	Adult Males	5 Jul \pm 8 days 27 Jun, 18 Jul (5)	2 Sep \pm 38 days 4 Jul, 5 Oct (7)	75 \pm 31 days 30, 97 days (4)
		Adult Females	17 Aug \pm 18 days 8 Aug, 18 Sep (5)	1 Oct \pm 6 days 21 Sep, 7 Oct (5)	46 \pm 19 days 16, 61 days (5)
2010	Pre-breeding Migration	Adult Male	16 May (1)	15 Jun (1)	31 days (1)
		Adult Females	31 May \pm 3 days 29 May, 5 Jun (4)	7 Jun 7 Jun, 8 Jun (3)	10, 10 days (2)
	Pre-breeding Migration	Adult Male	9 May (1)	23 Sep (1)	138 days (1)
	Breeding	Adult Female	10 Jun (1)	13 Oct (1)	126 days (1)
	Post-breeding Migration	Adult Females	14 Aug \pm 19 days 20 Jul, 16 Sep (15)	12 Oct \pm 8 days 1 Oct, 3 Nov (15)	64 \pm 11 days 31, 74 days (13)
	Post-fledging Dispersal	Juvenile Males	2 Oct \pm 6 days 23 Sep, 11 Oct (7)	19 Oct \pm 3 days 16 Oct, 22 Oct (4)	20 \pm 7 days 13, 29 days (4)
		Juvenile Females	28 Sep, 1 Oct (2)	17 Oct (1)	17 days (1)
On Land (Breeding)	Adult Male	8 Jun (1)	15 Jun (1)	7 days (1)	
	Adult Females	10 June 5 Jun, 16 Jun (3)	24 Jul (1)	44 days (1)	

Table 4 continued

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2011	Pre-breeding Migration	Adult Male	5 May (1)	30 May (1)	26 days (1)
		Adult Females	11 May \pm 18 days 29 Apr, 12 Jun (5)	6 Jun \pm 7 days 31 May, 17 Jun (5)	27 \pm 12 days 6, 37 days (5)
	Post-breeding Migration	Adult Females	30 Aug \pm 28 days 15 Jul, 28 Sep (10)	9 Oct \pm 5 days 3 Oct, 14 Oct (4)	73 \pm 8 days 67, 84 days (4)
	Post-fledging Dispersal	Juvenile Males	8 Oct \pm 6 days 30 Sep, 15 Oct (5)	19 Oct, 24 Oct (2)	10, 15 days (2)
Juvenile Females		25 Sep (1)	17 Oct (1)	23 days (1)	
2012	Pre-breeding Migration	Adult Female	21 May (1)	1 Jun (1)	12 days (1)

4.3.4. East Siberian Sea

Spectacled Eiders from breeding sites in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and western Beaufort Sea areas used the East Siberian Sea area during pre-breeding migration, breeding, and/or post-breeding migration. Adult females that used the East Siberian Sea during pre-breeding migration arrived in May and departed in late May to early June. Adult females that bred in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and western Beaufort Sea areas did not breed in the East Siberian Sea in the subsequent year, nor use the East Siberian Sea during post-breeding migration. Adult males that staged in the East Siberian Sea in May remained through breeding and molt until they departed in late September. Adult males moved on land in June, and remained on land for 4–30 days. Adult males that remained in the East Siberian Sea after breeding departed between 27 July and 15 October. Consequently, we found considerable variability in the duration of sustained occupancy among adult males, which ranged 87–165 days. A proportion of males that used the East Siberian Sea during post-breeding migration only, arrived in July, departed in October, and remained for 68–111 days (Table 5). Juveniles that fledged in the western Beaufort Sea did not use the East Siberian Sea during post-fledging dispersal.

Table 5. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the East Siberian Sea important area. Locations on land represent a subset of all locations occurring within the East Siberian Sea area within each year. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2008	Post-breeding Migration	Adult Males	21 Jul \pm 18 days 17 Jun, 7 Aug (6)	7 Oct \pm 4 days 2 Oct, 13 Oct (6)	80 \pm 16 days 68, 111 days (6)
	Pre-breeding Migration Breeding Post-breeding Migration	Adult Males	4 May \pm 8 days 28 Apr, 22 May (7)	22 Sep \pm 32 days 27 Jul, 14 Oct (5)	145 \pm 33 days 87, 165 days (5)
2009	Post-breeding Migration	Adult Males	13 Jul \pm 13 days 24 Jun, 6 Aug (7)	11 Oct \pm 6 days 3 Oct, 20 Oct (7)	91 \pm 12 days 71, 109 days (7)
	On Land (Breeding)	Adult Males	13 Jun \pm 10 days 4 Jun, 29 Jun (7)	4 Jul \pm 5 days 24 Jun, 9 Jul (7)	19 \pm 11 days 4, 30 days (7)
2010	Pre-breeding Migration	Adult Females	11 May 3 May, 20 May (3)	30 May 30 May, 8 Jun (3)	20 days 11, 37 days (3)
	Pre-breeding Migration Breeding Post-breeding Migration	Adult Males	8 May \pm 2 days 6 May, 11 May (5)	28 Sep 27 Sep, 15 Oct (3)	143 days 143, 158 days (3)
	Post-breeding Migration	Adult Male	24 Jun, 23 Jul (2)	4 Oct (1)	74 days (1)
	On Land (Breeding)	Adult Males	6 Jun \pm 3 days 1 Jun, 8 Jun (4)	21 Jun \pm 11 days 11 Jun, 2 Jul (4)	16 \pm 10 days 4, 24 days (4)
2011	Pre-breeding Migration	Adult Males	13 May \pm 18 days 21 Apr, 5 Jun (4)	–	–
	Pre-breeding Migration	Adult Female	3 May (1)	7 Jun (1)	36 days (1)
2012	Pre-breeding Migration	Adult Female	4 May (1)	–	–

4.3.5. Western Bering Strait

Spectacled Eiders from breeding sites in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and western Beaufort Sea areas used the western Bering Strait area during pre-breeding migration, post-breeding migration, and/or post-fledging dispersal. Adult males and females that arrived in March and April during pre-breeding migration remained for 9–72 days before they departed in April and May. Adults arrived at the western Bering Strait area approximately two weeks earlier during pre-breeding migration in 2011 than observed in 2009, 2010, and 2012. One juvenile female that migrated to the western Bering Strait in its first spring arrived on 17 June and remained until 5 July. Adult Spectacled Eiders did not remain in the western Bering Strait area during the breeding season.

During post-breeding migration, adult males arrived in June through September and remained for 25–126 days before they departed in September and October. Two adult females that used the western Bering Strait during post-breeding migration arrived in October and departed in November. Two juveniles that used the western Bering Strait during post-fledging dispersal arrived on 12 November and 17 October, and departed on 30 November and 30 October, respectively (Table 6).

Table 6. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the western Bering Strait important area. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2008	Post-breeding Migration	Adult Males	29 Jun \pm 16 days 5 Jun, 24 Jul (10)	6 Sep \pm 50 days 13 Jun, 31 Oct (13)	82 \pm 38 days 25, 126 days (10)
		Adult Males	8 Apr \pm 8 days 3 Apr, 19 Apr (4)	26 Apr \pm 2 days 24 Apr, 28 Apr (4)	20 \pm 7 days 9, 26 days (4)
2009	Pre-breeding Migration	Adult Females	10 Apr \pm 7 days 20 Mar, 21 Apr (7)	28 Apr \pm 4 days 23 Apr, 4 May (8)	20 \pm 7 days 9, 30 days (7)
		Adult Males	4 Sep \pm 48 days 16 Jun, 15 Oct (8)	23 Oct \pm 7 days 17 Oct, 5 Nov (6)	28 \pm 27 days 9, 80 days (6)
	Post-breeding Migration	Adult Females	9 Oct, 23 Oct (2)	4 Nov, 17 Nov (2)	26, 27 days (2)
		Adult Males	12 Apr \pm 11 days 30 Mar, 23 Apr (5)	5 May \pm 2 days 3 May, 7 May (6)	24 \pm 9 days 15, 35 days (5)
2010	Pre-breeding Migration	Adult Females	15 Apr \pm 6 days 7 Apr, 22 Apr (5)	9 May \pm 9 days 2 May, 23 May (6)	25 \pm 13 days 11, 42 days (5)
		Adult Male	23 Sep (1)	30 Oct (1)	38 days (1)
	2011	Pre-breeding Migration	Adult Males	28 Mar \pm 20 days 5 Mar, 23 Apr (4)	1 May 1 May, 2 May (3)
Adult Females			25 Mar \pm 29 days 17 Feb, 26 May (8)	4 May \pm 14 days 25 Apr, 6 Jun (8)	41 \pm 20 days 12, 72 days (8)
Post-fledging Dispersal		Juvenile Female	17 Jun (1)	5 Jul (1)	19 days (1)
		Juvenile Male	12 Nov (1)	30 Nov (1)	19 days (1)
2012	Pre-breeding Migration	Juvenile Female	17 Oct (1)	30 Oct (1)	14 days (1)
		Adult Females	1 Apr, 6 Apr (2)	22 Apr, 27 Apr (2)	17, 27 days (2)

4.3.6. Norton Sound

Adult Spectacled Eiders marked in the Yukon-Kuskokwim Delta in 2008 used Norton Sound during pre- and post-breeding migration. Females arrived to stage in Norton Sound in April, and departed in May. Males did not use Norton Sound during pre-breeding migration, and females did not remain in Norton Sound during the breeding season.

Three males used Norton Sound during post-breeding migration, arriving on 17 June, 23 June, and 30 July, and departing on 29 June, 2 July, and 9 October, respectively. Females that molted in Norton Sound arrived in July and August, departed in October, and remained for 41–88 days (Table 7).

Table 7. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the Norton Sound important area. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2008	Post-breeding Migration	Adult Males	17 Jun, 30 Jul (2)	29 Jun, 9 Oct (2)	13, 72 days (2)
		Adult Females	29 Jul \pm 16 days 7 Jul, 11 Sep (28)	5 Oct \pm 7 days 26 Sep, 21 Oct (27)	71 \pm 12 days 41, 88 days (27)
2009	Pre-breeding Migration	Adult Females	28Apr \pm 2 days 25 Apr, 29 Apr (4)	16 May \pm 1 day 15 May, 18 May (4)	20 \pm 2 days 17, 22 days (4)
		Adult Males	23 Jun (1)	2 Jul (1)	10 days (1)
	Post-breeding Migration	Adult Females	24 Aug \pm 19 days 23 Jul, 18 Sep (17)	24 Oct \pm 9 days 4 Oct, 1 Nov (14)	60 \pm 9 days 46, 77 days (14)

4.3.7. Yukon-Kuskokwim Delta

Adult Spectacled Eiders marked in the Yukon-Kuskokwim Delta used the Yukon-Kuskokwim Delta to stage and breed in subsequent years. Males and females arrived to stage offshore in May before moving on land. Males that departed terrestrial sites in June remained on land for 17–33 days, whereas females remained on land in the Yukon-Kuskokwim Delta for 52–112 days. Overall, females that departed in July and August remained in the Yukon-Kuskokwim Delta area for 65–142 days. Males that departed in June remained in the Yukon-Kuskokwim Delta area for 30–58 days (Table 8).

Table 8. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the Yukon-Kuskokwim Delta important area. Locations on land represent a subset of all locations occurring within the Yukon-Kuskokwim Delta area within each year. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2008	Post-breeding Migration	Adult Males	–	23 Jun \pm 16 days 13 Jun, 26 Jul (9)	–
		Adult Females	–	28 Jul \pm 16 days 6 Jul, 7 Sep (29)	–
	On Land (Breeding)	Adult Males	–	16 Jun \pm 4 days 12 Jun, 22 Jun (9)	–
		Adult Females	–	28 Jul \pm 16 days 6 Jul, 7 Sep (29)	–
2009	Pre-breeding Migration	Adult Males	5 May \pm 7 days 27 Apr, 14 May (4)	19 Jun \pm 5 days 12 Jun, 23 Jun (4)	46 \pm 12 days 30, 58 days (4)
	Breeding	Adult Females	11 May \pm 7 days 22 Apr, 21 May (17)	20 Aug \pm 19 days 18 Jul, 13 Sep (17)	102 \pm 22 days 65, 142 days (17)
	Post-breeding Migration	Adult Males	24 May \pm 4 days 21 May, 28 May (4)	19 Jun \pm 5 days 12 Jun, 23 Jun (4)	26 \pm 7 days 17, 33 days (4)
		Adult Females	21 May \pm 2 days 18 May, 26 May (18)	20 Aug \pm 19 days 14 Jul, 13 Sep (17)	90 \pm 20 days 52, 112 days (17)

4.3.8. Northern Bering Sea

Spectacled Eiders marked in the Yukon-Kuskokwim Delta, eastern Chukchi Sea, and western Beaufort Sea wintered in the northern Bering Sea during each year of our study. Adult males and females arrived simultaneously in October each fall, with little intra- and interannual variability in arrival date. Adults generally departed in April each year, although adults departed approximately two weeks earlier in spring 2011 than observed in springs 2009, 2010, and 2012. On average, adult Spectacled Eiders that wintered in the northern Bering Sea remained for 185 ± 25 days ($n = 55$). A limited sample of juvenile females ($n = 3$) that wintered in the northern Bering Sea arrived in October and departed in June. In 2008, four adult males also used the northern Bering Sea during post-breeding migration from the Yukon-Kuskokwim Delta; they arrived and departed in June (Table 9).

Table 9. Migratory timing and represented annual cycle phase(s) of Spectacled Eiders in the northern Bering Sea important area. We present the mean, standard deviation, and range of estimated arrival and departure dates (earliest, latest) and residency duration (least, greatest) within each year for each sex and age class. Sample sizes (n) are in parentheses. If $n \leq 3$, we present median and/or least, greatest.

