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LARGE-SCALE MOVEMENTS AND HABITAT CHARACTERISTICS OF KING EIDERS THROUGHOUT THE NONBREEDING PERIOD

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Abstract. King Eiders (*Somateria spectabilis*) breeding in western Canada and Alaska molt wing feathers and spend the winter in remote areas of the Bering Sea, precluding direct observation. To characterize timing of migration and habitat used by King Eiders during the nonbreeding period, we collected location data for 60 individuals (27 females and 33 males) over three years from satellite telemetry and utilized oceanographic information obtained by remote sensing. Male King Eiders dispersed from breeding areas, arrived at wing molt sites, and dispersed from wing molt sites earlier than females in all years. Males arriving earlier at wing molt sites molted flight feathers at higher latitudes. Distributions of molt and winter locations did not differ by sex or among years. Of the variables considered for analysis, distance to shore, water depth, and salinity appeared to best describe King Eider habitat throughout the nonbreeding period. King Eiders were located closer to shore, in shallower water with lower salinity than random locations. During the winter, lower ice concentrations were also associated with King Eider locations. This study provides some of the first large-scale descriptions of King Eider migration and habitat outside the breeding season.

Key words: distribution, habitat, migration, satellite telemetry, Somateria spectabilis, *wing molt, wintering.*

Movimientos a Gran Escala y Características del Hábitat de *Somateria spectabilis* en el Período No Reproductivo

Resumen. Los individuos de la especie *Somateria spectabilis* que crían en el oeste de Canadá y Alaska mudan las plumas de las alas y pasan el invierno en áreas remotas del Mar de Beiring, lo que hace imposible realizar observaciones directas. Para caracterizar el momento en que tiene lugar la migración y el uso de hábitat por parte de estas aves durante el período no reproductivo, obtuvimos datos sobre la ubicación de 60 individuos (27 hembras y 33 machos) a lo largo de tres años empleando telemetría satelital e información oceanográfica obtenida mediante sensores remotos. En todos los años, los machos se dispersaron desde las áreas de cría, llegaron a los sitios de muda de las plumas y se dispersaron desde estos sitios más temprano que las hembras. Los machos que llegaron más temprano a los sitios de muda de las alas mudaron sus plumas de vuelo en lugares ubicados a mayores latitudes. Las distribuciones de los datos de ubicación obtenidos en los sitios de muda e invernada no difirieron entre sexos ni entre años. De las variables consideradas en los análisis, la distancia a la costa, la profundidad del agua y la salinidad parecieron describir mejor el hábitat de *S. spectabilis* a lo largo del período no reproductivo. Las aves se ubicaron más cerca de la playa, y en aguas menos profundas y con menor salinidad que las de sitios seleccionados al azar. Durante el invierno, las menores concentraciones de hielo también se asociaron con la ubicación de *S. spectabilis*. Este estudio provee algunas de las primeras descripciones a gran escala de la migración y el hábitat de *S. spectabilis* por fuera del período reproductivo.

INTRODUCTION

Eider species spend most of their annual cycle in remote, inaccessible marine habitats, precluding direct observation and contributing to an incomplete understanding of their life histories (Petersen et al. 2000, 2006, Suydam 2000). They generally perform a distinct post-breeding migration to marine areas, where they

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congregate in flocks and molt all flight feathers. Molting may be a risky activity because the period of flightlessness may increase vulnerability to disturbance, stochastic events such as oil spills, and predation, and regrowing flight feathers may increase energy demands (Salomonsen 1968, King 1974, Hohman et al. 1992, Frimer 1994a). Eiders then move to wintering areas that are characterized by short periods of daylight and extremes of weather, temperature, and ice cover (Systad et al. 2000, Petersen and Douglas 2004). They generally form pair bonds at wintering areas and migrate as pairs to breeding grounds in the spring (Anderson et al. 1992). The timing of these life-history events during the nonbreeding period may be linked to productivity on the breeding grounds (Heitemeyer and Fredrickson 1981, Hepp 1984, Dugger 1997), and may vary by age, sex, and habitat conditions (Heitemeyer 1988). Female eiders rely heavily on endogenous reserves for egg laying (Korschgen 1977, Kellet 1999); therefore, body condition upon arrival at breeding grounds can influence clutch size and reproductive potential (Ankney and MacInnes 1978, Raveling 1979). Habitat changes, extreme weather events, or disturbance at locations where eiders gain reserves during winter and spring migration could influence their survival as well as reproductive output (Barry 1968, Coulson 1999, Petersen and Douglas 2004). In long-lived species such as eiders (Petersen et al. 2000, Suydam 2000), female survival may be an important factor contributing to general population declines (Flint and Grand 1997, Grand et al. 1998). Over 40% of the annual mortality of Spectacled Eiders (*Somateria fischeri*) occurs outside the breeding season (Flint and Grand 1997, Grand et al. 1998, Flint, Grand et al. 2000). Concern regarding apparent population declines of all four eider species in recent decades (Kertell 1991, Stehn et al. 1993, Suydam et al. 2000) has led to increased interest in location and timing of migration, demarcation of wing molt and wintering areas, and habitat characterization of these sites (Sea Duck Joint Venture Management Board, unpubl. data; U.S. Fish and Wildlife Service, unpubl. data). Identification of locations of and length of stay at molt and winter areas is critical for assessing the potential impacts on eider populations of climate and food web changes in the Bering Sea and increased anthropogenic use such as oil development and hunting pressure (Frimer 1994a, Flint et al. 1999, Grebmeier et al 2006). Grebmeier et al. (2006) suggested that declines in benthic standing stocks in the Bering Sea are linked to global warming trends and that these changes will have profound impacts on diving seabird populations.

At-sea wing molt and wintering areas of King Eiders (*S. spectabilis*) breeding in Alaska and western Canada are thought to be in marine environments along the shores of the Bering Sea, especially along the Chukotsk Peninsula, south of St. Lawrence Island, and along the Alaska Peninsula and Aleutian Islands (Suydam 2000; D. Dickson et al., Canadian Wildlife Service, unpubl. data). Aerial observations in Alaska (W. Larned and T. Tiplady, U.S. Fish and Wildlife Service, unpubl. data) have thus far been limited to a few known molt locations near St. Lawrence Island and in Kvichak Bay and Kuskokwim Bay. D. Dickson et al. (unpubl. data) used satellite telemetry to identify wing molt areas, but transmitters did not last beyond midwinter. This is one of the first avian studies we know of that combines satellite telemetry and data obtained by remote sensing to determine at-sea habitat use, and the first study of King Eider habitat use in the Bering Sea.

In 2002 and 2003, we obtained location data for 33 King Eiders during the entire annual cycle. Additionally, we collected wing molt location information for 27 eiders in 2004. Thus, we can describe the movements and habitat characteristics of areas used by this sample of King Eiders throughout the entire nonbreeding period. Our objectives were to: (1) determine temporal variation in molt and winter migration, (2) relate timing of individual movements to distance traveled, latitude of wing molt and wintering areas, and time spent at wing molt sites, (3) determine spatial variation of wing molt and wintering locations by sex and among years, and (4) describe oceanographic and physical characteristics of wing molt and wintering areas.

METHODS

STUDY SITES

Capture locations. We trapped King Eiders in Alaska at Kuparuk (70°20′N, 149°45′W) in early to mid-June of 2002–2004 and on

Teshekpuk Lake (70°26′N, 153°08′W) in 2004 only. The Kuparuk study site was located between the Colville and Kuparuk Rivers, and the Teshekpuk Lake study site was located about 80 km west of the Kuparuk study area and 10 km inland from the southeastern shore of Teshekpuk Lake.

Wing molt and winter locations. During the postbreeding period (late June through mid-September), Alaskan-breeding King Eiders generally move into the Bering Sea. The Bering Sea has a large, shallow, gently sloping coastal shelf that is less than 200 m deep and encompasses almost half the sea's total area. This shelf is broad (>500 km) in the northeast along the Alaskan coast and narrow (<100 km) in the southwest along the Siberian coast (Hood and Kelley 1974).

In winter, the Bering Sea is characterized by high winds, frequent storms, and complete ice cover over its shallow continental shelf region (Niebauer et al. 1999). The seasonal ice pack persists for six to eight months each year and generally reaches its maximum southern extent by March or April (Fay 1974). Major polynyas occur downwind of the Chukchi Peninsula, St. Lawrence Island, St. Matthew Island, and the Seward Peninsula (Stringer and Groves 1991). The amount of available daylight in the Bering Sea decreases to between four and six hours in late December and early January.

The Bering Sea is unusually productive for a body of water at high latitude. A number of mechanisms are thought to support this high productivity, including the broad shallow coastal shelf, the extensive seasonal ice coverage, and the convergence of current systems rich in nutrients (Walsh et al. 1989, Springer and McRoy 1993). The high density of benthic invertebrates in the Bering Sea is thought to be linked to its high primary productivity (Grebmeier 1993). King Eiders probably forage on benthic and epibenthic invertebrates while in marine systems (Frimer 1997, Suydam 2000).

LOCATION OF WING MOLT AND WINTERING AREAS

We obtained locations of King Eiders throughout the nonbreeding period using implantable satellite transmitters. King Eiders were captured on breeding grounds in early to mid-June using mist net arrays and decoys. Once captured, eiders were placed in a secure, dark kennel and transported to a nearby indoor facility or tent equipped for surgery. A 35 g satellite platform transmitting terminal (PTT) transmitter (Microwave Telemetry, Inc., Columbia, Maryland) was surgically implanted into the abdominal cavity of each eider following the techniques of Korschgen et al. (1996), using isofluorane as an anesthetic. Satellite transmitters were <3% of the average body mass of birds used in this study. Eiders were fitted with a U.S. Fish and Wildlife Service band. When birds were fully awake and recovered from anesthesia (usually after about two to three hours), we released them at their respective capture sites. At Kuparuk, transmitters were implanted into 21 King Eiders (10 female, 11 male) in 2002, 12 (3 female, 9 male) in 2003, and 15 (8 female, 7 male) in 2004. Twelve (5 female, 7 male) King Eiders were fitted with transmitters at Teshekpuk in 2004.