Year(s)	Annual Cycle Phase(s)	Age Sex	Arrival	Departure	Duration
2008	Post-breeding Migration	Adult Males	16 June, 17 June (2)	28 Jun \pm 13 days 12 Jun, 13 Jul (4)	13, 28 days (2)
2008– 2009	Wintering	Adult Males	13 Oct \pm 7 days 5 Oct, 1 Nov (15)	21 Apr \pm 13 days 2 Apr, 10 May (12)	192 \pm 12 days 174, 203 days (12)
		Adult Females	6 Oct \pm 8 days 28 Sep, 30 Oct (27)	24 Apr \pm 15 days 30 Mar, 16 May (17)	203 \pm 15 days 173, 223 days (17)
2009– 2010	Wintering	Adult Males	19 Oct \pm 7 days 4 Oct, 6 Nov (16)	13 Apr \pm 15 days 23 Mar, 30 Apr (6)	178 \pm 11 days 163, 190 days (6)
		Adult Females	25 Oct \pm 10 days 6 Oct, 6 Nov (18)	11 Apr \pm 4 days 6 Apr, 18 Apr (6)	177 \pm 12 days 158, 189 days (5)
2010– 2011	Wintering	Adult Males	15 Oct \pm 12 days 28 Sep, 31 Oct (6)	8 Apr \pm 25 days 4 Mar, 4 May (6)	174 \pm 35 days 125, 212 days (5)
		Adult Females	16 Oct \pm 10 days 1 Oct, 6 Nov (14)	18 Mar \pm 30 days 11 Feb, 26 May (8)	156 \pm 35 days 122, 233 days (8)
		Juvenile Female	23 Oct (1)	11 Jun (1)	–
2011– 2012	Wintering	Adult Females	17 Oct \pm 7 days 9 Oct, 25 Oct (4)	1 Apr, 6 Apr (2)	170, 172 days (2)
		Juvenile Female	13 Oct (1)	–	–

4.4. Site Fidelity

4.4.1. Western Beaufort Sea

Among 14 Spectacled Eiders, we recorded 18 potential returns to the western Beaufort Sea in subsequent years. Adult females ($n = 8$) displayed the greatest level of site fidelity. We recorded 11 returns out of 12 possible, including three females that returned to the western Beaufort Sea in two subsequent years following capture. All females that returned moved on land, presumably to breed. Among females that were initially captured on a nest and returned in subsequent years ($n = 4$), 75% ($n = 18/24$) of their on-land locations were within 5 km of the initial nest site; all locations were within 10 km of the initial nest site. Among five adult males, none returned to the western Beaufort Sea in the years following capture. A single female returned to the western Beaufort Sea in the second year following capture as a juvenile (Table 10).

Table 10. Site fidelity of Spectacled Eiders with satellite transmitters that provided data in subsequent years or annual cycle phases from each important area, 2008–2012. We present the number of returns out of the number of potential returns, and percentage. We did not calculate percentage if the number of potential returns was < 10. Sample sizes (*n*) are in parentheses. We stratified data from the eastern Chukchi Sea important area to show fidelity among Spectacled Eiders captured in the eastern Chukchi Sea and western Beaufort Sea, respectively.

Important Area	Annual Cycle Phase(s)	Fidelity			
		Overall	Adult Male	Adult Female	Juvenile Female
Northern Bering Sea	Interannual Wintering	40/40, 100% (40)	14/14, 100% (14)	25/25, 100% (25)	1/1 (1)
	Interannual Post-breeding Migration	18/19, 94.7% (19)	1/2 (2)	17/17, 100% (17)	–
Norton Sound	Inter-seasonal Pre- and Post-breeding Migration	4/4 (4)	–	4/4 (4)	–
	Inter-seasonal Post- and Pre-breeding Migration	4/20, 20.0% (20)	0/2 (2)	4/18, 22.2% (18)	–
Western Bering Strait	Interannual Post-breeding Migration	6/13, 46.2% (13)	6/12, 50% (12)	0/1 (1)	
	Interannual Pre-breeding Migration	9/12, 75% (12)	3/5 (5)	6/6 (6)	0/1 (1)
	Inter-seasonal Pre- and Post-breeding Migration	3/27, 11.1% (27)	3/9 (9)	0/17, 0.0% (17)	0/1 (1)
	Inter-seasonal Post- and Pre-breeding Migration	8/15, 53.3% (14)	6/13, 46.2% (12)	2/2 (2)	–

Table 10 continued

Important Area	Annual Cycle Phase(s)	Fidelity			
		Overall	Adult Male	Adult Female	Juvenile Female
Yukon-Kuskokwim River Delta	Interannual Pre-breeding Migration	23/31, 74.2% (31)	4/12, 33.3% (12)	19/19, 100% (19)	–
	Interannual On Land (Breeding)	23/31, 74.2% (31)	4/12, 33.3% (12)	19/19, 100% (19)	–
Eastern Chukchi Sea Rate of return among eiders captured during breeding in the eastern Chukchi Sea important area	Interannual Post-breeding Migration	4/5 (5)	1/2 (2)	3/3 (3)	–
	Interannual Pre-breeding Migration	2/2 (2)	1/1 (1)	1/1 (1)	–
	Interannual On Land (Breeding)	5/5 (5)	2/2 (2)	3/3 (3)	–
	Inter-seasonal Pre- and Post-breeding Migration	4/5 (5)	1/2 (2)	3/3 (3)	–
	Inter-seasonal Post- and Pre-breeding Migration	6/6 (6)	2/2 (2)	4/4 (4)	–

Table 10 continued

Important Area	Annual Cycle Phase(s)	Fidelity			
		Overall	Adult Male	Adult Female	Juvenile Female
Eastern Chukchi Sea Rate of return among eiders captured during breeding in the western Beaufort Sea important area	Interannual Post-breeding Migration	8/11, 72.7% (11)	0/2 (2)	8/8 (8)	0/1 (1)
	Interannual Pre-breeding Migration	2/4 (4)	–	2/4 (4)	–
	Inter-seasonal Pre- and Post-breeding Migration	7/7 (7)	–	7/7 (7)	–
	Inter-seasonal Post- and Pre-breeding Migration	9/17, 52.9% (12)	0/3 (3)	9/13, 69.2% (8)	0/1 (1)
Western Beaufort Sea	Interannual Pre-breeding Migration	11/18, 61.1% (14)	0/5 (5)	11/12, 91.7% (8)	0/1 (1)
	Interannual On Land (Breeding)	11/18, 66.6% (14)	0/5 (5)	11/1, 100% (8)	0/1 (1)
East Siberian Sea	Interannual Post-breeding Migration	14/15, 93.3% (12)	14/15, 93.3% (12)	–	–
	Interannual Pre-breeding Migration	1/2 (2)	–	1/2 (2)	–

4.4.2. Eastern Chukchi Sea

Eiders that used the eastern Chukchi Sea originated from capture locations in the eastern Chukchi Sea and western Beaufort Sea. Therefore, we stratified our assessment according to capture site.

Among Spectacled Eiders captured during breeding in the eastern Chukchi Sea, we found evidence of interannual fidelity during pre-breeding migration, breeding, and post-breeding migration, and inter-seasonal fidelity between pre- and post-breeding migration within and between years, respectively, although sample sizes were negligible. Only two adults (one male and one female) carried transmitters that provided sufficient data to detect fidelity during pre-breeding migration, and both staged in the eastern Chukchi Sea area in subsequent years. All Spectacled Eiders with active transmitters (two males and three females) that were captured during the breeding season returned to terrestrial areas of the eastern Chukchi Sea in the subsequent breeding season. Among females that were initially captured on a nest and returned in subsequent years ($n = 3$), 86.4% ($n = 19/22$) of their on-land locations were within 5 km of the initial nest site; all but one location was within 10 km of the initial nest site. Within the same year, one of two adult males and all three adult females used the eastern Chukchi Sea during pre- and post-breeding migration. All Spectacled Eiders that used the eastern Chukchi Sea area during post-breeding migration (two adult males, four adult females) returned to the eastern Chukchi Sea area during pre-breeding migration in the following year (Table 10).

Among Spectacled Eiders captured during arrival, breeding, and brood rearing in the western Beaufort Sea, we detected interannual fidelity to the eastern Chukchi Sea during pre- and post-breeding migration, as well as inter-seasonal fidelity between pre- and post-breeding migration within and between years, respectively. Among two adult males, eight adult females, and one juvenile female that could have used the eastern Chukchi Sea during subsequent post-breeding migrations, only the adult females returned. Only four adult females had transmitters that provided sufficient data to detect fidelity during pre-breeding migration; two staged in the eastern Chukchi Sea in subsequent years. Within the same year, all seven adult females that had transmitters that provided data used the eastern Chukchi Sea during pre- and post-breeding migration. Females exhibited intra-seasonal fidelity during post-breeding migration and pre-breeding migration in the following year; although males did not exhibit intra-seasonal fidelity to the eastern Chukchi Sea (Table 10).

4.4.3. East Siberian Sea

Adult males exhibited breeding and post-breeding site fidelity to the East Siberian Sea. Among 12 adult males that had transmitters that provided data, we recorded 14 returns out of 15 (93.3%) potential returns in subsequent years. Adult females used the East Siberian Sea during pre-breeding migration only. Two adult females provided sufficient data to record interannual pre-breeding fidelity to the East Siberian Sea, only one returned (Table 10).

4.4.4. Western Bering Strait

We detected interannual fidelity to the western Bering Strait during pre- and post-breeding migration, and inter-seasonal fidelity within and among years, respectively. Among 12 adult males and one adult female that could have used the western Bering Strait during subsequent post-breeding migrations, only six males returned. Five adult males, six adult females, and one juvenile female had transmitters that provided sufficient data to detect fidelity during pre-breeding migration; three adult males and all six adult females returned. Within the same year, few Spectacled Eiders used the western Bering Strait during both pre- and post-breeding migration. Among nine adult males, 17 adult females, and one juvenile female that used the western Bering Strait during pre-breeding migration, only three adult males returned during post-breeding migration. Among Spectacled Eiders that used the western Bering Strait during post-breeding migration and could have returned to stage the following year, we recorded 13 potential returns among 12 adult males, and two adult females. Six males and both females returned to the western Bering Strait during pre-breeding migration in the year following use during post-breeding migration (Table 10).

4.4.5. Norton Sound

We detected interannual fidelity to Norton Sound during post-breeding migration and inter-seasonal fidelity between pre- and post-breeding migration within and among years, respectively. Among two adult males and 17 adult females, all but one male used Norton Sound during post-breeding migration in subsequent years. Only four adult females had transmitters that provided sufficient data to detect inter-season fidelity during pre- and post-breeding migration in the same year; all four used Norton Sound during both seasons. Among two adult males and 18 adult females that used Norton Sound during post-breeding migration, only four adult females returned during pre-breeding migration the following year (Table 10).

4.4.6. Yukon-Kuskokwim Delta

Adult females displayed a greater level of interannual fidelity to the Yukon-Kuskokwim Delta than adult males. All 19 adult females that had transmitters that provided data returned to the Yukon-Kuskokwim Delta to stage and presumably breed in the year following capture. Among females that were initially captured on a nest and returned in subsequent years ($n = 12$), 71.8% ($n = 188/262$) of their on-land locations were within 5 km of the initial nest site; 98.1% ($n = 257/262$) were within 10 km of the initial nest site. Only four of 12 (33.3%) adult males returned to the Yukon-Kuskokwim Delta to stage and breed in the year following capture (Table 10).

4.4.7. Northern Bering Sea

We recorded complete interannual fidelity to the northern Bering Sea wintering area. Among 14 adult males, 25 adult females, and one juvenile female with transmitters that provided sufficient data, all used the northern Bering Sea in subsequent winters (Table 10).

4.5. Migratory Connectivity

4.5.1. Connectivity Overview

Spectacled Eiders that departed northern Alaska after the breeding season migrated through the eastern Chukchi Sea, East Siberian Sea, western Bering Strait, or directly to the northern Bering Sea. Spectacled Eiders that departed western Alaska migrated through Norton Sound, western Bering Strait, East Siberian Sea, or directly to the northern Bering Sea. Males that departed northern Russia migrated through the western Bering Strait or directly to the northern Bering Sea. During post-breeding migration, Norton Sound was exclusively used by Spectacled Eiders that departed the Yukon-Kuskokwim Delta, whereas the eastern Chukchi Sea was exclusively used by Spectacled Eiders that departed northern Alaska breeding areas (Table 11, Figure 4, Figure 5).

Adult Spectacled Eiders that returned to northern Alaska to breed migrated through the western Bering Strait, East Siberian Sea, and eastern Chukchi Sea, whereas Spectacled Eiders that returned to the Yukon-Kuskokwim Delta migrated through the western Bering Strait, Norton Sound, or directly from the northern Bering Sea wintering area. Males that presumably bred in northern Russia migrated through the western Bering Strait or directly from the northern Bering Sea. During pre-breeding migration, Norton Sound was exclusively used by Spectacled Eiders that returned to the Yukon-Kuskokwim Delta, whereas the eastern Chukchi Sea was exclusively used by Spectacled Eiders that returned to breeding areas in northern Alaska or Russia (Table 12, Figure 6, Figure 7).

Table 11. Post-breeding migratory connectivity of Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. We present the total number of departures within each age and sex class originating from each important area, and the number and proportion of arrivals to subsequently used areas. We did not calculate percentage if the total number of departures for a specific age and sex class was < 10.