We programmed transmitters with four duty cycles. Transmitters were on and transmitting location information to satellites for six hours every (1) 48 hr from June through September, (2) 84 hr from October through December, (3) 168 hr from January through March, and (4) 84 hr from April until the end of the battery life. Satellite transmitters used in this study had an average lifespan of 385 ± 15 (SE) days (n = 33, range = 99–519 days). We received location data from Service Argos (2001). Location data were filtered for accuracy using PC-SAS Argos Filter v. 5.1 (D. Douglas, U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska). The filtering program removed implausible locations based on location redundancy and tracking paths. The best location per transmission period was used for our analyses based on location class and number of locations received. Location class is a rating provided by Argos for each location to give some indication of potential error associated with the data. Locations were plotted using ArcView GIS (ESRI 1998). Definitions used to categorize events for analyses throughout the annual cycle are given in Table 1.

HABITAT CHARACTERISTICS

We used randomly selected King Eider locations and computer-generated random locations to investigate habitat characteristics at wing molt and wintering areas. We randomly selected King Eider locations during the 2002–

TABLE 1. Definitions of King Eider nonbreeding life history events as defined by satellite telemetry locations.

	Definition
Migration	A set of sequential locations indicating movement in a single direction during which an individual remains in no one area ≥1 week (Petersen et al. 1999).
Wing molt migration	The migration period from the last day at the breeding area to the first day at the wing molt location.
Wing molt site	An area where an eider spent ≥3 weeks with lowest daily movement rates between June and December prior to movement toward wintering areas.
Fall migration	The migration period from the last day at the wing molt site to the first day at the farthest-south wintering location.
Wintering area	An area where an eider spent ≥1 week between the end of the wing molt period and spring migration; King Eiders may have multiple wintering areas.
Spring migration	The period of migration from the last day at a wintering area to the first day on land at a subsequent breeding location; if there were no onshore locations for an eider during the subsequent breeding period, the first location at a June offshore staging area was used.
Breeding area	An area onshore where an individual was located after spring migration and prior to fall migration.

2003 wing molt and wintering periods to account for autocorrelation among an individual's locations and the variation in the number of locations obtained per individual (2–47 molt locations per individual; 10–40 winter locations per individual). We randomly selected five locations per individual during wing molt (n = 155 locations) and ten locations during the wintering period (n = 290 locations) to create two subsets of eider locations for use in habitat analyses. We created 6500 random points along the coastlines of Alaska and Russia extending from the coast to 80 m water depth to represent habitat available to King Eiders outside the breeding season. Foraging depths for King Eiders in the Bering Sea have not been recorded; therefore, we chose 80 m as the cutoff point for available habitat based on diving depths recorded for Spectacled Eiders foraging in the Bering Sea (Petersen et al. 2000). The large number of random points generated along coastlines used by King Eiders in this study, including the Bering Sea, Kamchatka Peninsula, Alaska Peninsula, Kodiak Island, and Kenai Peninsula coastlines, was required to adequately represent the habitat of such a large geographic area. We created all random subsets using Random Point Generator 1.27 extension (Jennes 2003) in ArcView.

We chose habitat variables based on availability of data and relevance to potential King Eider distribution as suggested by published literature on sea duck wing molt and winter ecology (Guillemette et al. 1993, Frimer 1995, Bustnes and Lonne 1997, Esler et al. 2000, Petersen and Douglas 2004). We used nine variables as potential indices of food resources and chemical and physical properties available at possible wing molt and winter sites. We included phosphate (μM), nitrate (μM), chlorophyll (μg/l), and apparent oxygen utilization (ml/l) as indices of primary productivity; surface salinity (ppm) and temperature (°C) as possible representations of freshwater inputs, upwellings, or polynyas; and water depth (m), distance from shore (km), and ice cover as physical characteristics of habitat. Data for salinity, temperature, phosphate, nitrate, chlorophyll, and apparent oxygen utilization were obtained from World Ocean Atlas 2001 (Conkright et al. 2002) as point data with a spatial resolution of 2° latitude by 2° longitude. We used monthly averages of salinity and temperature values and annual averages of all other World Ocean Atlas 2001 variables. We acquired weekly percent ice cover data from the National Ice Center (2004). Bathymetric data were obtained from ETOP02, a point database with a 0.25° spatial resolution compiled by the National Oceanic and Atmospheric Administration from Smith and Sandwell (1997) and Jakobsson et al. (2001). The depth value nearest a random point or eider location was assigned as the bathymetric value for that point. Distance from shore was calculated using ArcView GIS as the shortest distance from a random point or eider location to a 1:250 000 polyline shapefile (Soluri and

Woodson 1990) of the Russian and Alaskan coastlines.

STATISTICAL ANALYSES

We used two-way ANOVA to test for differences by sex and year in the timing of migration to molting sites (molt migration), residence at wing molt sites, fall migration, and spring migration. Significant differences among years were further examined using Tukey multiple comparison procedures. We calculated migration distance as the distance between as many subsequent locations that passed filtering requirements as possible per individual and corrected for curvature of the earth. Latitude of wing molt and wintering sites was calculated as the centroid of minimum convex polygons (Hooge and Eichenlaub 1997) created in ArcView GIS using the Lambert Equal Area Azimuthal projection. We then explored relationships among timing of molt, fall, and spring migration with distance of molt migration, number of days spent at wing molt locations, and latitude of wing molt and winter locations using Spearman rank-order correlations.

Differences in distributions of King Eiders during the wing molt and winter periods were examined using multiresponse permutation procedures (MRPP) in BLOSSOM (Cade and Richards 2001). We used the centroid of the minimum convex polygon (Hooge and Eichenlaub 1997) of the wing molt area and farthest-south wintering area of each individual as the sampling unit and compared distributions by sex and among years.

We examined the characteristics of habitats occupied during wing molt and winter periods using logistic regression with *a priori* candidate model sets (18 models for molt locations, 28 models for wintering locations). The best model in each candidate set was determined using Akaike's information criterion (AIC; Burnham and Anderson 2002). We report coefficients of determination (r^2) for best approximating models to describe variation explained by the model.

We examined collinearity among all habitat variables to exclude highly correlated variables from the analyses. Phosphate, nitrate, chlorophyll, and apparent oxygen utilization were all highly correlated, as was chlorophyll with temperature. We chose to retain chlorophyll in the analyses as the variable best reflecting primary productivity (Lalli and Parsons 2002) and removed the remaining variables. We removed ice cover as a variable in the candidate model set for molt site habitat analyses because ice cover was essentially zero during this period. We included the interactions of ice cover and distance to shore, ice cover and water depth, and chlorophyll and salinity. In the wing molt analysis, we examined models containing each parameter (distance to shore, water depth, chlorophyll, salinity, and chlorophyll * salinity) and all possible combinations of these parameters, as well as the null model. In the wintering analysis, we examined models containing each parameter (distance to shore, water depth, chlorophyll, ice cover, salinity, ice cover * distance to shore, ice cover * water depth, and chlorophyll * salinity) and all possible combinations of these parameters, as well as the null model. Means are presented ± SE. All statistical analyses were performed using SAS version 8 (SAS Institute 1990).

RESULTS

VARIATION IN TIMING AND DISTRIBUTION

Wing molt migration. Mean dates of dispersal from breeding areas and arrival at wing molt sites differed by sex (dispersal from breeding: $F_{1,59} = 75.3$, $P < 0.001$; arrival at molt site: $F_{1,59} = 65.8$, $P < 0.001$) and among years (dispersal from breeding: $F_{2,59} = 7.2$, $P < 0.001$; arrival at molt site: $F_{2,59} = 3.9$, $P = 0.02$). Female eiders dispersed from breeding areas and arrived at wing molt sites later than males in all years (Fig. 1). Male and female King Eiders dispersed from breeding areas more than a week earlier on average in 2004 than in 2002 and arrived at wing molt sites earlier in 2004 than in 2002 or 2003 (Fig. 1). King Eiders that arrived at wing molt sites earlier flew shorter distances during molt migration ($r_s = 0.30$, $P = 0.02$; Fig. 2). Male King Eiders that arrived at wing molt sites earlier molted at higher latitudes ($r_s = 0.42$, $P = 0.01$).

Wing molt sites. Average number of days spent at wing molt areas varied by year ($F_{2,55} = 5.0$, $P = 0.01$), with eiders spending significantly more days at wing molt sites in 2003 (74 ± 4 days) than in either 2002 (57 ± 3 days) or 2004 (53 ± 2 days). Number of days spent at wing molt sites did not vary by sex ($F_{1,55} = 2.4$, $P = 0.13$). Females dispersed from wing molt

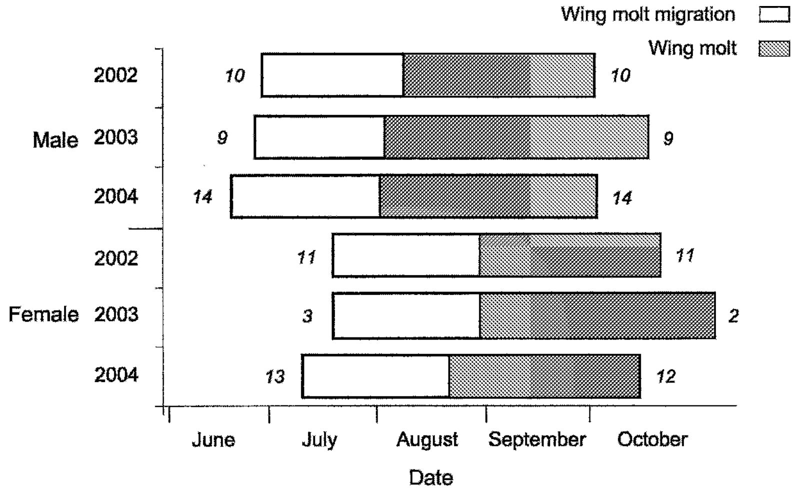

FIGURE 1. Mean number of days spent during wing molt migration and at wing molt sites for King Eiders marked at breeding sites in Alaska. Male and female King Eiders spent approximately the same amount of time on wing molt migration and at wing molt sites in 2002–2004, however males departed for wing molt sites, began wing molt, and departed for wintering sites earlier than females in all years. Sample sizes for the number of individual eiders used to calculate mean days of wing molt migration and duration at wing molt sites are represented by the italicized number before and after the bar graphs, respectively.