Important Area (Origin)	Age, Sex (Total Departures)	Important Area (Destination)							
		YKD	NS	CS	BS	ESS	WBS	NBS	Other
Yukon-Kuskokwim River Delta (YKD)	Adult Males (19)	X	3, 15.8%	–	–	1, 5.3%	11, 57.9%	4, 21.1%	–
	Adult Females (46)	X	45, 97.8%	–	–	–	–	–	1, 2.2%
Norton Sound (NS)	Adult Males (3)	–	X	–	–	2	–	1	–
	Adult Females (42)	–	X	–	–	–	–	42, 100%	–
Eastern Chukchi Sea (CS)	Adult Males (8)	–	–	X	–	2	4	1	1
	Adult Females (26)	–	–	X	–	–	3, 11.5%	23, 88.5%	–
	Juvenile Males (2)	–	–	X	1	–	–	–	1
	Juvenile Females (2)	–	–	X	–	–	–	2	–
Western Beaufort Sea (BS)	Adult Males (10)	–	–	7, 70.0%	X	3, 30.0%	–	–	–
	Adult Females (33)	–	–	33, 100%	X	–	–	–	–
	Juvenile Males (13)	–	–	12, 92.3%	X	–	–	–	1, 7.7%
	Juvenile Females (4)	–	–	3	X	–	1	–	–
East Siberian Sea (ESS)	Adult Males (23)	–	–	–	–	X	4, 17.4%	19, 82.6%	–
Western Bering Strait (WBS)	Adult Males (21)	–	–	–	–	5, 23.8%	X	16, 76.2%	–
	Adult Females (2)	–	–	–	–	–	X	1	1
	Juvenile Males (1)	–	–	–	–	–	X	–	1
	Juvenile Females (2)	–	–	–	–	–	X	–	2
Northern Bering Sea (NBS)	Adult Males (4)	–	–	–	–	–	4	X	–

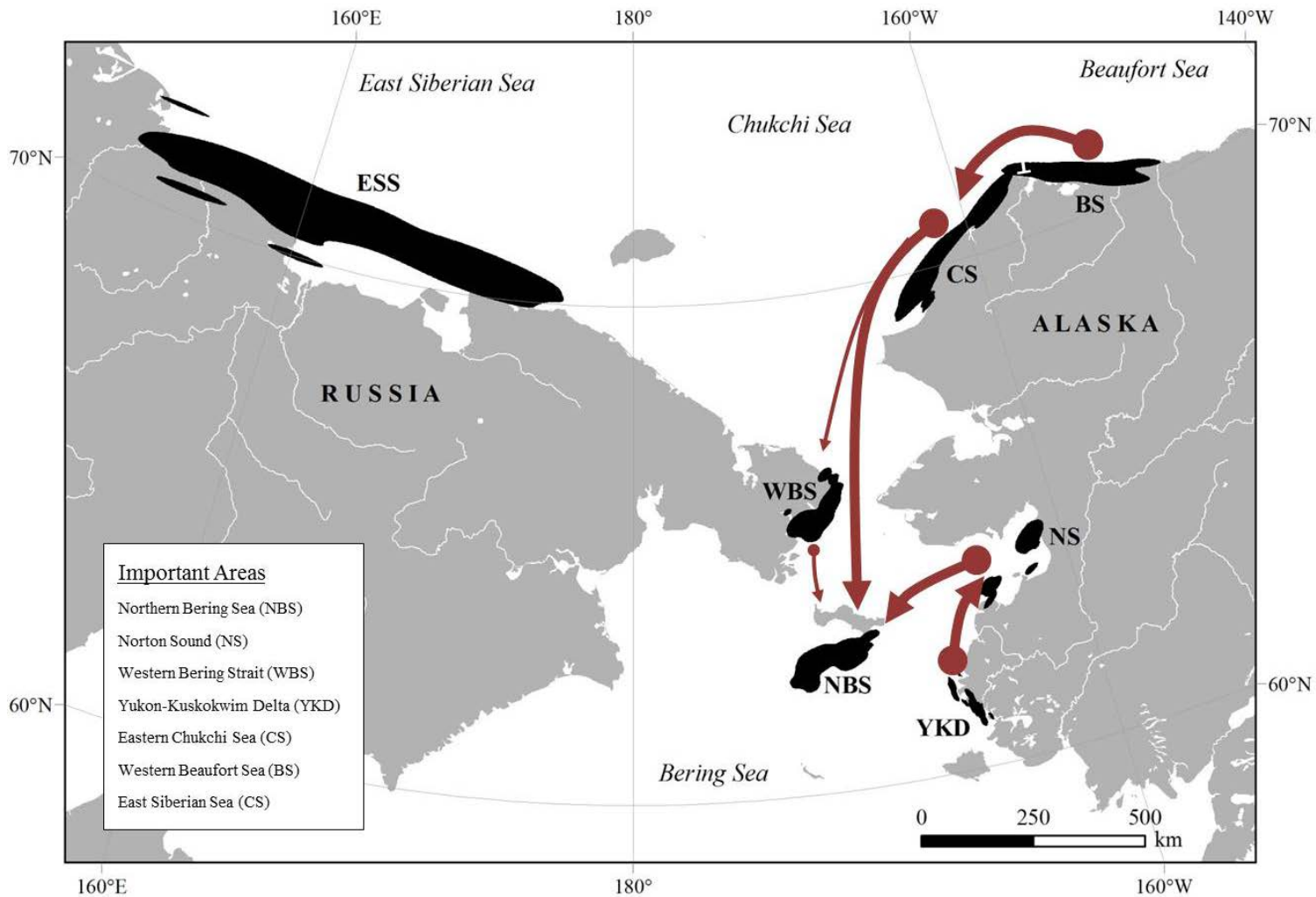


Figure 4. Post-breeding migratory connectivity of female Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. Large arrows represent connectivity where > 50% of departures from an important area with ≥ 10 departures arrived at a single important area (see Table 11). Small arrows represent connectivity where < 50% of all departures from an important area with ≥ 10 total departures arrived at a single important area or departures from an important area with < 10 total departures. Arrows indicate origin and subsequent destination, not migratory paths.

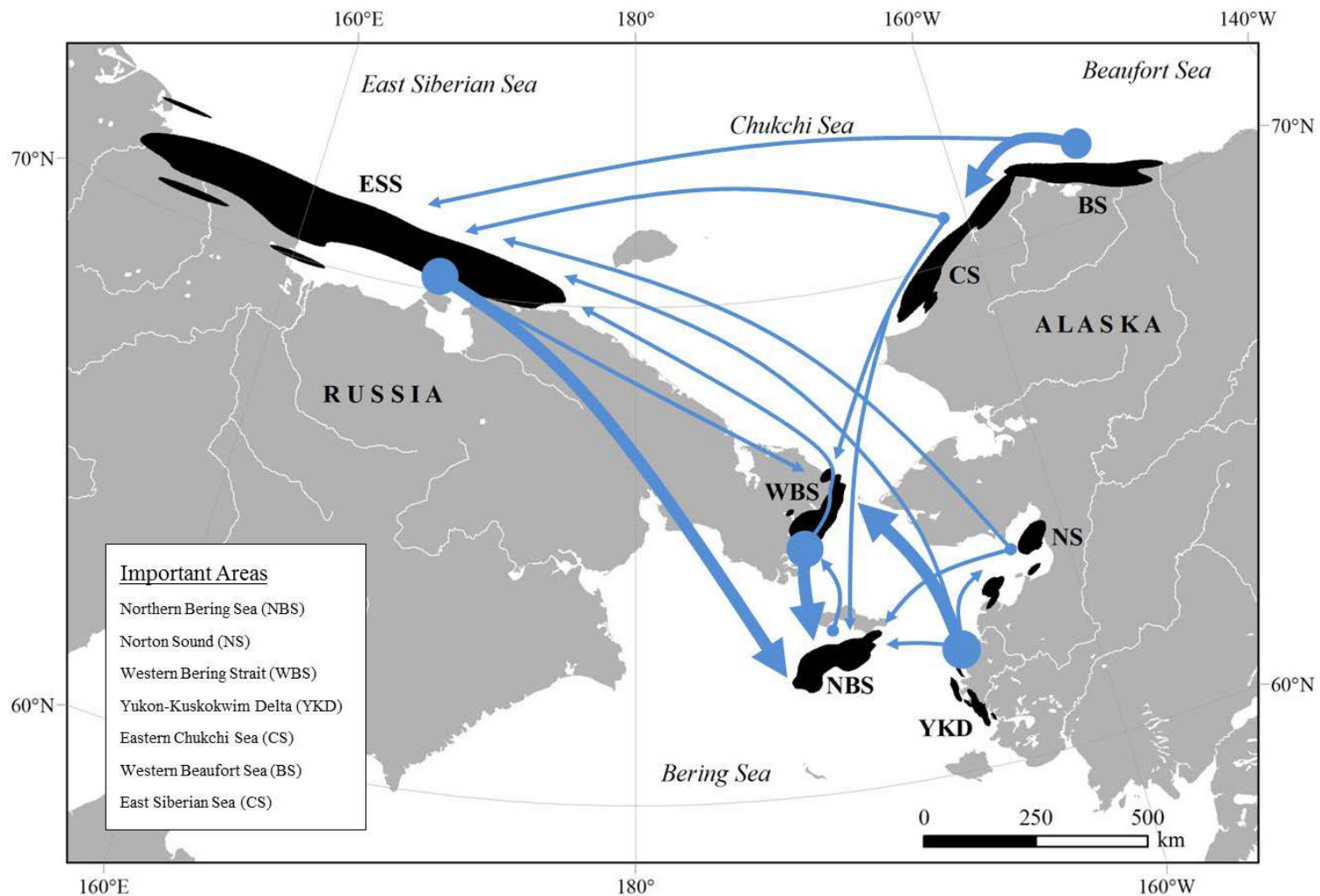


Figure 5. Post-breeding migratory connectivity of male Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. Large arrows represent connectivity where $> 50\%$ of departures from an important area with ≥ 10 departures arrived at a single important area (see Table 11). Small arrows represent connectivity where $< 50\%$ of all departures from an important area with ≥ 10 total departures arrived at a single important area or departures from an important area with < 10 total departures. Arrows indicate origin and subsequent destination, not migratory paths.

Table 12. Pre-breeding migratory connectivity of Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. We present the total number of departures within each age and sex class originating from each important area, and the number and proportion of arrivals to subsequently used areas. We did not calculate percentage if the total number of departures for a specific age and sex class was < 10. The Yukon-Kuskokwim Delta (YKD) and western Beaufort Sea (BS) were pre-breeding destinations, but not origins. The northern Bering Sea was not a pre-breeding destination.

Important Area (Origin)	Age, Sex (Total Departures)	Important Area (Destination)						
		YKD	NS	CS	BS	ESS	WBS	Other
Norton Sound (NS)	Adult Females (4)	4	X	–	–	–	–	–
Eastern Chukchi Sea (CS)	Adult Males (2)	–	–	X	–	2	–	–
	Adult Females (9)	–	–	X	9	–	–	–
East Siberian Sea (ESS)	Adult Females (3)	–	–	2	1	X	–	–
Western Bering Strait (WBS)	Adult Males (14)	–	–	2, 14.3%	–	10, 71.4%	X	2, 14.3%
	Adult Females (24)	4, 16.7%	3, 12.5%	11, 45.8%	1, 4.2%	5, 20.8%	X	–
Northern Bering Sea	Adult Males (25)	4, 16.0%	–	1, 4.0%	–	6, 24.0%	14, 56.0%	–
	Adult Females (36)	10, 27.8%	1, 2.8%	–	–	–	25, 69.4%	–
	Juvenile Females (2)	–	–	–	1	–	1	–

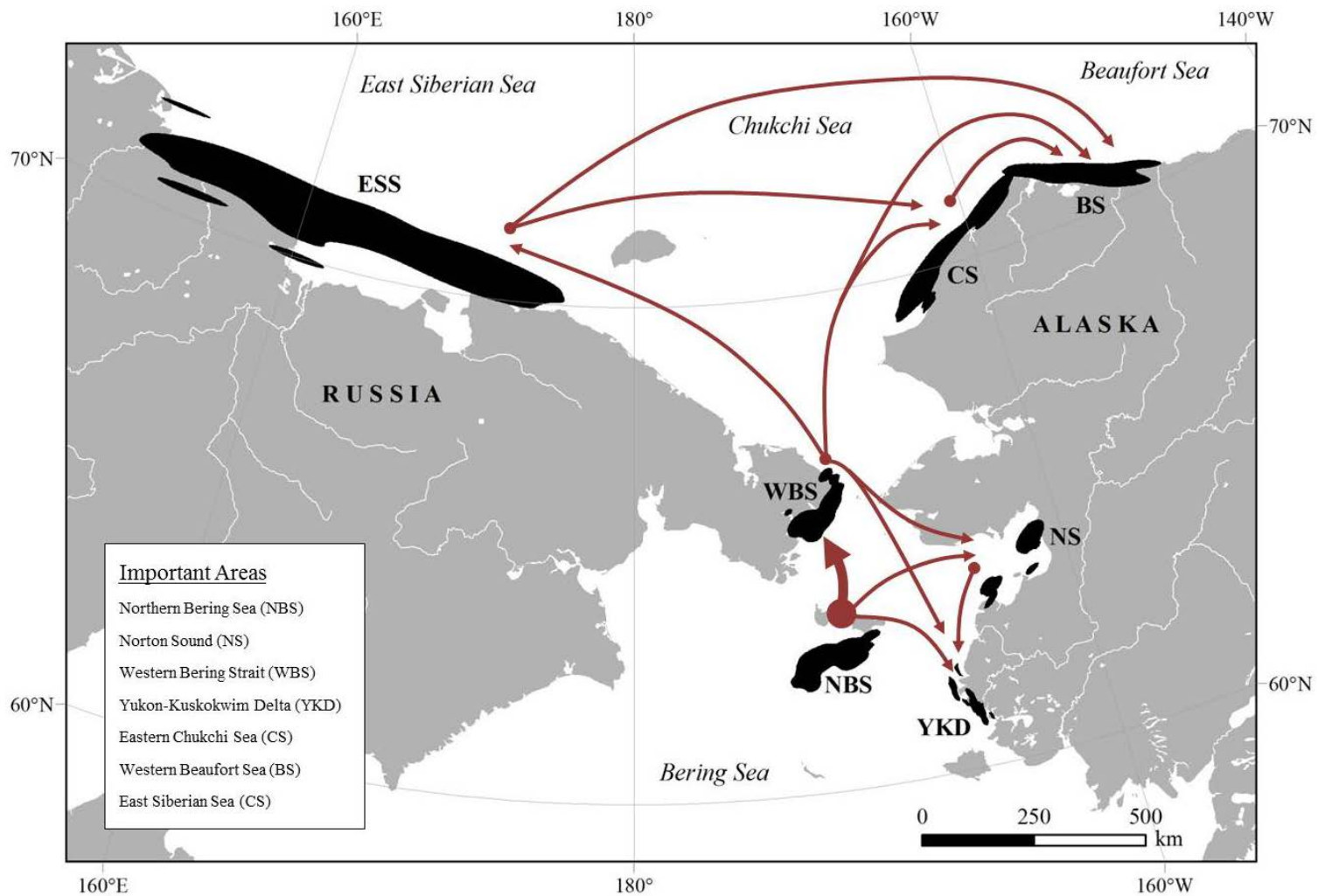


Figure 6. Pre-breeding migratory connectivity of female Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. Large arrows represent connectivity where > 50% of departures from an important area with ≥ 10 departures arrived at a single important area (see Table 12). Small arrows represent connectivity where < 50% of all departures from an important area with ≥ 10 total departures arrived at a single important area or departures from an important area with < 10 total departures. Arrows indicate origin and subsequent destination, not migratory paths.