sites later than males ($F_{1,55}$ = 5.6, P = 0.02; Fig. 1). Dispersal date from wing molt sites did not vary by year ($F_{2,55}$ = 1.6, P = 0.22). During wing molt, King Eiders were located in marine areas along the Chukotsk Peninsula and St. Lawrence Island, as well as in Anadyr, Olyutor, Karagin, Bristol, and Kuskokwim Bays, the Beaufort Sea, and the coast of Russia near Khatyrka (Table 2, Fig. 3). Multiple response permutation procedures did not distinguish differences in distribution of wing molt locations by sex (P = 0.57) or year (P = 0.44).

Wintering areas. Eiders wintered along the Chukotsk, Kamchatka, and Alaska Peninsulas, Olyutor and Bristol Bays, and the Gulf of Alaska (Table 2, Fig. 4). Multiple response permutation procedures did not distinguish differences in distribution of winter locations by sex (P = 0.16) or year (P = 0.59).

Spring migration. Arrival date at breeding areas the following year did not vary by sex ($F_{1,18}$ = 1.6, P = 0.22) or year ($F_{2,18}$ = 0.0, P = 0.92); however, female King Eiders that wintered farther south arrived earlier at breeding locations the following summer (r_s = −0.85, P = 0.01). Male spring arrival date was not correlated with wintering latitude (r_s = −0.45, P = 0.14). The year * sex interaction term was not significant in all previous two-way ANOVAs (all $P > 0.10$).

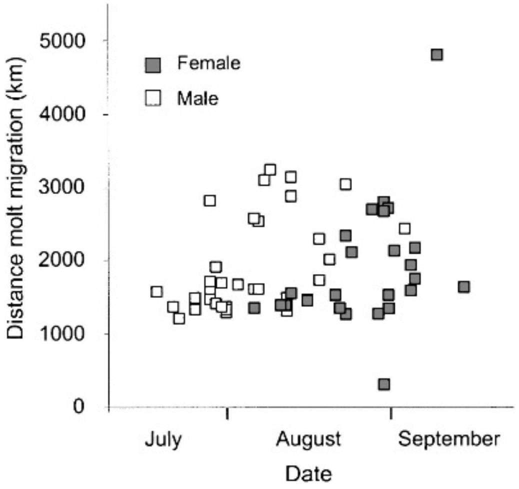

FIGURE 2. Correlation of date of arrival at wing molt sites with distance of wing molt migration for King Eiders marked at breeding sites in Alaska. Male and female King Eiders that arrived at wing molt sites earlier flew shorter distances during molt migration.

HABITAT CHARACTERISTICS

Wing molt sites. No one model best described habitat characteristics of King Eider locations

TABLE 2. Proportion of male and female King Eiders fitted with satellite transmitters on the North Slope of Alaska located in major wing molt and wintering areas in 2002–2004. Sample sizes (*n*, in parentheses) represent the number of marked eiders located during each season.

	2002		2003		2004	
Location	Male	Female	Male	Female	Male	Female
Wing molt area (*n*)	(11)	(10)	(9)	(2)	(14)	(13)
Russia						
Karagin Bay	0.18	0.10	0	0	0	0
Khatyrka	0	0	0	0	0.14	0.15
Anadyr Bay	0.18	0.10	0.44	0	0.07	0.08
Chukotsk Peninsula	0.18	0.50	0.33	1.00	0.43	0.46
Alaska						
St. Lawrence Island	0.18	0.10	0	0	0.21	0.08
Bristol Bay	0	0.20	0.11	0	0.07	0.15
Wintering area (*n*)	(10)	(8)	(9)	(2)		
Russia						
Kamchatka Peninsula	0.30	0	0.11	0		
Olyutor Bay	0.10	0.38	0.22	0		
Chukotsk Peninsula	0.10	0.12	0.22	0.50		
Alaska						
Bristol Bay	0.30	0	0	0		
Alaska Peninsula	0.10	0.38	0.33	0.50		
Gulf of Alaska	0.10	0.12	0	0		

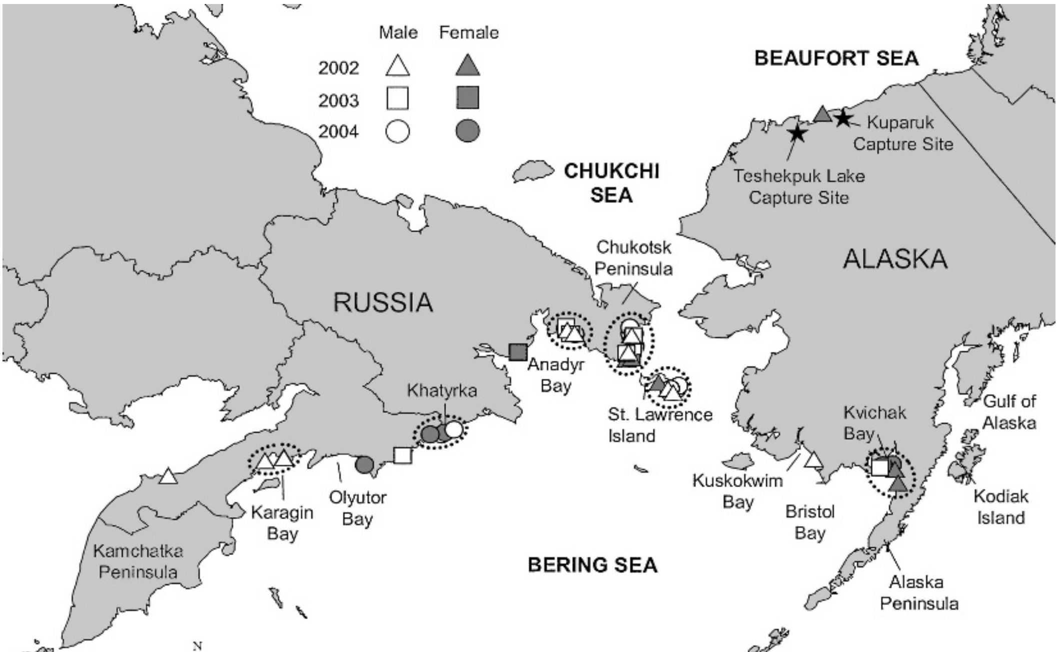

FIGURE 3. Distribution of male and female King Eiders during 2002–2004 wing molt periods. Areas where two or more marked eiders were located during wing molt over the three years of the study are outlined by a dotted grey line.

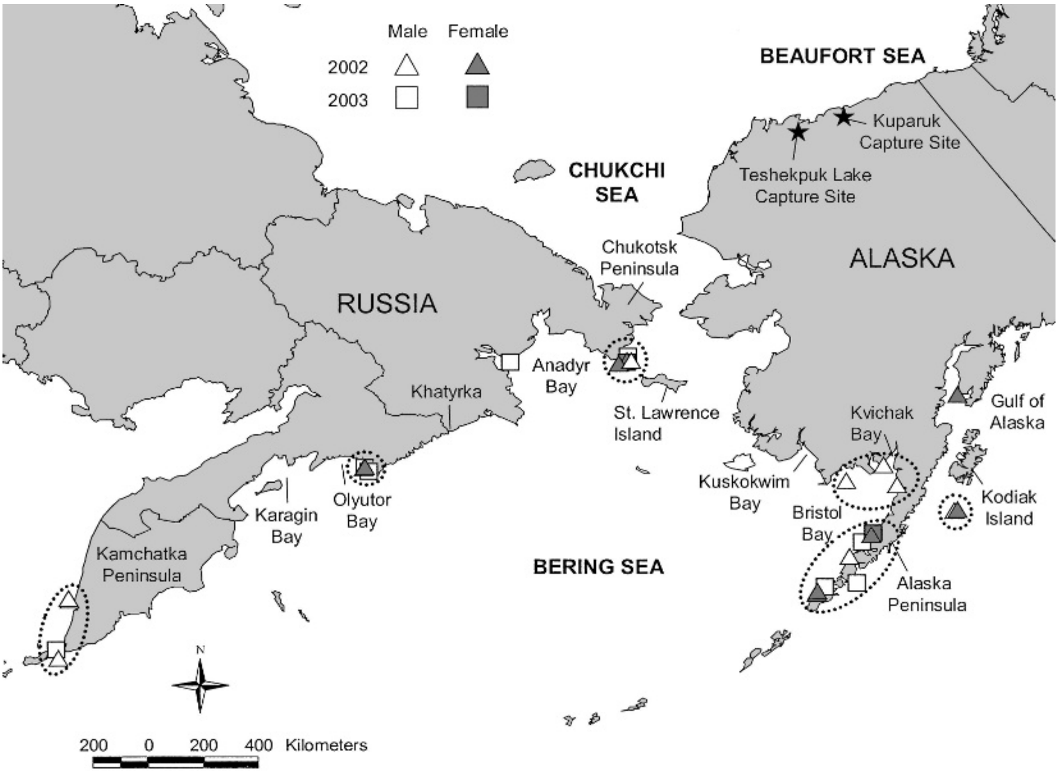

FIGURE 4. Distribution of male and female King Eiders during 2002–2003 wintering periods. Areas where two or more marked eiders were located during winter over the two years of the study are outlined by a dotted grey line.

during wing molt. The top two models suggested support for the parameters distance to shore, salinity, chlorophyll, a salinity * chlorophyll interaction, and water depth (top model: $r^2 = 0.38$; Table 3). King Eider wing molt sites were located closer to shore in areas with lower salinity and chlorophyll values and shallower water than random points (Table 4). Chlorophyll appeared to increase with increasing salinity up to a threshold point, after which chlorophyll values decreased rapidly.

Wintering areas. The model with parameters ice cover, distance to shore, water depth, salinity, and an ice cover * distance to shore interaction best described habitat at wintering locations (top model: $r^2 = 0.22$; Table 3). In winter, King Eider locations were closer to shore, in shallower areas with lower salinity and percent ice cover than random points (Table 4).