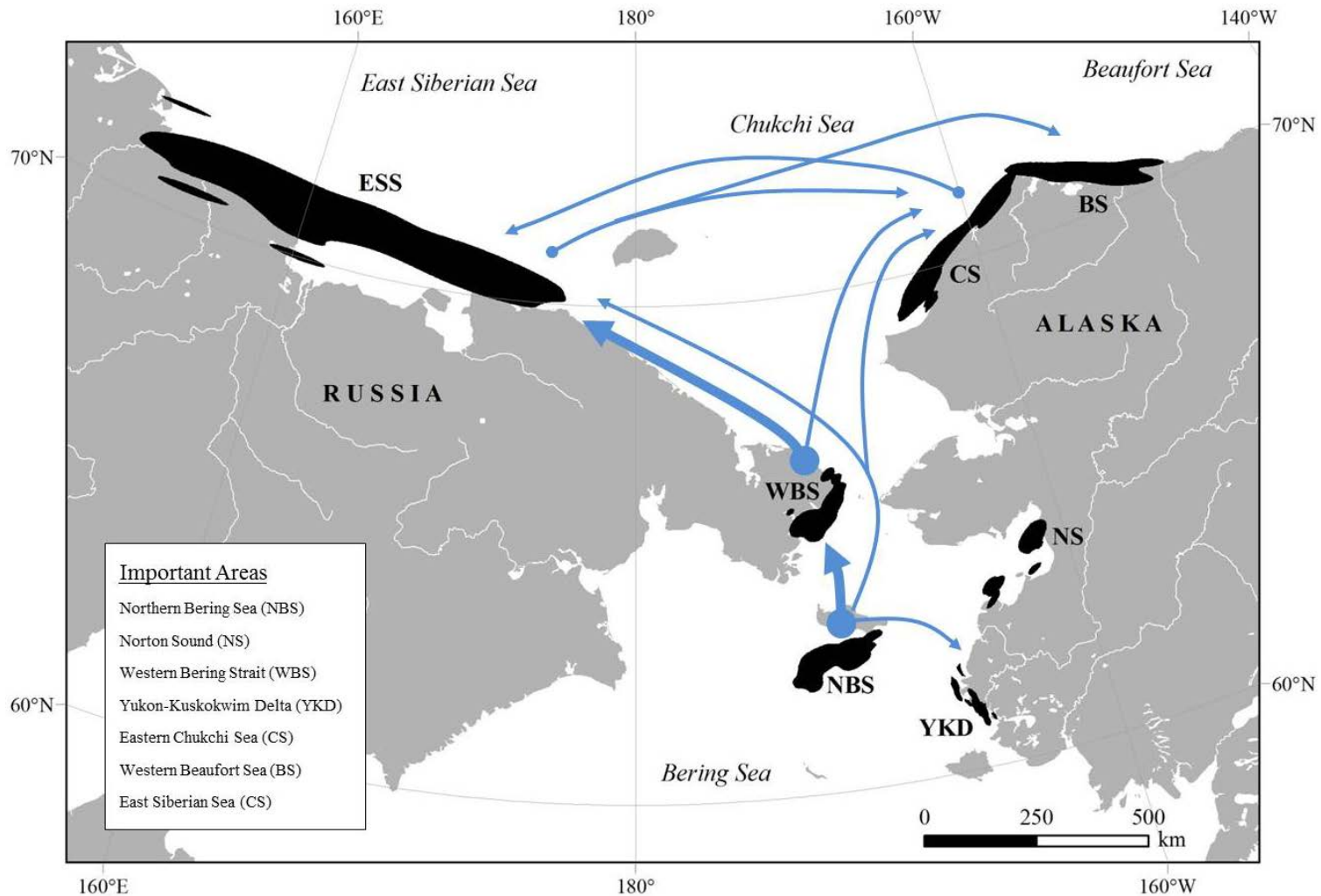


Figure 7. Pre-breeding migratory connectivity of male Spectacled Eiders with satellite transmitters that provided data among important areas, 2008–2012. Large arrows represent connectivity where $> 50\%$ of departures from an important area with ≥ 10 departures arrived at a single important area (see Table 12). Small arrows represent connectivity where $< 50\%$ of all departures from an important area with ≥ 10 total departures arrived at a single important area or departures from an important area with < 10 total departures. Arrows indicate origin and subsequent destination, not migratory paths.

4.5.2. Western Beaufort Sea

Ten adult males, 33 adult females, 13 juvenile males, and four juvenile females departed the western Beaufort Sea during post-breeding migration or post-fledging dispersal. All migrated to the eastern Chukchi Sea, except three adult males that migrated to the East Siberian Sea, one juvenile male that migrated to the Mackenzie River Delta, and one juvenile female that migrated to the western Bering Strait (Table 11, Figure 4, Figure 5).

Pre-breeding, 11 adult females and one juvenile female arrived in the western Beaufort Sea. Most adult females ($n = 9$, 81.8%) originated from the eastern Chukchi Sea; one each originated from the East Siberian Sea and western Bering Strait. The lone juvenile female originated from the northern Bering Sea wintering area (Table 12, Figure 6).

4.5.3. Eastern Chukchi Sea

Seven adult males, 33 adult females, 12 juvenile males, and three juvenile females arrived in the eastern Chukchi Sea during post-breeding migration or post-fledging dispersal. All originated in the western Beaufort Sea. Eight adult males, 26 adult females, two juvenile males, and two juvenile females subsequently departed the eastern Chukchi Sea. Adult males dispersed to the East Siberian Sea ($n = 2$), western Bering Strait ($n = 4$), northern Bering Sea ($n = 1$), and to a location off the northern coast of Russia between the East Siberian Sea and western Bering Strait ($n = 1$). Most adult females ($n = 23$, 88.5%) migrated to the northern Bering Sea wintering area; three migrated to the western Bering Strait. Of two juvenile males, one returned to the western Beaufort Sea, while the other migrated to an area in the Bering Sea between the northern Bering Sea and Norton Sound. Both juvenile females migrated to the northern Bering Sea (Table 11, Figure 4, Figure 5).

Thirteen adult females and 3 adult males arrived in the eastern Chukchi Sea during pre-breeding migration. Most (11 females, 2 males) originated from the western Bering Strait. Two adult females originated from the East Siberian Sea, and 1 adult male originated from the northern Bering Sea. Nine adult females and 2 adult males subsequently departed the eastern Chukchi Sea. All females migrated to the western Beaufort Sea, while both males migrated to the East Siberian Sea (Table 12, Figure 6, Figure 7).

4.5.4. East Siberian Sea

Thirteen adult males arrived in the East Siberian Sea during post-breeding migration. Males originated from the Yukon-Kuskokwim Delta ($n = 1$), Norton Sound ($n = 2$), eastern Chukchi Sea ($n = 2$), western Beaufort Sea ($n = 3$), and the western Bering Strait ($n = 5$). Twenty-three adult males subsequently departed the East Siberian Sea. Most ($n = 19$, 82.6%) migrated directly to the northern Bering Sea; the remainder migrated to the western Bering Strait (Table 11, Figure 5).

Five adult females and 16 adult males arrived in the East Siberian Sea during pre-breeding migration. Most (five females, 10 males) originated from the western Bering Strait. Six adult males originated from the northern Bering Sea. Three adult females subsequently departed for the eastern Chukchi Sea ($n = 2$) and western Beaufort Sea ($n = 1$) (Table 12, Figure 6, Figure 7).

4.5.5. Western Bering Strait

Nineteen adult males, three adult females, and one juvenile female arrived in the western Bering Strait during post-breeding migration or post-fledging dispersal. Adult males originated in the Yukon-Kuskokwim Delta ($n = 11$), eastern Chukchi Sea ($n = 4$), and East Siberian Sea ($n = 4$). All three adult females originated in the eastern Chukchi Sea, while the lone juvenile female originated in the western Beaufort Sea. Twenty-one adult males, two adult females, one juvenile male, and two juvenile females subsequently departed the western Bering Strait. Most adult males ($n = 16$, 76.2%) migrated to the northern Bering Sea; five migrated to the East Siberian Sea. Adult females migrated to the northern Bering Sea ($n = 1$) and an area north of St. Lawrence Island ($n = 1$). The juvenile male departed the western Bering Strait but remained near the eastern coast of the Chukotka Peninsula. One juvenile female migrated to southern Kuskokwim Bay, Alaska before moving to coastal sites on the Alaska Peninsula. The second juvenile female departed the western Bering Strait and migrated to an area off the northern coast of Russia between the East Siberian Sea and western Bering Strait (Table 11, Figure 4, Figure 5).

Fourteen adult males, 25 adult females, and one juvenile female arrived in the western Bering Strait during pre-breeding migration. All originated in the northern Bering Sea. Fourteen adult males and 24 adult females subsequently departed the western Bering Strait. Males migrated to the eastern Chukchi Sea ($n = 2$), East Siberian Sea ($n = 10$), and marine areas peripheral to the East Siberian Sea area ($n = 2$), while females migrated to the Yukon-Kuskokwim Delta ($n = 4$), Norton Sound ($n = 3$), eastern Chukchi Sea ($n = 11$), western Beaufort Sea ($n = 1$), and East Siberian Sea ($n = 5$) (Table 12, Figure 6, Figure 7).

4.5.6. Norton Sound

Three adult males and 45 adult females arrived in Norton Sound during post-breeding migration. All originated in the Yukon-Kuskokwim Delta. Three adult males and 42 adult females subsequently departed Norton Sound. One male and all females migrated to the northern Bering Sea. The remaining adult males ($n = 2$) migrated to the East Siberian Sea (Table 11, Figure 4, Figure 5).

Four adult females arrived in Norton Sound during pre-breeding migration. Three originated in the western Bering Strait, and one originated in the northern Bering Sea. All individuals subsequently departed for the Yukon-Kuskokwim Delta (Table 12, Figure 6).

4.5.7. Yukon-Kuskokwim Delta

Nineteen adult males and 46 adult females departed the Yukon-Kuskokwim Delta during post-breeding migration. Most males ($n = 11$, 57.9%) migrated to the western Bering Strait; four migrated to the northern Bering Sea, three to Norton Sound, and one to the East Siberian Sea. Most females ($n = 45$, 97.8%) migrated to Norton Sound; one migrated to Port Clarence, Alaska before moving to the northern Bering Sea (Table 11, Figure 4, Figure 5).

Four adult males and 18 adult females arrived in the Yukon-Kuskokwim Delta during pre-breeding migration. Most originated from the northern Bering Sea, including all four males and 10 females. Four females originated in Norton Sound, and another four originated in the western Bering Strait (Table 12, Figure 6, Figure 7).

4.5.8. Northern Bering Sea

Forty-one adult males, 66 adult females, and two juvenile females arrived in the northern Bering Sea wintering area at the conclusion of post-breeding migration or post-fledging dispersal. Nearly all of the important areas identified in our study were a migratory point of origin for Spectacled Eiders migrating to the northern Bering Sea. Individuals originated in the Yukon-Kuskokwim Delta (four adult males), Norton Sound (one adult male, 42 adult females), eastern Chukchi Sea (one adult male, 23 adult females, two juvenile females), East Siberian Sea (19 adult males), and the western Bering Strait (16 adult males, one adult female). Spectacled Eiders that departed the western Beaufort Sea did not migrate directly to the northern Bering Sea. We also recorded the movement of four adult males from the Yukon-Kuskokwim Delta to the northern Bering Sea in June before they continued post-breeding migration to the western Bering Strait (Table 11, Figure 4, Figure 5).

Twenty-five adult males, 36 adult females, and two juvenile females departed the northern Bering Sea as they initiated pre-breeding migration. Most adult males ($n = 14$, 56%) migrated to the western Bering Strait; six migrated to the East Siberian Sea, four to the Yukon-Kuskokwim Delta, and one to Norton Sound. Like males, most adult females ($n = 25$, 69.4%) migrated to the western Bering Strait; 10 migrated to the Yukon-Kuskokwim Delta and one to Norton Sound. Juvenile females migrated to the western Beaufort Sea and western Bering Strait, respectively (Table 12, Figure 6, Figure 7).

5.0. DISCUSSION

5.1. Winter

As first noted by Petersen et al. (1999) and reaffirmed in our study, the world population of Spectacled Eiders winters exclusively in the northern Bering Sea immediately south of St. Lawrence Island, Alaska. Our results suggest that Spectacled Eiders may have consistently wintered in the northern Bering Sea since telemetry and surveys began in 1993 (Petersen and Douglas 2004). Prior to 1993, the winter distribution of Spectacled Eiders was unknown; likely because the species concentrated away from traditional hunting areas in the northern Bering Sea and beyond visible distance of land-based observers on St. Lawrence Island. However, historical observations including traditional knowledge suggested that wintering areas may have existed elsewhere including nearshore areas of the Pribilof and Aleutian Islands, Alaska, and the Alaska Peninsula (Gabrielson and Lincoln 1959). During our study, the winter distribution of Spectacled Eiders did not change in three consecutive winters (2008/2009, 2009/2010, 2010/2011) and matched that of wintering Spectacled Eiders in 1993–1997 (Petersen et al. 1999, Cooper et al. 2013). While some juveniles migrated elsewhere during post-breeding dispersal, all adults occupied the northern Bering Sea important area for nearly half of their annual cycle and remained in this area until ice in the Bering Sea retreated northward in spring. Adults also demonstrated complete interannual winter fidelity to the northern Bering Sea during the 4 years of our study, further substantiating the importance of this area to the species.

Sea ice is a dominant physical feature in the northern Bering Sea throughout winter, and the distribution of open water (e.g., leads and polynyas) appears to control, in part, the distribution of wintering Spectacled Eiders as it does for other birds and mammals that must dive to feed and surface to breathe (Bump and Lovvorn 2004, Lovvorn et al. 2014). Ice in the northern Bering Sea originates from the north, before southward advection and melting over the Bering Sea shelf break (Niebauer et al. 1999). Spectacled Eiders generally arrived at the northern Bering Sea wintering area in October and used an ice-free area near St. Lawrence Island until ice began to form south of the island in December. As ice formed, the distribution of Spectacled Eiders shifted approximately 70 km to the west-southwest where they remained in lead-dominated pack ice through April (Cooper et al. 2013). Although predominant northerly winds in the region provide for a dynamic mosaic of ice and open water habitats south of St. Lawrence Island (i.e., ice expansion); occasional southerly winds push ice against the southern coast of the island which causes ice consolidation (i.e., lead closure and loss of open water). Loss of open water through ice consolidation can result in adverse consequences (e.g., exclusion from feeding areas) for species that depend on dynamic sea ice habitats (Barry 1968, Fournier and Hines 1994, Bump and Lovvorn 2004, Petersen and Douglas 2004).

Although dense sea ice conditions may have adverse consequences, ice also serves a critical role in minimizing energetic costs among sea ducks in Arctic marine environments. The thermal conductance of water is greater than that of air; therefore, sea ducks lose heat at a greater rate in water, requiring increased food intake and metabolic rate for thermostasis (De Vries and Van Eerden 1995). By resting on ice between feeding bouts, Spectacled Eiders reduce heat loss and metabolic rate, thereby conserving energetic reserves (i.e., fat) and reducing the frequency of energetically expensive feeding dives (Lovvorn et al. 2009). Ice may also act to reduce the effects of winter storms and resulting wave action which might preclude energetically efficient

feeding (Petersen and Douglas 2004). Although predominant northerly winds facilitate consistent formation of the St. Lawrence Island Polynya south of the island (Grebmeier and Cooper 1995), wintering Spectacled Eiders used iced areas southwest of the ice-free polynya, further supporting the importance of sea ice to the species.

Spectacled Eiders with implanted satellite transmitters wintered in areas with a mean water depth of 42 ± 13 m (Cooper et al. 2013), although Spectacled Eiders have been detected in areas where water depths can reach nearly 70 m (Petersen and Douglas 2004). Wintering Spectacled Eiders dive to feed on infaunal benthic invertebrates, strongly preferring bivalve molluscs (e.g., *Macoma calcaria*, *Nuculana radiata*, and *Ennucula tenuis*) over other benthic taxa including gastropods (Gastropoda), polychaetes (Polychaeta), ribbon and proboscis worms (Nemertea), amphipods (Amphipoda), crabs (Brachyura), and brittle stars (Ophiuroidea) (Lovvorn et al. 2003, Lovvorn et al. 2014). Substantial export production and limited predation by epibenthic predators in the northern Bering Sea supports some of the greatest densities of benthic infaunal biomass in the world ($300\text{--}400\text{ g m}^{-2}$; Cooper et al. 2002, Dunton et al. 2005, Lovvorn et al. 2005, Grebmeier et al. 2006a, Wei et al. 2010), which in turn supports a diverse community of apex predators including Spectacled Eiders, as well as other diving ducks, fish, whales, and walrus (McCormick-Ray et al. 2011, Lovvorn et al. 2010, Cooper et al. 2013). Although benthic fauna are abundant throughout the northern Bering Sea, the distribution of preferred prey in the Spectacled Eider wintering area appears to shift annually in response to patterns of export production, wind and current driven sediment deposition, and the dispersal and settlement of invertebrate larvae (Lovvorn et al. 2014). On a greater temporal scale, changing climatic conditions have been linked to notable changes (regime shifts) in the Bering Sea ecosystem (Hare and Mantua 2000, Grebmeier et al. 2006b). Of direct relevance to wintering Spectacled Eiders, decadal regime shifts have been implicated in the observed shift in dominant bivalve prey from *Macoma calcaria* to *Nuculana radiata* within the last 40 years (Richman and Lovvorn 2003, Lovvorn et al. 2009) and regime shifts appear to correlate with historical population declines of several species of North American sea duck, including Spectacled Eiders (Flint 2013). There is currently no evidence to support or refute the hypothesis that benthic resources are significantly depleted by wintering Spectacled Eiders. Although localized resources may become seasonally exhausted if the distribution of Spectacled Eiders is constrained to areas with a low abundance of prey (Doleman and Southerland 1997, Petersen and Douglas 2004, Merrill et al. 2010).

Decadal climate change and winter weather, and related variability in ice dynamics and the distribution, abundance, and composition of benthic faunal communities appear to determine the winter distribution of Spectacled Eiders. In a study to examine relationships between ice conditions, prey availability, prey consumption, and body condition among wintering Spectacled Eiders, Lovvorn et al. (2014) compared these parameters between winters when sea ice conditions were presumably favorable (2001: reduced sea ice concentration and greater access to benthic prey) and harsh (2009: greater sea ice concentration and reduced access to benthic prey). In both years, predominant prey consisted of bivalve molluscs, although diet composition shifted in response to the relative concentrations of bivalves at sites where Spectacled Eiders were sampled in each year. Eiders were sampled over a greater concentration of bivalves in 2001 when abundant open water permitted feeding in these areas. In 2009, increased ice concentration over the greatest densities of bivalve prey restricted the distribution of Spectacled Eiders to

relatively poor feeding areas. As a result, Spectacled Eiders carried less body fat in 2009, suggesting a strong relationship between sea ice dynamics, access to prey, and body condition.

Sea ice in the northern Bering Sea oscillates between ice expansion and consolidation regimes (Lovvorn et al. 2014). Regardless of ice conditions however, all Spectacled Eiders with implanted satellite transmitters remained in the northern Bering Sea important area. During ice expansion, Spectacled Eiders can move to preferred feeding areas as leads open or close in response to wind and currents (Bump and Lovvorn 2004). Spectacled Eiders may also remain in leads as they drift (Petersen and Douglas 2004). In contrast, the effects of ice consolidation on the distribution of persistent Spectacled Eiders are not well known, although we predict that wintering Spectacled Eiders become concentrated in areas where the aggregate of individuals maintain open water through body heat and movement. Further analysis is needed to better understand the relationship between ice conditions and the distribution of wintering Spectacled Eiders, which may have implications for individual body condition and survival if prevailing patterns change in the future.

Spectacled Eiders use only one wintering area, whereas other Beringian sea duck species are distributed across multiple wintering areas. Furthermore, Spectacled Eiders greatly outnumber other sea duck species within the northern Bering Sea area, indicating minimal overlap in winter distribution with other species (Bill Larned, U.S. Fish and Wildlife Service pers. comm.). In contrast, Common Eiders demonstrate site fidelity to several near-shore polynya associated wintering areas throughout the Bering Sea (Petersen and Flint 2002, Petersen et al. 2012), although none of these areas coincided with the Spectacled Eider wintering area. Similarly, King Eiders occurred in three distinct wintering regions including the northern Bering Sea, as well as near-shore areas in southwest Alaska and along the Kamchatka Peninsula, Russia (Phillips et al. 2006, Oppel et al. 2008), although overlap with wintering Spectacled Eiders was not apparent. Long-tailed Ducks marked in western Alaska demonstrated an even broader winter distribution which included areas as far west as the Sea of Okhotsk, Russia and as far east as southeast Alaska and coastal British Columbia, Canada (Petersen et al. 2003).

Winter endemism and fidelity to the northern Bering Sea is a unique life history trait of Spectacled Eiders, yet potential origins of these phenomena have not been investigated. We offer three hypotheses that warrant further study. First, subtle physiological or morphological differences among taxonomically similar species may contribute to regional partitioning of habitats used. For example, sympatric wintering King and Common eiders in northern Norway segregate according to dive depth and sea-floor substrate types (Bustnes and Lønne 1997); a relationship thought to result from historical competition which may have led to subtle adaptations to exploit different sources of food (Lovvorn and Jones 1991, Bustnes and Lønne 1997).

Second, Ploeger (1968) suggested that current segregation of taxonomically similar sea ducks across the Bering Sea may be attributable to fidelity to breeding areas used during the last glacial maximum (c. 20,000 bp). Ploeger proposed that breeding Spectacled Eiders were restricted to the southern coast of Beringia near the present day wintering area, while other species likely used circumpolar habitats. Subsequent sea level rise and flooding of the Bering Land Bridge presumably allowed northward expansion (c. 10,000 bp) of Spectacled Eiders into current breeding areas in coastal Alaska and Russia. If Spectacled Eiders wintered offshore of southern

Beringia breeding areas, the current distribution of wintering Spectacled Eiders may be a fidelity driven relic of distribution during the last glacial maximum. Although difficult to test this hypothesis, isolation and ecological or behavioral fidelity to historically used sites may provide explanation for current spatiotemporal patterns. Sonsthagen et al. (2011) tested Ploeger's hypothesis among circumpolar breeding Common Eiders presumed to once occupy glacial maximum refugia throughout the Arctic and Subarctic. Phylogeographic analyses found distinct population structure consistent with the potential distribution of Common Eiders during last glacial maximum and patterns of post-Pleistocene dispersal; evidence that supports the hypothesis that the current winter distribution of Beringian sea ducks may be a relic of historical dispersal events.

Third, Spectacled Eiders may realize specific benefits by wintering in the northern Bering Sea, including predictably abundant benthic prey, sea ice that supports conservation of energy by providing surfaces to roost, few predatory threats, benefits of social cohesion, and close proximity to areas used during pre- and post-breeding migration. Spectacled Eiders that return to winter in the northern Bering Sea can maximize fitness by taking advantage of known resources and conditions (Robertson and Cooke 1999). Individuals that disperse to alternate wintering areas risk encountering novel environmental conditions (e.g., different prey regime, competitors, or predators) for which they may be maladapted. In contrast, Spectacled Eiders appear to remain in the northern Bering Sea during severe ice conditions when departure may benefit individual survival. Persistence through harsh conditions may immediately affect individual survival or body condition, with carry-over effects through spring migration and breeding (Petersen and Douglas 2004, Opiel and Powell 2009, Lovvorn et al. 2014). In a study to assess factors hypothesized to influence King Eider movement within and among wintering areas, Opiel et al. (2009) found that mid-winter movement was likely when sea ice concentration increased, although movement was ultimately an individual-based decision independent of environmental cues. Among Spectacled Eiders, the benefits of returning to and remaining in the northern Bering Sea must outweigh the benefits of departing for an alternate wintering area; a hypothesis that warrants further research.

Spectacled Eiders that return to winter in the northern Bering Sea encounter several thousand potential mates, thereby maximizing individual likelihood of successful pair formation and breeding opportunity (Robertson and Cooke 1999). Recent observations of late-winter courtship in the northern Bering Sea suggest that Spectacled Eiders may form pair bonds during winter (Lovvorn et al. 2012). Although the timing of pair formation among Spectacled Eiders is not well known, genetic homogeneity among breeding populations (Scribner et al. 2001), equal rates of winter fidelity among sexes, and the spring migratory patterns of adult males suggest that Spectacled Eiders are: 1) seasonally monogamous, and 2) pair formation occurs before departing the northern Bering Sea wintering area. Although we might expect mid-winter departure to an alternate wintering site to be advantageous under harsh conditions, leaving may compromise an individual's opportunity to successfully breed if potential mates can only be secured in the northern Bering Sea. Furthermore, if successful pair formation requires winter congregation, fidelity to this region may be a relic of historical fidelity to a southern Beringia wintering area where reproductive benefits were realized (Ploeger 1968).

Spectacled Eiders occupy the northern Bering Sea wintering area for nearly half of their annual cycle, although questions regarding the basis for interannual fidelity and intra-winter persistence remain unanswered. Apparent benefits include abundant benthic prey that is typically accessible through openings in dynamic and energetically beneficial sea ice (Lovvorn et al. 2014). However, the density and movement of sea ice appears to control access to preferred feeding areas. Inability to access preferred prey during periods of increased ice concentration may carry long term costs including mortality or inability to reproduce (Petersen and Douglas 2004, Lovvorn et al. 2014). Strong interannual fidelity to the northern Bering Sea supports the hypothesis that winter conditions favor survival and reproduction. Interannual fidelity and observed courtship (Lovvorn et al. 2012) also supports the hypothesis that pair formation occurs during winter, further substantiating the importance of the northern Bering Sea to the species. Current conditions for greater individual fitness (i.e., abundant prey, energetic benefits of ice, potential mates) possibly precipitated from the species' historical distribution in southern Beringia (Ploeger 1968). Although this hypothesis is difficult to test, isolation during the last glacial maximum and persistent fidelity through time may explain the winter segregation of Spectacled Eiders from taxonomically similar sea duck species. Physiological or morphological differences among species and therefore differences in preferred habitats (e.g., water depth, prey community) may also influence winter segregation. Ultimately, the complex interaction of several factors may influence an individual eider's wintering strategy, including learned and genetically inherited behaviors, prior experiences (negative or positive), and social, physiological, or environmental cues.