DISCUSSION

TIMING OF NONBREEDING EVENTS

For King Eiders captured at breeding areas in Alaska, differences between sexes in dispersal dates from breeding grounds, arrival dates at wing molt sites, and departure dates from wing molt sites were consistent with those of eiders captured in western Canada (D. Dickson et al., unpubl. data), King Eiders molting flight feathers in Greenland (Frimer 1994b), and with other eider species (Petersen 1981, Petersen et al. 1999). The later timing of molt migration in 2004 suggests interyear variation in the timing of wing molt in King Eiders.

Migration is energetically costly, and mortality risks may be proportional to time spent migrating (Ketterson and Nolan 1976). We found that King Eiders arriving earlier at wing molt sites flew shorter distances during molt

TABLE 3. Selection results for models explaining variation in habitat characteristics of wing molt and wintering areas of King Eiders captured and fitted with satellite transmitters on the North Slope of Alaska in 2002–2004. Models were evaluated using Akaike's information criterion (AIC), number of estimated parameters (K), difference in AIC from the top model (ΔAIC), model weight (w_i), and model deviance (Dev). The four models with the lowest difference in AIC (ΔAIC) from the top model are presented, as well as the null model containing no factors.

Model	Dev	K	ΔAIC[a]	w_i
Wing molt				
Distance to shore, salinity, chlorophyll, chlorophyll * salinity	937.43	6	0	0.55
Distance to shore, depth, salinity, chlorophyll, chlorophyll * salinity	937.20	7	1.77	0.23
Distance to shore, salinity, chlorophyll	941.96	5	2.53	0.15
Distance to shore, depth, salinity, chlorophyll	941.47	6	4.04	0.07
Null model	1443.51	2	498.08	0.00
Wintering				
Ice, distance to shore, depth, salinity, ice * distance to shore	1773.09	7	0	0.98
Ice, distance to shore, depth, salinity, ice * depth	1792.69	7	7.60	0.02
Ice, distance to shore, depth, ice * distance to shore	1798.36	6	13.27	0.00
Ice, distance to shore, depth, salinity, chlorophyll	1786.44	7	13.35	0.00
Null model	2264.00	2	480.90	0.00

[a] The lowest AIC value was 947.43 for the top wing molt habitat model and 1785.09 for the top wintering habitat model.

migration, potentially incurring fewer costs than birds flying farther and arriving later. Intraspecific competition for food resources may be high at molt sites closer to breeding areas, forcing later arrivals to undergo longer migrations (Gauthreaux 1985). Mehl et al. (2004) suggested that the flocking nature of King Eiders during migration may allow them to follow other individuals to alternative wintering areas. However, limited data on wing molt sites (n = 10) of individuals in subsequent years suggests that King Eiders, especially males, show fidelity to wing molt locations (Phillips and Powell 2006). This fidelity would be consistent with that seen in Steller's Eiders (*Polysticta stelleri*), which exhibited high return rates to wing molt sites along the Alaska Peninsula (Flint, Petersen et al. 2000), and with other waterfowl species (Bowman and Brown 1992, Bollinger and Derksen 1996). King Eiders may use a combination of strategies, with individuals following flocks to molt locations in some years and exhibiting site fidelity in others.

DISTRIBUTION OF WING MOLT AND WINTERING AREAS

Unlike Spectacled and Steller's Eiders (Petersen 1980, Petersen et al. 1999), male and female King Eiders exhibited no sexual segregation at wing molt sites. The apparent lack of successfully breeding females in this study may explain our inability to detect any sexual segregation. There is some evidence that female eiders that successfully raise young to fledging may molt flight feathers closer to the breeding grounds (Petersen et al. 1999), possibly in terrestrial

TABLE 4. Mean values ± SE of habitat variables associated with locations of King Eiders captured on the North Slope of Alaska in 2002–2004 and random points during wing molt and winter.

	Wing molt		Winter	
	Eider location	Random point	Eider location	Random point
Distance to shore (km)	6.1 ± 0.4	68.3 ± 0.7	11.1 ± 0.8	64.3 ± 0.7
Water depth (m)	19.3 ± 2.5	44.1 ± 0.4	37.9 ± 3.2	45.8 ± 0.4
Salinity (ppm)	33.7 ± 0.3	35.2 ± 0.0	34.6 ± 0.1	35.2 ± 0.0
Chlorophyll (μg/l)	0.8 ± 0.1	1.3 ± 0.0	1.2 ± 0.1	1.3 ± 0.0
Ice cover (%)			22 ± 2	32 ± 1

environments (Knoche 2004). During the course of this study, we found three of our marked hens incubating eggs, but their early dispersal from breeding areas suggests none successfully fledged young. The distribution of wintering sites also did not differ between male and female King Eiders. This lack of sexual segregation has been seen in other waterfowl species that, like King Eiders, form pair bonds on wintering grounds (Hepp and Hair 1984) or use marine habitats during winter (Diefenbach et al. 1988).

Wing molt sites used by King Eiders in this study were similar to those used by eiders marked by D. Dickson et al. (unpubl. data), with the addition of molting areas located in the Alaskan Beaufort Sea, Olyutor Bay, and on the west side of the Kamchatka Peninsula. Almost 50% of King Eiders marked in this study molted flight feathers along the Chukotsk Peninsula. The Chukotsk Peninsula was also a heavily used wing molt location for Common Eiders (*S. mollissima*) captured at breeding colonies on barrier islands in the Beaufort Sea (Petersen and Flint 2002) and Spectacled Eiders from breeding areas on the Yukon-Kuskokwim Delta and the North Slope of Alaska (Petersen et al. 1999).

We found previously unreported wintering areas in Olyutor Bay, at the southernmost tip of the Kamchatka Peninsula, and in Anadyr Bay. However, we did not receive any wintering locations of King Eiders marked in this study from the Pribilof Islands, where several hundred King Eiders were killed in an oil spill in 1996 (Flint et al. 1999), nor did we receive locations from Prince William Sound or the southern mainland coast of Alaska, where King Eiders have also been reported to overwinter (Suydam 2000). Both wing molt and wintering sites for our sample of King Eiders were widely dispersed along the coastlines of the Bering Sea, supporting the findings of Pearce et al. (2004) of little population structure in King Eiders. This wide distribution during winter contrasts with the wintering strategies reported for other eider species. Spectacled Eiders are the most restricted in their wintering range, with almost the entire population wintering in a small polynya south of St. Lawrence Island (Petersen et al. 1999). Petersen and Flint (2002) concluded that Common Eiders move the minimum distance possible from breeding areas to suitable wintering locations and that they probably exhibit fidelity to these sites.

HABITAT CHARACTERISTICS

We found that King Eiders inhabited relatively shallow, nearshore areas with low salinity throughout the nonbreeding period. Postbreeding King Eiders in western Greenland were primarily observed within 1 km of the coast (Mosbech and Boertmann 1999); however, W. Larned and T. Tiplady (unpubl. data) found molting eiders >20 km offshore south of St. Lawrence Island and in Kvichak Bay. While King Eiders foraged predominantly in water 15–25 m deep during wing molt in Greenland (Frimer 1995, Bustnes and Lonne 1997), eiders generally moved far offshore into deeper water to rest at night (Frimer 1995). Although we did not find salinity to be highly correlated with distance to shore, lower salinity values at King Eider locations may have been a reflection of freshwater inputs, suggesting that King Eiders molted wing feathers near estuaries.

In our habitat models, we intended chlorophyll to reflect the potential food resources at available eider locations and random points. We expected that higher chlorophyll would reflect higher primary productivity and, as a result, higher benthic biomass (Grebmeier 1993). During wing molt, King Eider locations were described by lower chlorophyll values and a chlorophyll * salinity interaction that reflected lower chlorophyll values at low salinity. Benthic biomass in the Bering Sea is unusually high (Grebmeier et al. 1988), and food resources at King Eider wing molt sites may not be limited despite an indication of lower primary productivity in these areas based on chlorophyll values. Alternatively, low salinity at King Eider use areas during wing molt may have affected chlorophyll values at those locations.

King Eiders occupied wintering areas with lower percentage ice cover than random points. In contrast, Common and Spectacled Eiders have shown a high tolerance for ice obstruction. Common Eiders in the Gulf of St. Lawrence foraged in small openings within areas of >75% ice cover (Guillemette et al. 1993). Petersen and Douglas (2004) found that although population indices of Spectacled Eiders were negatively correlated with extreme ice conditions at core wintering areas, Spectacled Eiders did not move from these areas when ice began to cover them. Multiple wintering locations for birds in our study may reflect that King Eiders are less restricted in their habitat requirements during winter than Spectacled and Common Eiders and thus may have the ability to move away from areas with high ice concentrations to those with more available foraging habitat.

We did not address a number of habitat characteristics that may influence King Eider use of wing molt and wintering areas in our analyses. For example, shelter from wind and wave action was thought to be an important habitat characteristic of King Eider wing molt sites in Greenland (Frimer 1994a) and Harlequin Duck (*Histrionicus histrionicus*) wintering areas in Prince William Sound (Esler et al. 2000). In addition, sea ducks may require protection from human disturbance and predation and the presence of conspecifics at wing molt and wintering areas (Salmonsen 1968, Guillemette et al. 1993, Frimer 1994b, Mosbech and Boertmann 1999).

The inability of eiders to fly away from disturbance during wing molt may make them vulnerable to catastrophic events such as oil spills or extreme weather events, and higher energy requirements during this period could increase the impacts of changes in food webs (Grebmeier et al. 2006), disturbance from increased human development, or pollution. A broad distribution and multiple locations in winter suggest King Eiders have more flexibility in habitat requirements during winter than Spectacled and Common Eiders (Petersen et al. 1999, Petersen and Flint 2002, Petersen and Douglas 2004). However, dispersed locations across such a large geographic area may expose King Eiders to a wider variety of risks, making it difficult for managers to pinpoint potential causes of declines. King Eiders do appear to be less tolerant of severe ice cover than other eider species (Guillemette et al. 1993, Petersen and Douglas 2004); therefore, climate changes in the Bering Sea may allow King Eiders to winter farther north in the future as sea ice cover declines.

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