5.2. Pre-breeding Migration

Prior to our study, the spatiotemporal distribution of Spectacled Eiders during pre-breeding migration was inferred from ground-based observations in western and northern Alaska (Dau and Kistchinski 1977, McCaffery et al. 1999). Dau and Kistchinski (1977) proposed that Spectacled Eiders congregated in the vicinity of the Bering Strait in the southern Chukchi or northern Bering seas before dispersing to breeding areas in March or April. McCaffery et al. (1999) proposed that Spectacled Eiders migrated directly to western Alaska from the northern Bering Sea wintering area or possibly staged somewhere in the northern Bering Sea before arriving in early May. Our results supported these hypotheses. Spectacled Eiders dispersed from the northern Bering Sea wintering area in March and April as sea ice retreated northward. Most eiders then congregated in nearshore areas of the western Bering Strait near Mechigmenskiy Bay, Russia before dispersing to secondary areas near each of the three breeding regions. Initial migratory destinations also included staging areas immediately offshore of breeding areas in the Yukon-Kuskokwim Delta, the eastern Chukchi Sea, and the East Siberian Sea. Spectacled Eiders also staged in southern Norton Sound in route to the Yukon-Kuskokwim Delta. Eiders arrived at lower latitude staging areas (e.g., western Bering Strait and southern Norton Sound) in April, and higher latitude areas (e.g., eastern Chukchi Sea and East Siberian Sea) in May. Among Spectacled Eiders, the timing of arrival at pre-breeding areas has been attributed to the availability of open water along migratory routes and the emergence of habitat at terrestrial breeding areas (Petersen et al. 2000).

The temporal frequency of data collection during our study precluded detection of pre-breeding migratory routes and estimates of the duration of migratory flight. However, results suggest that Spectacled Eiders used direct over-water routes or followed coast lines during spring migration, and moved from one area to another within one transmitter duty cycle (4–7 days). We detected migratory (i.e., ‘transient’) locations over the Chukotka Peninsula, which may suggest that some Spectacled Eiders use a short overland route when moving between the western Bering Strait and the East Siberian Sea. Within each year, we found little variation in the timing of migration and routes used among adults, which should be expected if adults form pair bonds during winter, migrate together to breeding areas, and experience the same environmental conditions during migration.

Despite our efforts to characterize the spatiotemporal distribution of young Spectacled Eiders during their first and second spring, only one female eider marked as a juvenile had a transmitter that provided sufficient data. In the first spring, this female migrated from the northern Bering Sea to the western Bering Strait in June and remained through July before migrating to the East Siberian Sea. In the second spring, this eider departed the northern Bering Sea and arrived in the western Beaufort Sea in June, although we were unable to record the use of intermediate staging areas. During each spring, this individual departed the northern Bering Sea wintering area approximately 2 months later than adults. Although this individual migrated to breeding areas in northern Russia and Alaska, it is unlikely that this female successfully nested in its first or second year given the timing of migration and seasonally constrained breeding period at northern latitudes (Petersen et al. 2000).

Spatiotemporal patterns of spring migration among Spectacled Eiders were consistent with patterns exhibited by other sea duck species that migrate from wintering areas in the Bering Sea

to breed in coastal Alaska and Russia. Spectacled, King, and Common eiders that migrated to breeding areas in northern Alaska used the same coastal or over-water routes through the western Bering Strait and eastern Chukchi Sea in April through June (Petersen and Flint 2002, Oppel et al. 2008, Petersen 2009). In our study, all adult females that staged in the eastern Chukchi Sea continued migration to breeding areas in northern Alaska. Males also staged in the eastern Chukchi Sea, but subsequently migrated to breeding areas in northern Russia; a pattern also observed among King Eiders (Oppel et al. 2009). Like King Eiders, female Spectacled Eiders briefly staged in the Beaufort Sea before moving inland to breed in northern Alaska (Phillips et al. 2007). The short duration during which these species remained offshore suggests that pre-breeding eiders merely wait in western Beaufort Sea until snow and ice melt allows access to terrestrial breeding habitat (Phillips et al. 2007).

Oppel et al. (2008) found that King Eiders initiated spring migration later from more northern wintering areas, although the timing of arrival at breeding areas in northern Alaska was the same regardless of sex or migratory origin. Similarly, Petersen and Flint (2002) observed that Common Eiders that migrated to western Alaska initiated spring migration earlier than Common Eiders destined for higher latitude staging and breeding areas. In general, the timing of migration among Spectacled Eiders matched these patterns; Spectacled Eiders arrived later at staging and breeding areas north of the Bering Strait likely due to the persistence of ice and snow, although pre-breeding arrival to each important area was synchronous regardless of migratory origin. For example, we noted contrasting strategies of spring migration among adult females that returned to breed in the Yukon-Kuskokwim Delta in 2009 ($n = 17$). Females that used intermediate staging areas (i.e., western Bering Strait, southern Norton Sound) departed the northern Bering Sea wintering area ($\bar{x}_8 = 9 \text{ April} \pm 9 \text{ days}$) earlier ($t_{15} = 6.03$, $p < 0.001$) than those that migrated directly to the Yukon-Kuskokwim Delta ($\bar{x}_9 = 2 \text{ May} \pm 7 \text{ days}$). However, regardless of migratory strategy, Spectacled Eiders arrived at the Yukon-Kuskokwim Delta in mid-May ($t_{15} = 1.19$, $p = 0.25$; direct: $\bar{x}_9 = 10 \text{ May} \pm 8 \text{ days}$; indirect: $\bar{x}_8 = 15 \text{ May} \pm 6 \text{ days}$).

Our study was not designed to evaluate the disadvantages or realized benefits of these and other migratory strategies, although we expect each strategy to involve trade-offs between distances and routes traveled during pre-breeding migration, prey availability at staging areas, and preparedness for breeding (e.g., the timing of pair formation, body condition). For example, Spectacled Eiders that migrated directly from the northern Bering Sea to the Yukon-Kuskokwim Delta traveled approximately 600 km less than Spectacled Eiders that used intermediate staging areas. Although we expect greater flight distances to result in greater energetic costs (Newton 2008), Spectacled Eiders that staged at intermediate sites may realize benefits (e.g., prey) not available to direct migrants. These benefits are not apparent and warrant additional study.

Although we sought to generalize our data to present broad spatiotemporal patterns exhibited by Spectacled Eiders, we detected considerable inter-individual variation in the timing of pre-breeding migration, duration of site occupancy, and migratory connectivity to suggest that migratory strategies are individually based. For example, adults arrived at the western Bering Strait staging area as early as 17 February, but as late as 26 May, and Spectacled Eiders remained for as few as nine days, but at most 72 days. Furthermore, our assessment of pre-breeding migratory connectivity revealed that individuals originating from the same staging area may disperse to several destinations including breeding areas or secondary staging areas. For

example, adults that initially stopped in the western Bering Strait staging area continued pre-breeding migration to each of the important areas (excluding the northern Bering Sea) identified in our study.

Individual variation in migratory strategy may be influenced by several interacting factors including inherent or learned behaviors (e.g., realized benefits of site fidelity), environmental conditions (e.g., weather), social cohesion (e.g., migratory behaviors of a mate), prey availability, or physical condition (Newton 2008). We presume that Spectacled Eiders seek to maximize survival and reproductive potential by varying their strategy in response to these and other factors, although some factors such as social cohesion or inherent and learned behaviors that are independent of environmental variability may have indirect negative effects on survival and fitness when environmental conditions rapidly deteriorate. For example, we detected considerable interannual fidelity to staging areas where stochastic weather events and resultant shifts in sea ice or re-freezing can lead to loss of open water, starvation, and mass mortality of sea ducks (Barry 1968, Fournier and Hines 1994, Newton 2007). Petersen (2009) tracked the pre-breeding migration of Common Eiders from the northern Bering Sea to northern Alaska and concluded that the timing of migration varied annually in response to sea ice conditions. Sea ice and terrestrial melt is later in relatively cold springs, which delays access to staging and breeding areas. In contrast, departure from wintering areas, arrival at staging areas, and the timing of nest initiation occurs earlier in relatively warm springs (McLaren and Alliston 1985, Parker and Mehlum 1991). Although Spectacled Eiders may alter the timing of migration in response to their environment, our data suggest that Spectacled Eiders may not exercise interannual plasticity in migratory routes or destinations which could have negative consequences if stochastic events change otherwise predictable conditions during pre-breeding migration.

Individual migratory plasticity in response to environmental cues may translate to survival and reproductive success in light of the energetic expense of migration and breeding (Newton 2008). Arctic nesting waterfowl (Anatidae) depend on stored energy (i.e., body fat) to fuel migration, maintain homeostasis when fasting (e.g., food limitations, nest incubation or guarding), and supplement feeding during egg formation (Parker and Holm 1990, Flint and Grand 1999, Oppel et al. 2010). If environmental conditions during pre-breeding migration influence survival and reproductive success, we should expect Spectacled Eiders to stage in areas where environmental conditions allow the net accumulation of energy (i.e., open water with access to high quality prey; Lovvorn et al. 2014). Recurring polynyas occur at each of the staging areas identified in our study, although wind direction and currents may interact to either open or close polynyas throughout spring (Stringer and Groves 1991, Barber and Massom 2007). Polynyas are generally associated with greater rates of primary production and therefore increased biological activity throughout the trophic hierarchy (Karnovsky et al. 2007, Heide-Jørgensen et al. 2013). However, the location of a polynya may not always be associated with the distribution of prey as polynya associated primary production may be advected down-stream in a current driven system as is the case at the northern Bering Sea wintering area (Grebmeier and Cooper 1995, Grebmeier and Barry 2007). Unfortunately, the distribution and abundance of benthic infauna has been inadequately quantified at most of the staging areas identified in our study including the western Bering Strait, Yukon-Kuskokwim Delta, East Siberian Sea, and Norton Sound. Therefore prey availability is unknown at most sites used by pre-breeding Spectacled Eiders.

Energy development and ongoing concerns regarding the effects of climate change on marine ecosystems in the Arctic have prompted extensive assessment of benthic infaunal biomass at staging areas in the eastern Chukchi and western Beaufort seas. A synthesis of data collected in the eastern Chukchi Sea from 1971 to 1995 estimated benthic biomass within the area used by Spectacled Eiders to range between 47 and 220 g m⁻² (Dunton et al. 2005), although considerable variation has been detected among studies. Feder et al. (1994a) estimated that mean infaunal biomass ranged between 43 and 70 g m⁻², although Grebmeier et al. (2006a) estimated mean infaunal biomass ranged between 200 and 400 g m⁻², and Schonberg et al. (2014) estimated mean infaunal biomass as high as 645 g m⁻² in the Chukchi Sea. Within the eastern Chukchi Sea staging area, dominant benthic taxa appear to include echinoderms (primarily sand dollars, Clypeasteroidea), barnacles (Cirripedia), amphipods, and bivalve molluscs (Bivalvia), although these taxa appear to be disproportionally dispersed (Feder et al. 1994b, Grebmeier et al. 2006a, Schonberg et al. 2014). Therefore, the results of large-scale surveys have not adequately captured the distribution and abundance of prey in areas of the eastern Chukchi Sea specifically used by Spectacled Eiders and other sea ducks. Dunton et al. (2005) also synthesized data in the western Beaufort Sea where infaunal biomass within the area used by Spectacled Eiders ranged between 50 and 100 g m⁻², with the greatest biomass detected offshore of the Colville River Delta. In comparison, Grebmeier et al. (2006a) estimated mean infaunal biomass in this region to be < 200 g m⁻², although Carey (1991) estimated mean biomass to be 77 g m⁻² and attributed lower values to active ice scouring at shallower depths. Polychaete worms appear to dominate benthic infaunal communities in the nearshore Beaufort Sea (Carey 1978). However, the short duration during which the Beaufort Sea is used by King and Spectacled eiders during pre-breeding migration (Phillips et al. 2007) and evidence that King Eiders may use a terrestrial source of nutrients for egg production (Oppel et al. 2010) suggest that western Beaufort Sea benthos are not an important source of nutrients prior to breeding.

Although our description of the pre-breeding spatiotemporal distribution of Spectacled Eiders is the most comprehensive to date, implications of these patterns have yet to be assessed. If Spectacled Eiders initiate migration in response to environmental cues (e.g., sea ice and temperature), which cues are most influential and how might these change under projections of future climate change? Consequently, what outcomes (e.g., resultant shift in pre-breeding spatiotemporal distribution) may be important to the recovery and conservation of Spectacled Eiders? We demonstrated that Spectacled Eiders exhibit fidelity to staging areas that are connected to specific breeding areas. Therefore, change in conditions at any one of the areas used during pre-breeding migration could have significant implications for one or more breeding populations (Oppel et al. 2009). However, habitat parameters such as prey, predator, and competitor abundance at areas used throughout pre-breeding migration have not been adequately assessed, making it difficult to determine the importance and sensitivity of these sites beyond spatiotemporal use. Without continued assessment of the spatiotemporal distribution of Spectacled Eiders and habitats used during pre-breeding migration, consequences of habitat change will likely be realized as a function of the timing of arrival to breeding areas, reproductive success, annual recruitment, individual survival, and ultimately variation in population demographics.

5.3. Breeding

Listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1993) prompted an increase in research attention at terrestrial breeding areas where causes for the population decline were initially thought to have originated. Research has focused on the breeding and terrestrial feeding ecology of the species, habitat use, variability in the demographics of breeding populations, and identification of threats at breeding areas (e.g., Franson et al. 1995, Flint and Grand 1997, Grand and Flint 1997, Petersen et al. 2000). In addition to focused studies, annual aerial and ground-based surveys provide indices of breeding population size in northern and western Alaska (Julian Fischer, U. S. Fish and Wildlife Service pers. comm.). Our results provided further insight into breeding site fidelity, connectivity between areas used during pre-breeding migration, breeding, and post-breeding migration, and the phenology of Spectacled Eiders that presumably attempted to breed. We assumed that satellite telemetry locations occurring on land within the breeding season (May through September; Petersen et al. 2000) were associated with breeding activities (e.g., nest site selection, nest initiation and guarding, incubation, and brood rearing). However, we could not distinguish breeding from other activities that Spectacled Eiders may exhibit on land.

Four out of seven important areas were used during the breeding season. Consistent with the northern Alaska breeding range, Spectacled Eiders used terrestrial areas of the eastern Chukchi Sea and western Beaufort Sea areas. Likewise, Spectacled Eiders used terrestrial areas of the East Siberian Sea and Yukon-Kuskokwim Delta areas, consistent with breeding ranges in western Alaska and northern Russia, respectively.

The timing of Spectacled Eider breeding activity during our study was consistent with observations by Bart and Earnst (2005) in northern Alaska and studies summarized by Petersen et al. (2000). The breeding phenology of Spectacled Eiders was also consistent with that of other sea duck species that breed in northern and western Alaska, and northern Russia. Adult Spectacled Eiders arrived on land in the Yukon-Kuskokwim Delta in mid- to late May, whereas Spectacled Eiders arrived on land at northern breeding areas (i.e., East Siberian Sea, eastern Chukchi Sea, and western Beaufort Sea) in late May through mid-June. Overall, adult males remained on land for 7–33 days, moving offshore in June and July. Adult females remained on land for 26–112 days, departing as early as July and as late as September. Juveniles captured as pre-fledging ducklings in northern Alaska remained on land through September.

Comparatively, Common Eiders initiated nests in the Yukon-Kuskokwim Delta in May through early June, suggesting arrival in early to late May (Wilson et al. 2012), and King and Common eiders generally arrive in northern Alaska in early June (Petersen 2009, Opper and Powell 2010). Like Spectacled Eiders, male King and Common eiders depart breeding areas within the first week of nest incubation, whereas the timing of female departure depends on breeding success (Goudie et al. 2000, Powell and Suydam 2012). Females that successfully raise a brood to fledge are expected to remain at terrestrial breeding areas with ducklings through September, whereas unsuccessful females may move to marine areas at any time after failing to reproduce (Petersen et al. 2000). Interannual variability in breeding phenology has been attributed to the timing of pre-breeding migration, snow and ice melt at breeding areas, and the condition of breeding adults (Dau 1976b, Grand and Flint 1997, Pearce et al. 1998).

Among seasonally monogamous waterfowl species, adult females exhibit greater fidelity to breeding areas than males (Rohwer and Anderson 1988, Anderson et al. 1992). Among *Somateria* eiders, female-biased fidelity (i.e., apparent absence of fidelity among males) has been attributed to the propensity for males to follow philopatric females during spring migration (Rohwer and Anderson 1988, Bustnes and Erikstad 1993, Phillips and Powell 2006). Consistent with theory, we found complete breeding site fidelity among adult female Spectacled Eiders in our study. Furthermore, we detected fine-scale interannual fidelity to specific nest sites. Among females captured on nests, most locations that occurred on-land in the following year (98.1%, $n = 302/308$) were located within 10 km of an individual's initial nest site. One female used areas within 5 km of its initial nest site in two consecutive breeding seasons. Of note, we recaptured two adult females on nests in 2008 in the Yukon-Kuskokwim Delta; both females were initially captured in 1997 on nests located within 500 m of their 2008 nest sites. In contrast, only six out of 19 males demonstrated breeding site fidelity; most migrated to breeding areas in northern Russia in subsequent years, which is also consistent with behaviors exhibited by male King Eiders (Phillips and Powell 2006). Over 95% of the world population of Spectacled Eiders breeds in northern Russia. Therefore, if pair formation occurs at the wintering area where breeding populations are mixed, we expect that males are more likely to pair with a female that demonstrates fidelity to breeding sites in northern Russia.

Anderson et al. (1992) proposed three hypotheses regarding the evolution of breeding site fidelity among waterfowl. First, female Spectacled Eiders may realize ecological advantages by returning to breeding areas with predictably suitable nesting habitat (e.g., food resources, concealment from predators). Nest site suitability is especially important to females because of the high energetic cost of reproduction (e.g., egg production, fasting during incubation) and susceptibility to predators during incubation and brood rearing. By returning to breeding areas where breeding success was realized in the past, females may maximize the likelihood of securing resources without expending energy to search for alternative breeding sites. However, female fidelity to breeding areas may prompt population declines if fidelity persists when the suitability of breeding habitats deteriorate (e.g., increasing predator density). Male Spectacled Eiders do not tend nests or broods and generally leave breeding sites after nest initiation (Petersen et al. 2000). Therefore, female-biased fidelity among Spectacled Eiders may be a consequence of the species' breeding ecology, specifically female-biased parental investment and resource needs.

Second, fidelity to breeding sites may persist as long as demographic processes allow an individual to occupy the same breeding area in subsequent years. Dispersal is unlikely to occur when individuals do not compete for optimal habitat or mates. Spectacled Eiders are considered semi-colonial breeders as nests are generally clustered rather than randomly distributed across suitable habitat (Petersen et al. 2000, Bart and Earnst 2005). Suitable habitat is not limiting throughout the species' breeding range and solitary nests are also common, although Spectacled Eiders are not territorial (Petersen et al 2000). Therefore, intraspecific competition does not appear to limit access to preferred nest sites. Spectacled Eiders share nesting habitat with several species including other waterfowl, gulls and terns (Laridae), and jaegers (Stercorariidae) (Petersen et al. 2000, Bart and Earnst 2005). Interspecific competition for nest sites appears to be minimal as well, as species initiate nests at different times and use different resources (Mickelson 1975). Eiders that nest among heterospecifics may in fact benefit from the agonistic behavior of other species, realized as hazing of potential predators (Ahlén and Andersson 1970,

Kellett and Alisauskas 1997). Spectacled Eiders appear to arrive at breeding sites having already formed pair bonds. Therefore mate competition is unlikely to occur at breeding areas, further limiting the effect of demographic processes on breeding site fidelity of females.

Third, sex-biased breeding site fidelity may also result from genetic processes such as inbreeding avoidance or kin selection. Inbreeding causes substantial loss of genetic diversity and retention of deleterious traits which may result in depressed fitness (e.g., inability to breed or depressed survival of offspring, Allendorf et al. 2013). Spectacled Eiders appear to form pair bonds during winter when non-breeding aggregations presumably consist of females that demonstrate fidelity to each of three primary breeding areas (Lovvorn et al. 2012). Pair formation appears to be random as evidenced by interannual variability in the spring dispersal of adult males during our study. Genetic evidence also supports the hypothesis that Spectacled Eider pair formation is a random process (Scribner et al. 2001). Among waterfowl, there is no evidence to reject or support the hypothesis that random mating (i.e., male-mediated gene flow) evolved as a mechanism to avoid inbreeding (Anderson et al. 1992). Therefore we propose that inbreeding avoidance among Spectacled Eiders is a bi-product of the species' ecology; females annually select a mate from a global pool of potential mates at the wintering area. Although behaviors involved with courtship and mate selection among Spectacled Eiders have not been studied, it is unlikely that females recognize male kin among thousands of potential mates at the wintering area, thereby further avoiding inbreeding.

Natal site fidelity (or philopatry) among female Spectacled Eiders may have also evolved as a product of selectively nesting near relatives. Kin selection is an evolutionary strategy through which individuals indirectly improve fitness by supporting the reproductive success of relatives (Clutton-Brock 2002). Selectively nesting near kin may improve an individual's ability to defend a nest site, provide opportunities to parasitize the nest of a relative that is in better condition or more vigilant during incubation, or provide opportunities for shared brood rearing (Waldeck et al. 2007, Tiedemann et al. 2011). Relatedness among nesting Spectacled Eiders has not been studied, although female Common Eiders appear to selectively nest in kin groups, and females on neighboring nests are more genetically related than females that are dispersed (McKinnon et al. 2006, Sonsthagen et al. 2010). If kin selection conveys reproductive benefits, female philopatry increases the likelihood that female relatives will be encountered at the breeding area. Female Spectacled Eiders do not appear to compete for resources at breeding areas nor demonstrate agonistic behavior (Petersen et al. 2000). Therefore, we would expect unrelated females to realize the same benefits as kin if forming nesting or brood rearing coalitions (Öst et al. 2005). Furthermore, the occurrence of kin recognition among Spectacled Eiders is unknown, although discriminating kin from non-kin is theoretically necessary for Spectacled Eiders to selectively associate with relatives (Hamilton 1964). Alternatively, Hamilton (1964) proposed that kin selection may evolve in a population that does not disperse, thereby maintaining genetic relatedness among members. In this respect, we propose that related female Spectacled Eiders may unintentionally associate because of fine-scale philopatric tendencies and related reproductive benefits influenced by other mechanisms (e.g., site familiarity, prior success, learned migratory patterns).

Due in part to long term mark-recapture and telemetry studies, it is well understood that the breeding success and demography of migratory birds is predicated by individual response to

environmental conditions in previous seasons (Webster et al. 2002, Norris and Marra 2007). In our study, we detected strong pre-breeding migratory connectivity to each of three primary breeding areas. Of note, the western Bering Strait was used by male and female Spectacled Eiders returning to each breeding area, although not exclusively. Pre-breeding, most adults used the eastern Chukchi Sea before they arrived at terrestrial areas in northern Alaska; Opper et al. (2009) detected the same pattern among King Eiders. Therefore, demographic change within a breeding population of Spectacled Eiders may be linked to habitat change at specific sites used during pre-breeding migration.

Female Spectacled Eiders demonstrate strong fidelity to breeding areas; whereas males may disperse to a different breeding area in alternate years. Female fidelity presumably confers reproductive benefits, realized through annual return to predictably suitable habitats. However, female return and reproductive success may be linked to conditions encountered in previous seasons (e.g., winter and pre-breeding migration). Spectacled Eiders demonstrated strong pre-breeding migratory connectivity among the important areas identified in our study. Therefore, variability in breeding population demographics may be a product of habitat change or stochastic processes at areas used during pre-breeding migration.

5.4. Post-breeding Migration

Following the breeding season, Spectacled Eiders undergo molt migration to marine areas where individuals are flightless for approximately 3–4 weeks (Petersen et al. 2000). Satellite telemetry data collected by Petersen et al. (1999) provided the first comprehensive assessment of the post-breeding movement of adult Spectacled Eiders and found concentrated use of molting areas between the Indigirka and Kolyma river deltas in the East Siberian Sea, Ledyard Bay in the eastern Chukchi Sea, Mechigmenskiy Bay in the western Bering Strait, and eastern Norton Sound. Each of these areas coincided with important areas identified in our study, and our sample of Spectacled Eiders did not use any new areas, which suggests that the post-breeding distribution of Spectacled Eiders has not changed significantly in the past 20 years. Persistent use of regional molting areas also suggests that underlying environmental conditions (e.g., benthic prey availability) have not changed, which may otherwise preclude contemporary use. However, historical and contemporary environmental data is lacking throughout the post-breeding distribution of Spectacled Eiders making it difficult to assess fine-scale changes (e.g., shift in prey distribution) and potential impacts on the species.

Unlike pre-breeding migration, we detected substantial variability in the timing of adult arrival and duration of use of important areas during post-breeding migration. Adult Spectacled Eiders arrived in the East Siberian Sea, eastern Chukchi Sea, western Bering Strait, and Norton Sound in June through October. Males depart breeding areas after females initiate nests (Petersen et al. 2000), and therefore arrived at post-breeding areas as early as three months before females. The timing of female departure from breeding areas is dependent on breeding success (see Section 5.3. Breeding). Unsuccessful females initiated post-breeding migration as early as June, while females that successfully raised a brood to fledge arrived at molting areas in September and October. Adult Spectacled Eiders remained at post-breeding areas through October, when they departed for the northern Bering Sea. Our findings were consistent with Petersen et al. (1999) who found that male Spectacled Eiders arrived at molting areas in July, unsuccessful breeding females arrived in July through August, females with broods arrived in September, and all individuals remained at molting areas through October.

Our study was the first to characterize the post-fledging migratory movement of juvenile Spectacled Eiders from northern Alaska. Adult females and their offspring moved offshore in early September, although adults departed the western Beaufort Sea 1–2 weeks prior to their offspring. In contrast, Regehr et al. (2001) found that adult female Harlequin Ducks (*Histrionicus histrionicus*) migrated to wintering areas with their broods. Juvenile Spectacled Eiders departed the western Beaufort Sea in late September through early October, and most arrived in the eastern Chukchi Sea in early to mid-October. Juveniles remained in the eastern Chukchi Sea for at most four weeks. Juveniles also used the western Bering Strait where at least one individual remained until late November. We detected considerable variability in migratory movement after juveniles departed the western Beaufort Sea. Juvenile locations were widespread and ranged as far south as the Alaska Peninsula, whereas adults demonstrated direct movements between important areas and migrated no further south than the northern Bering Sea. Similarly, Pearce and Petersen (2009) observed broad dispersal among juvenile Common Mergansers (*Mergus merganser*) following departure from natal areas in south-central Alaska. Likewise, Swennen (1990) observed broad dispersal among juvenile Common Eiders after departing natal areas in The Netherlands. Among many bird species, the post-fledging dispersal

of juveniles can be described as wandering or exploratory as movement appears to be random and indirect (Newton 2008). *Somateria* eiders generally migrate in cohesive flocks. Therefore, juvenile Spectacled Eiders that deviated from the migratory patterns of adults may have joined flocks of other sea duck species including King, Common, or Steller's eiders that demonstrate a much broader non-breeding distribution.

Important areas used during pre-breeding migration were also used during post-breeding migration, suggesting that these sites offer sufficient resources to support Spectacled Eiders through two seasonal migrations and critical phases of the annual cycle, including pre-breeding fat accumulation and post-breeding feather growth (see section 5.2. Pre-breeding Migration). As observed during pre-breeding migration, Spectacled Eiders appeared to use direct over-water routes or follow coast lines during post-breeding migration, and moved from one area to another within one transmitter duty cycle (4–7 days). Molting areas in the East Siberian Sea, eastern Chukchi Sea, and western Bering Strait were located on direct routes between breeding areas in northern Alaska or Russia and the northern Bering Sea, although not all of the Spectacled Eiders in our study followed direct routes from breeding to wintering areas. Furthermore, we noted differences in migratory routes between sexes originating from each breeding area. For example, among females departing western Alaska, 45 of 46 migrated to Norton Sound to molt. In contrast, only three of 19 males migrated to Norton Sound; most migrated to the western Bering Strait or East Siberian Sea. Similarly, all 33 females that departed breeding areas on the western Beaufort Sea coast migrated to the eastern Chukchi Sea to molt. In contrast, males migrated to the eastern Chukchi Sea, East Siberian Sea, or western Bering Strait.

Sex-biased movement among migratory animals is generally attributed to an evolved mechanism to avoid inbreeding or competition for mates and resources during the breeding season (Pusey 1987). However, few studies have investigated sex-biased movement during post-breeding migration. Phillips and Powell (2006) and Knoche et al. (2007) found that King Eiders exhibited strong molt site fidelity in consecutive years, regardless of the breeding areas used in each year. Post-breeding site fidelity has also been observed among Harlequin Ducks (Breault and Savard 1999, Iverson and Esler 2006) and Steller's Eiders (Flint et al. 2000b). We found a similar pattern among Spectacled Eiders; males and females exhibited strong interannual fidelity to important areas during post-breeding migration. Spectacled Eiders may realize ecological benefits by returning to post-breeding areas where known environmental conditions or cohesion with conspecifics favor survival (Newton 2008). However, fidelity could be disadvantageous if it results in greater migratory distances and therefore energetic expense to reach molting areas and ultimately the northern Bering Sea wintering area. For example, males that departed the Yukon-Kuskokwim Delta to molt in the East Siberian Sea migrated approximately 3,800 km before reaching the northern Bering Sea, whereas Spectacled Eiders molting in Norton Sound migrated approximately 900 km to the wintering area. Likewise, males departing the western Beaufort Sea to molt in the East Siberian Sea migrated approximately 3,900 km before reaching the wintering area, whereas Spectacled Eiders molting in the eastern Chukchi Sea migrated approximately 1,400 km. In theory, these patterns must have originated as a result of realized advantages although underlying mechanisms remain unknown.

Migratory strategies may be influenced by several interacting factors including inherent or learned behaviors, environmental conditions, social cohesion, prey availability, or physical condition (see section 5.2. Pre-breeding Migration, Newton 2008). Specific to spatiotemporal

patterns observed during our study, we propose two hypotheses to explain different strategies of post-breeding migration among male and female Spectacled Eiders. First, migratory birds that care for young depart breeding areas later and in poorer physical condition than birds without parental responsibilities (Newton 2008). Therefore, we presume that male Spectacled Eiders are afforded time and energetic reserves needed for long-distance migration. In contrast, females that remain at breeding areas to care for nests and young depart breeding areas in relatively poor physical condition and experience a shorter post-breeding season, thus requiring shorter migratory distances to reach post-breeding areas and successfully molt before winter. In our study, male Spectacled Eiders departed breeding areas as early as three months before females, and average male body mass in spring was 1518 ± 133 g ($n = 32$), whereas average female body mass during late brood rearing was 1120 ± 57 g ($n = 15$). If males departed breeding areas immediately after nest initiation, they would have migrated in better physical condition than females that departed after brood rearing. In this respect, the breeding ecology of Spectacled Eiders favors post-breeding migratory strategies in which males are capable of migrating longer distances to presumably better post-breeding habitats, whereas females may be constrained to migrate shorter distances to the nearest post-breeding area. However, the relative quality of habitat (e.g., benthic prey availability) at post-breeding areas is unknown. Furthermore, the ecology of Spectacled Eiders at each molting area has not been studied. Therefore, it remains unknown if males that migrate greater distances benefit by molting in areas with more abundant, nutrient rich, or easily accessed prey than at other molting sites.

Second, Spectacled Eiders may exhibit fidelity to the post-breeding areas they used as ducklings. During our study, juvenile Spectacled Eiders that fledged in northern Alaska migrated through the eastern Chukchi Sea and western Bering Strait at the same time as adults during post-breeding migration. If juveniles learn the location of post-breeding molting areas during their first migration, we propose that Spectacled Eiders may return to learned molting areas in subsequent years. Individual adherence to learned migratory strategies could have produced the patterns of post-breeding migratory connectivity and fidelity observed during our study. Female Spectacled Eiders that exhibited fidelity to northern and western Alaska breeding areas consistently molted in the eastern Chukchi Sea and Norton Sound, respectively. Regardless of breeding area, most of the males in our study migrated to the East Siberian Sea. Although the natal origin of adults in our study is unknown, over 95% of the world population of Spectacled Eiders breeds in northern Russia. Therefore, we propose that most of the adult males marked during our study initially fledged in northern Russia, possibly followed adults to adjacent post-breeding areas in the East Siberian Sea, and therefore return to the East Siberian Sea to molt regardless of where they subsequently bred. In contrast, female Spectacled Eiders demonstrate strong philopatry and return to natal areas to breed as adults (Petersen et al. 2000). Therefore, we propose that the post-breeding movement of adult females also replicates post-fledging dispersal from natal areas. Although molt site fidelity among sea ducks is common, the foundations of this behavior relative to natal dispersal have yet to be investigated.

The post-breeding spatiotemporal distribution of Spectacled Eiders was similar to patterns exhibited by other Beringian sea duck species, although we also found considerable differences among species in the location of molting areas. King Eiders depart breeding areas in northern Alaska and stage in the western Beaufort Sea before continuing post-breeding migration through the eastern Chukchi Sea to the western Bering Strait, Kamchatka Peninsula, or northern Bering Sea (Phillips and Powell 2006, Knoche et al. 2007, Phillips et al. 2007, Oppel et al. 2008, Oppel

et al. 2009). King Eiders do not appear to molt in the eastern Chukchi Sea as observed among Spectacled Eiders (Petersen et al. 1999, Opper et al. 2009). Similar to Spectacled Eiders, male King Eiders initiate post-breeding migration from northern Alaska in June, earlier than females, and King Eiders complete molt by late October (Phillips et al. 2006, Opper et al. 2008). In contrast, Petersen and Flint (2002) found that Common Eiders that breed in northern and western Alaska molt directly offshore of breeding areas through October. Unlike Spectacled Eiders, Common Eiders from each breeding area remained allopatric through post-breeding migration and used separate wintering areas. Steller's Eiders depart breeding areas in northern Alaska and Russia and migrate through the Bering Strait en route to molting areas on the north side of the Alaska Peninsula (Petersen 1981, Flint et al. 2000b, Philip Martin, U. S. Fish and Wildlife Service pers. comm.). Similar to King and Common eiders, Steller's Eiders appear to pass through the eastern Chukchi Sea and western Bering Strait, although Steller's Eiders do not use these areas to molt (Philip Martin, U. S. Fish and Wildlife Service pers. comm.). Long-tailed Ducks that breed in the Yukon-Kuskokwim Delta remain to molt, or undertake molt migration to the western Bering Strait or St. Lawrence Island in July where they remain through September (Petersen et al. 2003). Unlike Spectacled Eiders, Long-tailed Ducks from the Yukon-Kuskokwim Delta did not molt in Norton Sound or the East Siberian Sea. Long-tailed Ducks from breeding areas in northern Alaska molt along barrier islands in the near-shore Beaufort Sea (Howell et al. 2003, Flint et al. 2004). Causal mechanisms of disparate post-breeding migratory patterns may echo mechanisms that potentially explain spatiotemporal differences among species during winter (see section 5.1. Winter). In this respect, differences in evolutionary history (e.g., competition, use of glacial refugia) or finite differences in species-specific habitat requirements (e.g., prey, water depth) may be contributing factors.

The post-breeding distribution of Spectacled Eiders echoed pre-breeding distribution, reinforcing the importance of important areas used during both migratory periods. Specifically, the East Siberian Sea, eastern Chukchi Sea, western Bering Strait, and Norton Sound important areas appear to be positioned along critical migratory corridors linked to each of three breeding areas. Spectacled Eiders appear to have consistently used the same post-breeding areas for the past 20 years, although local changes in habitat characteristics and implications for Spectacled Eider recovery and conservation remain unknown. We observed patterns of sex-biased post-breeding dispersal among adults. Males migrated greater distances to molt and ultimately reach the wintering area in the northern Bering Sea, whereas females followed more direct migratory routes. Juveniles exhibited broad dispersal after departing natal areas in northern Alaska.

5.5. Management Implications

Spectacled Eiders exhibited strong migratory connectivity and site fidelity throughout the annual cycle. These patterns create spatiotemporal bottlenecks; instances where a considerable proportion of a breeding population or the global population seasonally masses in an important area (Iwamura et al. 2013). Stochastic weather events or anthropogenic disturbance within important areas may negatively affect a breeding population or the global population, with outcomes resonating throughout the annual cycle as carry-over effects (Oppel et al. 2009). The potential for Spectacled Eiders to adapt to these disturbances is unknown.

Marine habitat at areas important to Spectacled Eiders may also change in response to climate. Specifically, short- and long-term climate-driven change in benthic communities and sea ice are likely to influence spatiotemporal distribution and population demographics (Lovvorn et al. 2009, 2014). North American sea duck populations appear to fluctuate in response to oceanic regime shifts which characterize abrupt and relatively short-term climate-driven changes in marine ecosystems (Overland et al. 2008, Biggs et al. 2009, Flint 2013). Long-term climate change has also been linked to changes in community composition and sea ice dynamics in the northern Bering Sea (Grebmeier et al. 2006b).

If Spectacled Eiders maintain fidelity to areas subject to stochastic disturbance or undergo long-term habitat change, managers should expect concurrent change in population status. If Spectacled Eiders respond to habitat change by exploiting new areas or changing migratory patterns, managers should also be prepared to redefine the spatiotemporal distribution of the species and reassess implications for management.

5.6. Considerations for Future Research

Our study did not capture spatiotemporal information from several groups including adult males and females known to breed in northern Russia and juveniles that fledged in western Alaska and northern Russia. Our description of the spatiotemporal distribution of Spectacled Eiders would be improved by supplementing our dataset with information from these strata. Furthermore, our ability to characterize the spatiotemporal distribution of juveniles that fledged in northern Alaska was affected by a high rate of post-release mortality and only one juvenile had a transmitter that provided data after this individual's first winter. Similarly high mortality rates were observed among juvenile Common Mergansers during their first winter (Pearce and Petersen 2009) and over winter survival in sea ducks is thought to be lower in juveniles than adults (Pearce et al., 2005, Esler and Iverson 2010). We could not determine the cause of mortality or transmitter failure within our sample, although future telemetry projects that use coelomically implanted transmitters may improve data collection by adopting processes intended to maximize the survival of marked birds (e.g., pre-screening candidates for surgery; Sexson et al. 2014).

Fidelity to nest sites or brood rearing areas produced a concentration of locations at each study site. Concentrated locations at each study site biased our delineation of important areas to include study sites, but exclude other terrestrial areas where Spectacled Eiders may occur. Therefore, the important areas identified during our study, especially those areas that include capture sites (i.e., western Beaufort Sea, eastern Chukchi Sea, and Yukon-Kuskokwim Delta), are specific to our sample of Spectacled Eiders. Future efforts to supplement or replicate our study should consider alternate study sites to capture spatiotemporal data from Spectacled Eiders originating from other breeding areas.

To assess the effect of habitat or climate change on the spatiotemporal distribution of Spectacled Eiders, additional data and analysis are needed to detect changes in spatiotemporal patterns and relate these changes to key environmental variables including the availability of benthic resources. The contemporary distribution and abundance of benthic infauna has not been quantified at most of the important areas identified in our study. Recurrent benthic sampling in marine areas used by Spectacled Eiders is needed to assess habitat use and change over time and will provide context to spatiotemporal patterns. Continued efforts to collect spatiotemporal data from Spectacled Eiders will allow detection of change in response to environmental conditions, as well as anthropogenic activities.

Spectacled Eiders demonstrated strong migratory connectivity. Due to carry-over effects, changes in the status of breeding populations may reflect processes occurring during non-breeding seasons. Therefore, in lieu of additional telemetry or benthic sampling, continued efforts to monitor Spectacled Eider breeding population sizes and reproductive potential are critical to indirectly detect the effects of habitat change away from breeding areas.

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under US administration.



The Bureau of Ocean Energy Management

As a bureau of the Department of the Interior, the Bureau of Ocean Energy (BOEM) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS) in an environmentally sound and safe manner.

The BOEM Environmental Studies Program

The mission of the Environmental Studies Program (ESP) is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments.