Final Wildlife Research Report ADF&G/DWC/WRR–2016–7

# Seasonal Movements and Distribution of Pacific Steller's Eiders (*Polysticta stelleri*)

Daniel H. Rosenberg, Michael J. Petrula, Denny Zwiefelhofer, Tuula Hollmen, Douglas D. Hill, and Jason Schamber

2016

Alaska Department of Fish and Game Division of Wildlife Conservation

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This project was funded by U.S. Department of Interior, Fish and Wildlife Service Grant E-5-HP-1: Habitat Conservation Planning for Alaska Coastal Species: Studies Related to Listed and Candidate Marine Birds.

This Wildlife Research Report was reviewed and approved for publication by Daniel H. Rosenberg, Waterfowl Program Coordinator for the Division of Wildlife Conservation.

Wildlife Research Reports are available from the Alaska Department of Fish and Game's Division of Wildlife Conservation, P.O. Box 115526, Juneau, Alaska 99811-5526; phone (907) 465-4190; email: dfg.dwc.publications@alaska.gov; website: www.adfg.alaska.gov. The report may also be accessed through most libraries, via interlibrary loan from the Alaska State Library or the Alaska Resources Library and Information Service (www.arlis.org).

Please cite this document as follows:

Rosenberg, D. H., M. J. Petrula, D. Zwiefelhofer, T. Hollmen, D. D. Hill, and J. L. Schamber. 2016. Seasonal movements and distribution of Pacific Steller's eiders. Alaska Department of Fish and Game, Final Wildlife Research Report ADF&G/DWC/WRR-2016-7, Juneau.

An abridged version of this report was published in *Arctic*:

Rosenberg, D. H., M. J. Petrula, J. L. Schamber, D. Zwiefelhofer, T. E. Hollmen, and D. D. Hill. 2014. Seasonal movements and distribution of Steller's eiders (*Polysticta stelleri*) wintering at Kodiak Island, Alaska. Arctic 67:347–359.

**Cover Photo:** Male Steller's eider. ©2007 Milo Burcham.

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# Executive Summary

The Pacific population of Steller's eiders (*Polysticta stelleri*) is recognized as having 2 distinct breeding populations: one population that occurs in Russia and another that occurs in Alaska. The Russian breeding population is estimated to be much larger (>100,000 birds) than the Alaska breeding population (<1,000 birds). The 2 breeding populations are defined by international boundaries, not as biological entities. Both populations mix on nonbreeding areas that are located primarily in Alaska. The Pacific population is thought to have declined by 50% in recent decades, which prompted a listing of the species as rare in the Yakutsk Republic of Russia; and the Alaska breeding population was recently listed as *Threatened* under the provisions of the United States' Endangered Species Act in response to the population decline and a severe contraction of their breeding distribution.

Causes of the long-term decline are unknown because little is understood about the life-history of Steller's eiders, particularly habitat use and linkages among stages throughout the annual cycle. Other studies of long-distance migrants have demonstrated that ecological conditions at one life-cycle stage may influence demographic attributes in another; thus, understanding migratory connectivity among seasonal habitats is important to distinguish cross-seasonal effects and their influence on population dynamics. Such information is often unattainable because of the difficulty following individuals' migratory movements. This is especially true with sea ducks because they often migrate long distances and occupy remote habitats. However, satellite telemetry has recently been used for many sea duck species to describe large-scale movements, identify critical habitats and link important life-history stages. In particular, satellite telemetry was used successfully to characterize the seasonal movements of Steller's eiders breeding on the North Slope of Alaska and wintering in Norway.

We used satellite telemetry to track the movements of Steller's eiders (*Polysticta stelleri*) wintering at Kodiak Island, Alaska. Our objectives were to determine the timing and patterns of migration, identify critical habitat, and describe affiliations among wintering, breeding, and molting areas. As well, we wished to identify the relationship of birds wintering at Kodiak Island to the Alaska breeding population. Despite previous efforts to track Steller's eiders breeding on the North Slope using satellite telemetry, the nonbreeding distribution and seasonal movements of this population remain poorly described.

We captured 114 Steller's eiders in Women's Bay and Kalsin Bay, which are part of the larger Chiniak Bay at Kodiak Island, from late February to early March during 2004–2006. Kodiak Island is the largest island in the Kodiak Archipelago, located in the northwestern Gulf of Alaska separated from the Alaska Peninsula by Shelikof Strait. Kodiak Island is characterized by fjord-like ports and bays that remain relatively ice-free during the winter. Birds were captured over open water using floating mist nets with decoys. Of the 114 birds captured in the 3 years of the study we implanted 36 birds with satellite transmitters: 10 in 2004, 21 in 2005, and 5 in 2006. Transmitters were inserted into the coelomic cavity by an experienced veterinarian using standard aseptic surgical techniques. In 2004 and 2006, birds were released within 2–5 hours of surgery. However, in 2005 we attempted to reduce post-surgical mortality by holding birds in captivity in an outdoor pool on-site pre- and post-surgery. All birds were released within 1 km of the capture sites.

We used Service Argos Inc., compatible PTT-100 implantable transmitters which were equipped with temperature and battery voltage sensors. The amount of data we received was limited by the battery life of the transmitters; thus, to conserve battery life we programmed transmitters with various ON/OFF duty cycles based on predicted periods of seasonal movements. Transmitter signals were analyzed using Argos Data Collection and Location Systems processing. We filtered Argos data to remove implausible locations and aberrant locations; filter criteria were based on travel distance, travel rate, and redundancy from previous or subsequent locations. We plotted filtered bird locations using ESRI ArcMap™ 10.0.

We monitored the movements of 24 birds (17 females and 7 males) that departed Kodiak Island (11 of the 36 birds tagged died and 1 transmitter failed soon after surgery). Spring departures appeared to vary by year and among individuals, but males and females had similar departure dates. Most birds departed in mid-April although among individuals departure was protracted by 10 to 35 days between late March and late April. Protracted spring departures appeared to result in asynchronous movements throughout spring migration which included variation in timing of stopovers. In general, most birds appeared to use a single intercontinental migration corridor between Kodiak Island and respective summer locations. Specifically, birds primarily followed the Alaska coastline, but also used overland crossings of the Alaska Peninsula and offshore pathways across Bristol Bay and the Bering Sea south of St. Lawrence Island. In Russia, the migration corridor included an overland route from the Gulf of Anadyr, across the Chukotka Peninsula to the Russian Arctic coast where birds' final movements were over coastal tundra wetlands.

Birds spent the summer at inland sites of coastal Russia or in nearshore waters of Russia and Alaska. Inland sites included those from the Chukotka Peninsula to the Taymyr Peninsula, including the New Siberian Islands. However, half of the birds were located on the Indigirka–Jana lowlands, suggesting this may be a relatively high-density nesting area. Birds arrived to inland locations between 4 June and 28 June, although arrival date varied annually. Most birds stayed for a period that was suggestive of breeding activity. Only one bird returned to a breeding location in a consecutive summer and used an inland site on the Indigirka River Delta ~300 km from the site used in the previous summer at the Indigirka–Yana lowlands. Birds that spent the summer in nearshore waters were likely nonbreeding birds. The nearshore sites used by these birds included the northern Gulf of Anadyr and the mouth of the Amguema River in Chukotka, Russia, as well as Hagemeister Island and the Kuskokwim Shoals in the eastern Bering Sea of Alaska.

All birds migrated long distances from Russian breeding areas to molting locations in Alaska. Males began molt migration much earlier (~42 days on average) than females, but arrived at molting areas only 18 days prior to females. Males spent a much longer time migrating, on average, than did females (55 and 15 days, respectively). Birds primarily followed the northern coastline of Russia making short stops of 1–7 days at several coastal locations but did not cross overland to the Gulf of Anadyr; rather they appeared to follow the coast around the Chukotka Peninsula. From here, birds seemingly moved to molting areas fairly rapidly, possibly within 1–2 days. Molt migration was shorter in duration than spring migration. Among nonbreeding birds, most appeared to fly directly to molt locations; a couple of birds made a few stops but completed migration within 1–2 duty cycles.

Most birds used known molting locations that included sites along the Alaska Peninsula (Port Heiden, Seal Islands Lagoon, or Nelson Lagoon), St. Lawrence Island, and the Kuskokwim Shoals (Martin et al. 2015, Jones 1965, Petersen 1981, Fredrickson 2001). However, ~20% of birds used Kamishak Bay, which was not documented as a molt location. Males and females used the same molt locations regardless of breeding status, but timing of molt was different between sexes. Males arrived ~3 weeks prior to females; although, females' length of stay at molting areas was abbreviated relative to males which resulted in nearly simultaneous departure. In general, males arrived between late-July to mid-August and females arrived in late-August to early September. Most birds departed molting areas in mid- to late-November. Three of 4 birds returned to the same molting location in a consecutive year, suggesting fidelity to molt locations.

All but one bird in our study returned to Kodiak Island in the following winter, suggesting high return rates. A nonbreeding male returned to a winter location on the Alaska Peninsula. Most birds returned to their respective capture location (i.e., specific bay). Only one female returned to a bay adjacent to the capture location.

In 2 years (2004 and 2006) of this study, we encountered nearly 50% mortality within 2 weeks of post-surgery release. Most of this mortality was additive and associated with transmitter implantation; thus, the rate we observed was much higher than natural mortality. Although we don't know with certainty the causes of mortality in our study, the winter period appeared to be an especially challenging interval for birds that undergo implantation and may have been an ultimate factor in the high mortality we observed. Holding birds in captivity in 2005 dramatically improved post-surgery survival (85% survived >2 weeks). However, the monetary costs of building and maintaining a captive facility were appreciable. Our estimate of annual survival was 0.69 and similar among sexes. This estimate was lower than was estimated for molting Steller's eiders on the Alaska Peninsula and for spectacled eiders and common eiders. However, our sample sizes were small and we cannot exclude the possibility that we violated the assumption that the marking instrument was independent of fate, which may have biased our estimate low.

Steller's eiders appeared to have diffuse connectivity between breeding and nonbreeding areas; this suggests a lack of subpopulation structure throughout the Pacific population and supports a pattern of genetic homogeneity among birds at multiple life-history stages. However, fidelity to discrete molting areas and winter sites suggests the potential for demographic independence among birds using these areas. This study provided the first complete description of the annual cycle of Pacific Steller's eiders by characterizing the timing and patterns of migration, identifying critical habitat, and delineating affiliations among seasonal habitats. This information can help managers predict and mitigate possible future impacts of habitat changes on the Pacific population of Steller's eider, and develop action plans to protect important habitat resources and birds using those regions.

# Abstract

We used satellite telemetry to characterize the annual movements and habitat use of Pacific Steller's eiders (Polysticta stelleri) wintering at Kodiak Island, Alaska in 2004–2006. Descriptions of broad-scale patterns in seasonal distribution and links among annual cycle stages are critical for interpreting population trends and developing conservation strategies. We captured birds in Chiniak Bay at Kodiak Island in late February and early March and monitored the movements of 24 satellite-tagged birds (16 ASY females, 1 SY female and 7 ASY males) that departed from Kodiak Island (11 of 36 birds originally tagged died and 1 transmitter failed soon after surgery). All birds used the same intercontinental migration corridor during spring, but fine-scale patterns and chronology of spring migration appeared to vary by year and among individuals. Thirteen females and 3 males migrated to known breeding areas along the Arctic coast of Russia from the Chukotka Peninsula to the Taymyr Peninsula; 5 birds spent the summer in nearshore waters of Russia and Alaska. Twelve birds migrated rapidly to molt sites in Alaska close to Kodiak Island. Molting areas were broadly distributed in coastal Alaska and included St. Lawrence Island, Kuskokwim Shoals, Kamishak Bay and 3 sites along the Alaska Peninsula. Most birds (92%) returned to Kodiak Island the following winter. Steller's eiders appear to have diffuse connectivity between breeding and nonbreeding locations, but exhibit fidelity to molting and wintering areas.

***Key Words***: Alaska, Bering Sea, breeding, Kodiak Island, migration, molting, *Polysticta stelleri*, Russia, satellite telemetry, sea duck, site-fidelity, Steller's eider, waterfowl, wintering, Arctic, threatened and endangered species.

***Project Data***: *Description of data* – Latitude/longitude coordinate and sensor data were acquired by Service Argos from 24 satellite transmitters. *Format* – Latitude/longitude coordinate and sensor data were stored in Microsoft Excel and DBASE files. As well, latitude/longitude data were depicted on maps of Russia and Alaska created in ArcMap 10.0 and stored as shapefiles (.shp). *Custodian* – All data are archived at ADF&G regional headquarters in Anchorage. For additional information, contact Dan Rosenberg at ADF&G, 525 W. 67th Ave., Anchorage, Alaska 99518 (907-267-2453; dan.rosenberg@alaska.gov), Mike Petrula (907-267-2159; mike.petrula@alaska.gov), or Jason Schamber (907-267-2206, jason.schamber@alaska.gov).

# Introduction

Connectivity between life-history stages of sea ducks is poorly known. Understanding linkages is critical as ecological conditions during any one of these periods can influence individual fitness (Angelier et al. 2009, Sorensen et al. 2009), seasonal distribution (Ward et al. 2005), and population dynamics (Sillett and Holmes 2002, Norris and Marra 2007) of migratory birds. The influence of seasonal conditions may be immediate (e.g., reduced survival) or extend into subsequent life-history stages and effect individual survival and reproduction (Norris and Marra 2007). However, determining migratory connectivity in sea ducks has been difficult because they often occupy remote and inaccessible areas that are seldom surveyed, particularly during the nonbreeding period. Satellite telemetry has afforded researchers the ability to observe broad-scale movements of many sea duck species and describe their affiliations between critical habitats during the annual cycle (Petersen et al. 1999, Phillips et al. 2006, Oppel et al. 2008). In particular, satellite telemetry has been used to study the movements of Steller's eiders breeding in Alaska (Martin et al. 2015) and wintering in Norway (Petersen et al. 2006).

The Steller's eider (*Polysticta stelleri*) is a Holarctic sea duck (*Mergini*) found at higher latitudes (>48°N latitude) with a range that includes Arctic and sub-Arctic regions of northern Europe, Russia, and Alaska, USA. Two distinct populations are recognized and are distinguished by their Atlantic and Pacific distributions (Palmer 1976, Nygård et al. 1995, Kertell 1991, Dau et al. 2000, Fredrickson 2001). The Atlantic population, which is the smallest of the 2 populations (recent estimates are 30,000–50,000 birds; Nygård et al. 1995), breeds along the western Arctic coast of Russia; and winters in coastal waters of northern Europe, northeastern Russia, and the Baltic Sea (Petersen et al. 2006). The Pacific population (~200,000 birds; Fredrickson 2001) is delineated by 2 breeding areas: a relatively large Russian population breeds along the Arctic coast of Siberia and a smaller Alaska population breeds almost exclusively on the Arctic Coastal Plain concentrated near Barrow (Fig.1); this distribution is significantly diminished from the historical breeding range in Alaska (U.S. Fish and Wildlife Service [USFWS] 2002). Both populations winter together, primarily in coastal waters of Alaska from Cook Inlet and Kodiak Island, west along the Alaska Peninsula to the eastern Aleutian Islands (Fredrickson 2001).

The current size of the Pacific population of Steller's eiders is unclear, but the most reliable estimate (~87,000 birds) stems from a long-term annual survey of spring migrants along the southwestern Bering Sea coastline (Larned and Bollinger 2009). This minimal count likely represents a large portion of the Russian breeding population and the entirety of the Alaska breeding population. Independent surveys of the 2 breeding areas yielded conservative estimates of the Russian population at ~129,000 birds (Hodges and Eldridge 2001) and fewer than 1,000 birds in the Alaska population (Kertell 1991, Flint and Herzog 1999, Ritchie et al. 2006, Larned et al. 2009, Rojek 2007). Contemporary estimates of the Pacific population are believed to be 50% lower than the largely qualitative estimate of ~400,000 in the mid-1960s (Palmer 1976). This apparent long-term decline prompted the listing of the Steller's eider as a rare species in the Yakutsk Republic of Russia (Solomonov 1987, Kertell 1991). The Alaska breeding population of Steller's eider was listed as *Threatened* in 1997 (Federal Register 62(112): 31748–31757, U.S. Fish and Wildlife Service 2002) in response to a contraction of its historical breeding range in Alaska.

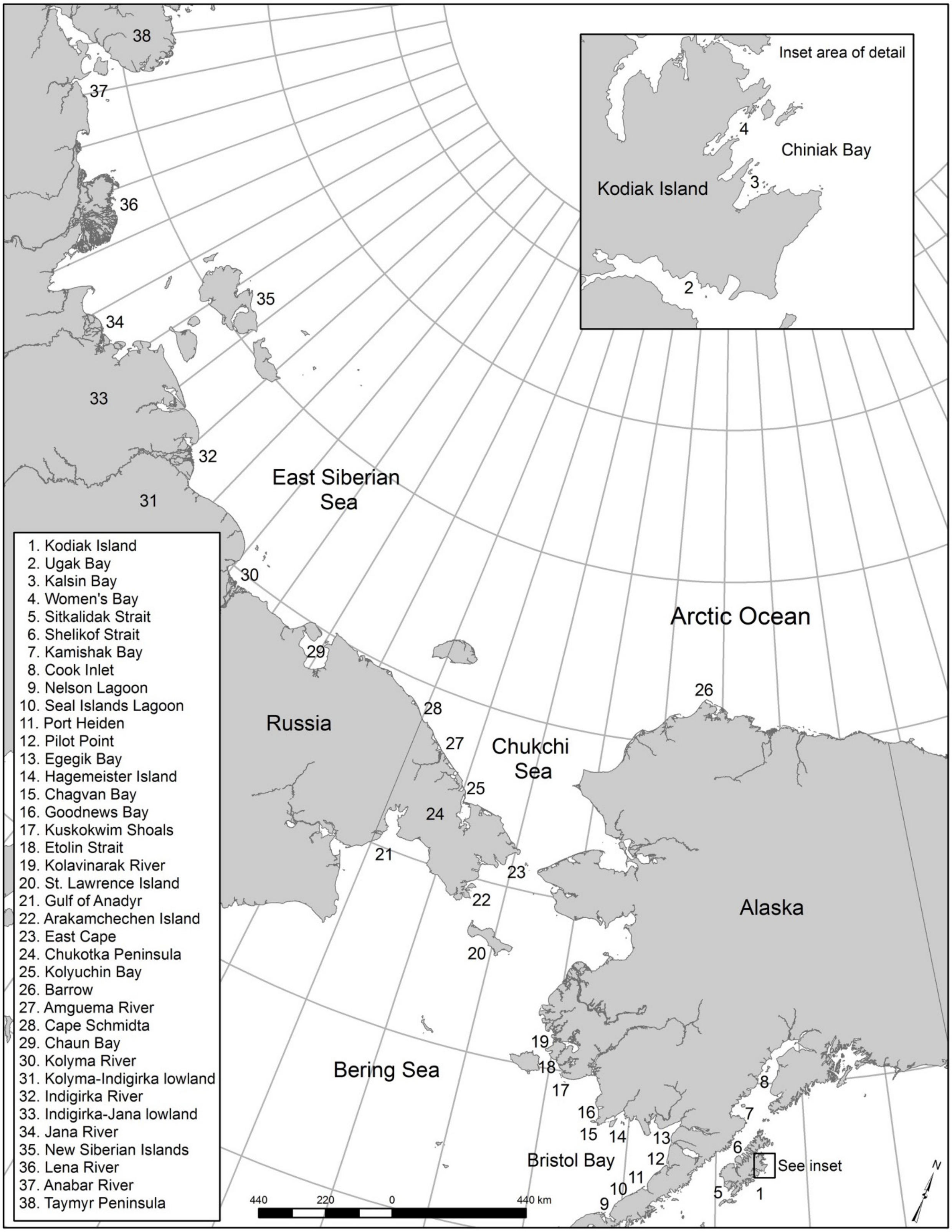

**Figure 1. Place names of key seasonal use areas of Steller's eiders referenced in this report.**

Factors contributing to the decline of Steller's eiders are unknown. Although, previous studies have provided fundamental information regarding annual distribution of the Pacific population (Jones 1965, Dau et al. 2000) and partial delineation of migration routes and seasonal habitat use of the Alaska breeding population (Martin et al. 2015); few detailed data are available that describe timing and patterns of migration and habitat use throughout the annual cycle (Fredrickson 2001). Understanding connectivity between staging, breeding, molting, and wintering areas (U.S. Fish and Wildlife Service 2002, Flint et al. 2000) can aid managers in identifying population-limiting factors and help guide conservation efforts.

Managers are tasked with the recovery of the Alaska breeding population, but conservation actions are limited. No mechanism for population decline has been identified and effects of range contraction on historical population change are poorly quantified. Identifying nonbreeding habitat unique to either population is difficult because both the Alaska and Russian breeding populations mix on staging, molting, and wintering areas throughout much of their range. Thus, without good information about their temporal and spatial distribution during the nonbreeding season focal conservation actions are difficult to achieve. Government regulators are required to assume that birds from the Alaska population are distributed throughout the entire nonbreeding range when reviewing actions that may jeopardize the continued existence of this threatened population.[1] Therefore, a clearer understanding of nonbreeding habitat use and seasonal affiliations may facilitate effective regulatory controls.

We used satellite telemetry to track individual Steller's eiders wintering at Kodiak Island in Southcentral Alaska to provide additional information on the distribution, habitat use, and timing and pattern of annual movements of the Pacific population. Approximately 5,000 Steller's eiders winter at the Kodiak Archipelago (Larned and Zweifelhofer 2002), which is near the eastern extent of the Pacific population's winter range and ~550 km from the largest wintering aggregations on the Alaska Peninsula. Although, the only linkage identified between Kodiak Island and the Pacific population has been the recovery of 3 birds marked with leg bands while molting at the Alaska Peninsula (C. Dau, USFWS, personal communication), we suspect that these birds are representative of most other small discrete wintering groups.

Our objectives were to: 1) identify staging, breeding, molting, and wintering areas, 2) document migration routes and timing of movements throughout the annual cycle, 3) identify connectivity between annual cycle stages, and 4) compare the relationship of Kodiak Island birds to the Alaska breeding population.

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[1] Section 7 of the Endangered Species Act requires that federal agencies insure against jeopardy "in consultation with and with the assistance of the Secretary . . . ." 16 U.S.C. § 1536(a)(2) (1999). The joint USFWS/National Marine Fisheries Service regulations describing this consultation process, including the "may affect" threshold for initiating consultation, appear at 50 C.F.R. § 402.14 (2000).

# Methods

## STUDY AREA

We used satellite telemetry to determine the annual movements of Steller's eiders wintering in northeastern bays of Kodiak Island, Alaska (57.73°N, -152.48°W) from 2004–2006. Kodiak Island is the largest island in the Kodiak Archipelago, located in the northwestern Gulf of Alaska and separated from the Alaska Peninsula by Shelikof Strait (Fig. 2). Kodiak Island is ~160 km long and ranges 16–96 km wide. The coastline is characterized primarily by numerous fjord-like bays and inlets that remain relatively ice-free during the winter.

We captured Steller's eiders in Women's Bay and Kalsin Bay, which are part of the larger Chiniak Bay, from late-February to early March, 2004–2006. The 2 capture sites were ~15 km and ~20 km, respectively, from the community of Kodiak (Fig. 2).

## BIRD CAPTURES

We used floating mist nets and decoys to capture birds over open water (Kaiser et al. 1995). Captured birds were immediately removed from mist nets, placed in small pet carriers with raised mesh liners and transported by skiff to shore and by vehicle to a surgical unit. The total transport time for a bird between removal from the mist net and arrival at the surgical unit was <30 minutes. At the surgical unit, birds were weighed (±1.0 g), measured (culmen, total tarsus and wing-cord; nearest 1.0 mm), and banded with a U.S. Geological Survey metal leg band (left leg) and a blue colored tarsal band engraved with a unique white alphanumeric code (right leg). Birds were sexed and assigned to either a second year (SY) or after–second year (ASY) age class based on plumage characteristics (Palmer 1976, Gustafson et al. 1997). We determined the eligibility of a bird for satellite implant surgery based on its age class (SY and ASY) and body condition to ensure that a bird was fit to carry a transmitter and that the transmitter weight to body mass ratio was near or below 5%. A bird was considered fit if it had >average body mass and no signs of past or present injury, lesions, or physical abnormalities.

## SURGERY AND HANDLING

Surgical procedures for satellite transmitter implantation were similar in all years and were performed by an experienced veterinarian following protocols developed by Korschgen et al. (1996) with some modifications (Mulcahy and Esler, 1999, Robert et al. 2000). At minimum, one veterinarian and one trained anesthetist performed the surgery using standard aseptic surgical techniques. Birds were anesthetized with isoflurane gas (IsoFlo®; Abbott Laboratories, North Chicago, Illinois 60064, USA) delivered in oxygen. Satellite transmitters were inserted in the coelomic cavity through an incision made along the ventral midline (~3 × 2 cm) between the distal end of the keel and the pubic bone. An additional incision was made for the antenna to exit at a dorsal position nearest the intersection of the pubis and synsacrum. The right abdominal air sac was then breached and the antenna was passed through a trochar inserted dorsally. The transmitter was then inserted into the air sac and all incisions were closed with absorbable sutures.

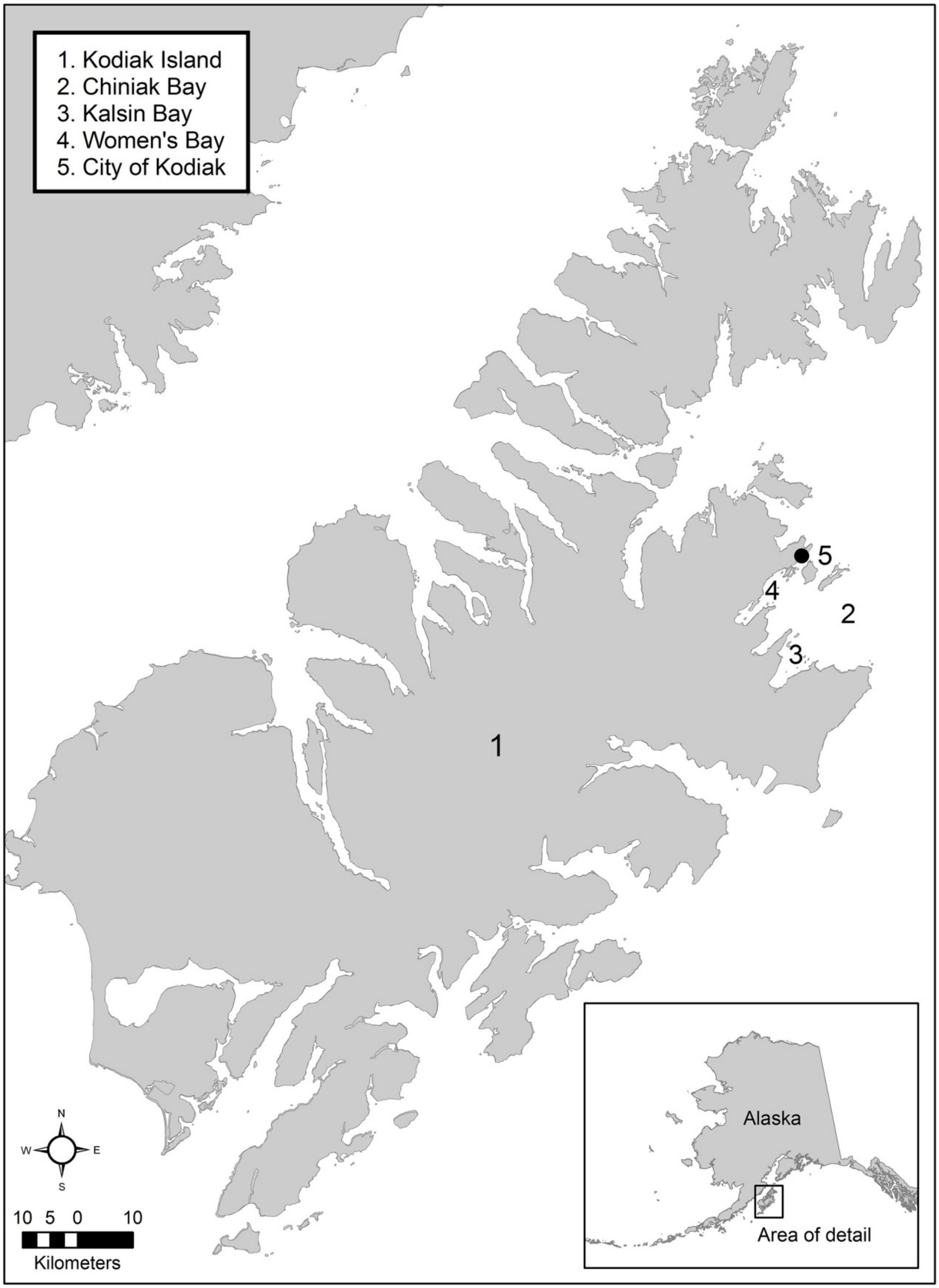

**Figure 2. Study area at Kodiak Island, Alaska where wintering Steller's eiders were implanted with satellite transmitters in March of 2004–2006. Steller's eiders were marked at 2 smaller bays within Chiniak Bay: Women's Bay and Kalsin Bay.**

We followed similar handling procedures for satellite-tagged birds in 2004 and 2006; however, we modified handling protocols in 2005. Specifically, in 2004 birds were subjected to relatively minimal handling: they were returned to pet carriers post-surgery and allowed to recover from anesthesia for 2–5 hours before being released to the water within 1 km of their capture site. We elected to follow similar procedures in 2006[2] because of the logistical and monetary constraints associated with handling procedures used in 2005.

We modified handling procedures in 2005 in response to high rates of post-release mortality in 2004 (see Results). Once captured, birds were divided into 2 treatment groups. The first group (7 females, 5 males) consisted of birds held in captivity both pre- (6–13 days, mean = 8.5 days, SD ± 2.2) and post-surgery (8–12 days, mean = 9.8 days, SD ± 1.8). This group was selected from a larger pool of candidates (*n* = 19) based on sex, age, initial body condition at capture and changes in body condition and behavior during captivity (i.e., response and acclimation to capture and handling). Post-surgery, they were placed back in captivity for recovery. The second group (8 females, 1 male) was held in captivity post-surgery only (10–14 days, mean = 10.8 days, SD±1.6)[3] to facilitate rehabilitation. We selected birds for surgery based on sex, age, and initial body condition.

Birds were held in captivity pre- and post-surgery under identical conditions. The captive facility included a covered, outdoor, aluminum tank (7.3 m x 2.4 m)[4] equipped with water intake and outflow. Seawater was pumped to reservoirs elevated above the tank and gravity fed to the tank, creating a current that provided for continuous surface drainage. Screen material (i.e., nylon netting, hardware cloth), small mammal traps, and an electric fence provided security from potential predators. Water depths ranged from 0.6 m to 1.8 m. We provided 4 haulout platforms (0.3 m × 1.2 m) covered with Nomad™ carpet matting (3M). Food and water was provided *ad libitum*. Birds were fed Mazuri Sea Duck Diet[5] in bowls and as free-floating pellets. Supplemental krill was provided. Freshwater for drinking was provided in pet bowls. Birds were screened from observers and monitored throughout the day. Birds were recaptured every 2–5 days to evaluate body condition and health. We released captive birds (at capture sites) once they remained dry at the ventral incision site; had normal hematocrits, total plasma solids, and leukocytes (buffy coat); gained mass; and exhibited no signs of trauma or lethargy.

## SATELLITE TELEMETRY

### Transmitter Specifications

We used Service Argos, Inc. compatible PTT-100 implantable transmitters (PTTs; Microwave Telemetry Inc., Columbia, MD). The weight of PTTs ranged 39–41 g; and approximate dimensions were 58 mm × 33 mm × 9–15 mm thick. A 21.6 cm long Teflon-coated, multi-strand, stainless steel antenna exited from the posterior dorsal end of the transmitter and protruded 2 cm before bending at a 90-degree $^{\text{angle}}$; a Dacron collar was placed at the juncture of

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[2] 2006 birds were not held in captivity (2005 protocols) due to the small number of implants and high cost of maintaining birds in captivity.

[3] Data are from 6 surviving birds. Three birds from the post-held-only group died in captivity and are not included.

[4] University of Alaska Fairbanks/National Marine Fisheries Service Kodiak Fisheries Research Center (KFRC).

[5] http://mazuri.com/PDF/5681.pdf

the transmitter and antenna to facilitate suturing and prevent infection at the dorsal exit wound. All PTTs that we used were reinforced to withstand considerable external pressure; and were equipped with temperature and battery voltage sensors.

Data Acquisition and Analysis

Birds require a small-sized transmitter. A small-sized transmitter has a small-sized battery, which limits the battery power available, and, therefore, limits the life span of the transmitter. The PTTs we used were designed with an approximate 10 month lifespan if allowed to operate continuously. Thus, to conserve limited battery power and maximize data collection, we programmed the PTTs with various ON/OFF (duty) cycles based on predicted periods of seasonal bird movements. All PTTs remained ON for 5–6 consecutive hours during which time location data was transmitted and received. PTTs were programmed with OFF times that varied from a minimum of 24 hours to a maximum of 120 hours depending on the life-cycle stage of the birds. For example, we increased the frequency of ON hours (i.e., data collection) during spring migration and summer residency at the expense of collecting data during fall migration and the winter period.

PTT signals were analyzed using Argos Data Collection and Location Systems (Service Argos, Inc., Landover, MD). We accepted all Argos Standard Location Processing with class codes 1, 2 or 3 (Service Argos 2007). When standard processing criteria were not met during a transmission cycle (generally fewer than 4 signals during a satellite overpass), we used Argos Auxiliary Location Processing (class codes A, B). We used the PC-SAS Argos-Filter algorithm (D. Douglas, US Geological Survey, Alaska Science Center, Anchorage, Alaska) to remove implausible locations and aberrant locations associated with Class codes A, B, and 0, which is typical for data obtained through the Argos 'Doppler' system (Fancy et al. 1988); filter criteria were based on travel distance, travel rate, and redundancy from previous or subsequent locations (Ely et al. 1997). We plotted filtered bird locations using ESRI ArcMap™ 10.0 (Environmental Systems Research Institute, Redlands, CA, USA). We did not include in our analyses data from birds that either died (verified by temperature sensor) or had transmitters fail within 30 days of post-surgery release.

We assigned seasonal status (spring departure, breeding, molting, wintering, and migration) to birds by correlating dates and patterns of movement with geographical locations and information from published literature, historical accounts, and surveys.

We used the best location in each duty cycle selected by the filter program for mapping and distance calculations. We selected from all plausible locations to determine migration routes. As well, we estimated dates of spring migration from Kodiak Island by using the median date between 2 sequential locations (last date at Kodiak Island and first date after departing Kodiak Island) and rounding towards the first location in the sequence. We followed this pattern throughout the annual cycle (e.g., median date between last location at breeding area and first location after departing breeding area to indicate last date at breeding area). We did not estimate arrival and departure dates between seasonal use areas for an individual if we did not receive a location for ≥8 consecutive days between movements.

A potential breeding area was assigned to a bird if it spent ≥10 days after its arrival in spring or within any 10-day period between 17 June and 10 July at an interior location before departing to a suspected molting area (Solovieva 1999, Petersen et al. 2006). However, if a bird spent time at 2 or more locations we used the last location. Our assignment of a breeding area was not intended as an indication of breeding status. We received the last data from a satellite transmitter on 30 December 2006.

### CONTAMINANTS, BLOOD, AND VIRUS SAMPLING

Blood and virus samples were collected within one hour of capture and birds not slated for surgery were released within 1 km of the capture site.

In 2004 and 2005, we collected ≤5 ml blood from birds not undergoing surgery. However, for birds undergoing surgery, we collected blood samples for genetic analysis only (1 to 3 drops) in 2004, and ~2 ml of blood were collected in 2005. Blood was collected via jugular venipuncture using a 21 or 22 gauge needle and a 5 cc syringe. Once collected, blood was transferred to serum tubes and processed. Blood samples collected for genetic analyses were placed in vials containing Longmire preservative and archived at the Molecular Ecology Lab, U.S. Geological Survey, Anchorage, Alaska.

A virus sample was collected from each captured bird using a Dacron-tipped swab inserted gently into the cloaca then transferred to a vial containing viral transport media. All samples were preserved in liquid nitrogen. Blood serum and virus samples were archived at the Alaska SeaLife Center, Seward, Alaska.

In 2004, 30 Steller's eiders (17 males, 12 females, and 1 unknown sex) were tested for blood lead levels (Brown et al. 2006). A portable blood analyzer (LeadCare®; ESA, Inc., Chelmsford, MA 01824, USA) was used to obtain immediate blood lead data in the field, providing an on-site tool for clinical assessment of individual birds. During post-surgical recovery, ~3–5 ml of blood was collected via jugular or medial metatarsal venipuncture, of which 0.05 ml was utilized for this analysis.

Field methods used in this study were approved in different years by either the Institutional Animal Care and Use Committee (IACUC) of the Alaska SeaLife Center or the Alaska Department of Fish and Game's IACUC. Capture and handling of birds followed guidelines of The Ornithological Council (Gaunt et al. 1997).

### ANALYTICAL METHODS

Because our data were not normally distributed, we used a randomization procedure in Poptools Macro (v.3.1.1; Hood 2009) in Microsoft Excel 2007 to assess the probability that males and females differed in departure dates from Kodiak Island. First, we calculated the difference in overall mean dates between males and females. We then randomly reassigned dates to sexes, without replacement, to retain the original sample size for each sex, and recalculated the difference in departure dates between sexes. We repeated this process over 1,000 iterations, and we report the *P*-value as the proportion of random trials with greater differences between sexes than observed in the actual data +1 divided by the number of trials +1 (Davidson and Hinkley

1997). Conditional on the sample of departure dates, this proportion represents the probability that differences observed between sexes occurred by random chance. We also used a randomization procedure to assess the probability that sexes differed in the distance traveled during spring migration, the dates they began the molt migration and arrived to molt locations, and differences in the length of time spent at molt areas. Spring migration distance was estimated using the sum distance between consecutive directional locations calculated as great circle routes by the filter program. We assumed straight-line travel by birds between successive locations; thus, distance estimates likely represent minimum distances traveled. Because sample sizes were small in some years, we could not quantitatively examine annual variation in the timing of life-history stages; however, we offer a qualitative assessment of these events.

We examined whether males and females used different molt sites by calculating the centroid of minimum convex polygons at each molt location created using ArcMap 10.0. We then used the centroids as the sampling unit in a multi-response permutation procedure in BLOSSOM (Cade and Richards 2001). We also calculated the centroid of minimum convex polygons for each individual bird during summer to assign a terminal summer location. As well, we determined the kernel home range distribution to calculate 95% and 50% probability contours for 3 areas that we considered important to spring migrants based on number of birds that used these areas and length of stay.

We used a known-fate model to estimate survival of satellite-tagged birds because PTTs were equipped with a temperature sensor that allowed us to verify fate of the birds (Murray 2006). We used the Kaplan–Meier product-limit estimate in the known-fate-model procedure with a logit link in program MARK (White and Burnham 1999) to estimate monthly survival rates. Known-fate models assume that markers do not affect an individual’s fate; therefore, we excluded 11 birds from this analysis because they died within the first month of marking, suggesting that the PTT implant may have contributed to mortality. However, we are uncertain if marking impacted survival of other birds that died later in our study; thus, we recommend cautious interpretation of our survival estimates. Known-fate models also assume that censoring is unrelated to mortality. We were unable to assess whether we violated this assumption. However, in addition to censoring known mortalities, we also censored data from transmitters where it appeared birds were still alive but the transmitters had failed, such as when there was an indication of battery failure by a drop in the battery voltage sensor, or when a temperature sensor indicated that the bird was alive at the time of last transmission.

We were unable to consider a full time-varying model of monthly survival probability because of our small sample size, but were able to consider 2 models. We compared the fit of a model for time-invariant monthly survival probability ($\varphi.$) to a sex-specific model of time-invariant monthly survival probability ($\varphi._{\mathrm{sex}}$) and selected the best approximating model using $\mathrm{QAIC}_c$ (Burnham and Anderson 2002). We present $\mathrm{QAIC}_c$ weights ($w_i$) as evidence of relative model importance. We used the derived estimates function to obtain estimates of annual survival based on the best model. Annual survival rate was calculated as the product of monthly survival rates (i.e., monthly survival rate).

# Results

We captured 114 Steller's eiders during the 3 years of the study: 40 in 2004, 46 in 2005, and 28 in 2006. Of these, 36 birds were implanted with satellite transmitters: 10 in 2004, 21 in 2005, and 5 in 2006. Mean body mass[6] of all ASY female and ASY male Steller's eiders captured was 802.2 ± 40.8 g (*n* = 49) and 802.7 ± 39.2 g (*n* = 41), respectively. Mean body mass of SY females and SY males captured was 748.5 ± 54.7 g (*n* = 12) and 774.2 ± 39.3 g (*n* = 11), respectively. Mean body mass of all female and male Steller's eiders implanted with satellite transmitters was 819.8 ± 23.4 g (*n* = 25) and 828.3 ± 32.7 g (*n* = 11), respectively. The ratio of transmitter mass to bird body mass ranged from 4.6 percent for the largest bird, an 874 g male, to 5.2 percent for the smallest bird, a 773 g female.

We monitored the movements of 24 satellite-tagged birds (16 ASY females, 1 SY female and 7 ASY males) that departed from Kodiak Island (11 birds died and one bird's PTT failed a few days post-surgery). As the study progressed, we monitored fewer birds in each season due to mortality and transmitter failure (Fig. 3). Individual transmitter performance (number of transmissions, location quality, and longevity) varied significantly throughout the study. Individual transmitters provided location data from 71 to 654 days ($\bar{x}$= 307.2 ± 194.0 days) and the total number of locations per individual ranged 181–1,215 ($\bar{x}$ = 720.7 ± 305.0 locations). We received 3,623 locations from 5 birds in 2004, 12,668 locations from 16 birds in 2005, and 1,005 locations from 3 birds in 2006. We used 13.9% of all location data in our analyses. Sample size at a given life-history stage (e.g., breeding, molting, wintering) varied throughout the study because transmitter performance and individual migration patterns varied. Of the 24 satellite-tagged birds that departed Kodiak Island, 11 birds had transmitters that lasted for more than one year (Fig. 3).

## MOVEMENTS AND DISTRIBUTION

### Spring Migration

Spring departure dates from Kodiak Island, on average, were not significantly different (*P* =0.16) between males ($\bar{x}$=12 April ± 4.3 days, *n* = 7) and females ($\bar{x}$=16 April ± 9.1 days, *n* = 16). Median departure dates from Kodiak Island for all birds in each year were on 23 April 2004 (*n* = 5, range = 14–24 April), 13 April 2005 (*n* = 16, range = 22 March–26 April), and 7 April 2006 (*n* = 3, range = 26 March–19 April), which suggests that spring departure dates varied by year (Table 1), but small sample sizes and differences in bird handling across years precluded the use of inferential statistics.

In 2005, we marked a male and female pair at capture in Women's Bay, Kodiak. The male departed Kodiak and arrived in Port Heiden on the Alaska Peninsula about 4–5 days before the female. The pair joined in Port Heiden and remained together through the nest initiation period.

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[6] Body mass was measured up to one hour post capture, after birds were transported to the surgical suite. Due to defecation, feather drying, and dehydration, body mass declined by an average of 4.6% (range = 4.5–4.8%) from measurements taken when birds were weighed immediately after removal from nets.

From Kodiak, most birds migrated westerly ~315–550 km to staging areas in protected bays and lagoons on the north side of the Alaska Peninsula from Egegik Bay south to Seal Islands Lagoon with the majority of birds (71%) staging at Port Heiden. However, 2 birds appeared to stage at either Pilot Point or Egegik Bay and 2 other birds migrated northwest to stage in lower Cook Inlet at Kamishak Bay (Table 2). Although a few birds stopped briefly along the south side of the Alaska Peninsula before crossing overland, most birds arrived on the north side of the Alaska Peninsula in ≤4 days[7] after leaving Kodiak Island. Arrival dates and length of stay on the Alaska Peninsula appeared to vary by year.[8] In the respective years of the study, the last bird departed the Alaska Peninsula and continued northward migration on 7 May 2004, 11 May 2005, and 13 May 2006.

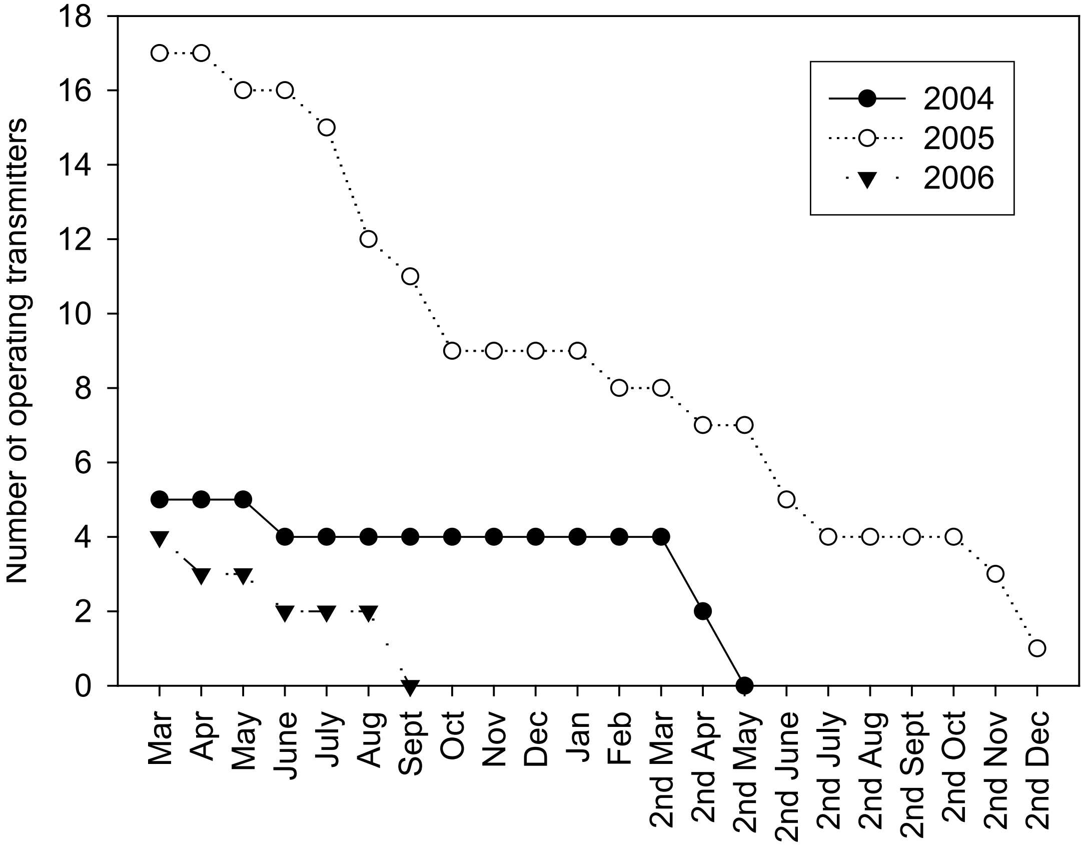

**Figure 3. Depreciation of satellite transmitter function in each year of a 3-year study (2004–2006), characterizing the annual movements of Steller's eiders wintering at Kodiak Island, Alaska. Causes for loss of satellite transmitter signals were unknown, but likely were due either to bird mortality or battery failure.**

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[7] Duty cycles were from 3.5 to 5.5 days in 2006.

[8] Small sample sizes and differences in handling precluded use of inferential statistics.

**Table 1. Dates of arrival to and departure from winter sites across years of individual satellite-tagged Steller's eiders wintering at Kodiak Island, Alaska 2004–2006. Status is indicated as censored when it could not be determined due to transmitter failure or mortality.**

| PTT | Sex | Year | Status[a] | Capture site | Depart | Arrival | Return site | 2nd depart | 2nd return |
|---|---|---|---|---|---|---|---|---|---|
| 20375 | F | 2004 | Censored | Women's Bay | 24 April | | | | |
| 20376 | F | 2004 | B | Women's Bay | 24 April | 1 December | Women's Bay | | |
| 20377 | M | 2004 | NS | Women's Bay | 18 April | 25 January | Women's Bay | 15 March | |
| 23888 | M | 2004 | NS | Women's Bay | 14 April | 15 February | Seal Isl. Lagoon[b] | | |
| 23889[c] | F | 2004 | NB | Women's Bay | 23 April | 23 November | Women's Bay | | |
| 23887 | M | 2005 | NS | Women's Bay | 13 April | | | 6 April | |
| 23891 | F | 2005 | NS | Kalsin Bay | 25 April | 29 November | Kalsin Bay | 4 April | |
| 23893 | F | 2005 | B | Women's Bay | 13 April | | | | |
| 23894 | F | 2005 | B | Women's Bay | 22 April | 19 November | Ugak Bay[d] | | |
| 24124 | F | 2005 | B | Women's Bay | 13 April | 18 November | Women's Bay | 7 April | 22 November |
| 24126 | F | 2005 | B | Women's Bay | 24 April | | | | |
| 25760 | M | 2005 | B | Kalsin Bay | 6 April | | | | |
| 25761 | F | 2005 | B | Kalsin Bay | 14 April | | | | |
| 25768 | M | 2005 | Censored | Women's Bay | 14 April | | | | |
| 25786 | F | 2005 | B | Women's Bay | 16 April | 21 November | Women's Bay | 8 April | |
| 25813 | M | 2005 | NB | Kalsin Bay | 12 April | 26 November | Kalsin Bay | | |
| 27595 | F | 2005 | B | Women's Bay | 11 April | | | | |
| 27597 | M | 2005 | B | Kalsin Bay | 8 April | 18 November | Kalsin Bay | 26 March | |
| 27598 | F | 2005 | B | Women's Bay | 17 April | 21 November | Women's Bay | 10 April | |
| 27599 | F | 2005 | B | Kalsin Bay | 9 April | | | | |
| 29302[e] | F | 2005 | NS | Women's Bay | 26 April | 19 November | Women's Bay | | |
| 25816 | F | 2006 | B | Women's Bay | 19 April | | | | |
| 24125 | F | 2006 | Censored | Women's Bay | 5 April | | | | |
| 25784 | F | 2005 | Censored | Women's Bay | 18 April | | | | |

[a] Summer status: B=used inland location and suspected of breeding; NB=used inland location and suspected of nonbreeding; NS=used nearshore location.

[b] Seal Island Lagoon is located along the Alaska Peninsula.

[c] Remained paired with 27597 from capture at Kodiak Island until battery failed 169 days later.

[d] Ugak Bay is adjacent to Kalsin Bay on Kodiak Island.

[e] Second year age class.

After leaving the Alaska Peninsula, most satellite-tagged birds (71%) migrated ~450 km north and crossed western Bristol Bay to the next major staging area at the Kuskokwim Shoals, located on the northwest side of Kuskokwim Bay (Fig. 4, Table 2). However, a few birds (45%) staged farther to the southeast of the Kuskokwim Shoals at Chagvan Bay or Goodnews Bay; a portion of these birds later moved to the Kuskokwim Shoals or farther north to Etolin Strait (Fig. 4). Median arrival dates to the Kuskokwim Shoals appeared to vary by year.[9] In 2005, birds arrived earlier than in the other 2 years, but resided for a longer period of time (median stay = 25.5 days, range = 1–30 days); while in 2006, birds arrived later than in other years and resided for a shorter period of time (median stay = 10.5 days, range = 7–30 days). In 2004, a nonbreeding male remained at the Kuskokwim Shoals for 75 days (until 17 July) before migrating to a molting area in Nelson Lagoon and was not included in the "median stay" calculations.

From staging areas in western Alaska, most birds crossed the Bering Sea traveling ~880 km northwesterly to the next major staging area, the protected lagoons of the northern Gulf of Anadyr (Ruddera Bay; Fig. 4). However, a few birds did not cross the Bering Sea, but remained in Alaska waters for the summer. At minimum, 83% of birds staged in the northern Gulf of Anadyr and all birds that migrated to Russian breeding areas staged there, with one exception. A female migrated northeast of St. Lawrence Island to the east coast of Chukotka. Based on a few locations, this bird appeared to migrate north to East Cape (Mys Dezhneva) and then west to the Chukchi Sea.

The minimum recorded time for birds to fly between the Kuskokwim Shoals and the Gulf of Anadyr was 35.2 hours, but flight times were potentially shorter because movements of birds did not coincide with the duty cycle programming of their transmitters. Several birds traveled routes of up to 100 km southwest of St. Lawrence Island, while others stopped briefly in nearshore waters of St. Lawrence Island. All birds except 2 traveled from Kuskokwim Bay or Etolin Strait within 72 hours (1–2 duty cycles). Median arrival dates to the Gulf of Anadyr appeared to vary by year.[10] In general, the duration of stay was shorter than at Alaska Peninsula or Kuskokwim Shoals sites (Fig. 5). Mean residence times were 10 days (range = 8–13, $n$ = 3) in 2004, 4 days (range = 1–13, $n$ = 12) in 2005, and 5 days (range = 2–6, $n$ = 5) in 2006.[11] In 2005, a nonbreeding male and a nonbreeding female remained in the northern Gulf of Anadyr for 46 and 69 days, respectively, and were not included in the calculations of residence times.

From the Gulf of Anadyr birds proceeded northerly across the Chukotka Peninsula (minimum overland distance of about 215 km). Birds arrived on coastal lagoons between the Chuckchi and East Siberian seas in the general region of the Amguema River; where they remained briefly, and then rapidly migrated west to the Kolyma–Indigirka lowlands (Figs. 1 and 4).

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[9] Small sample sizes and differences in handling precluded use of inferential statistics.

[10] Small sample sizes and differences in handling procedures precluded use of inferential statistics.

[11] Duty cycles were from 65 to 130 hours in 2006, making estimates more variable.

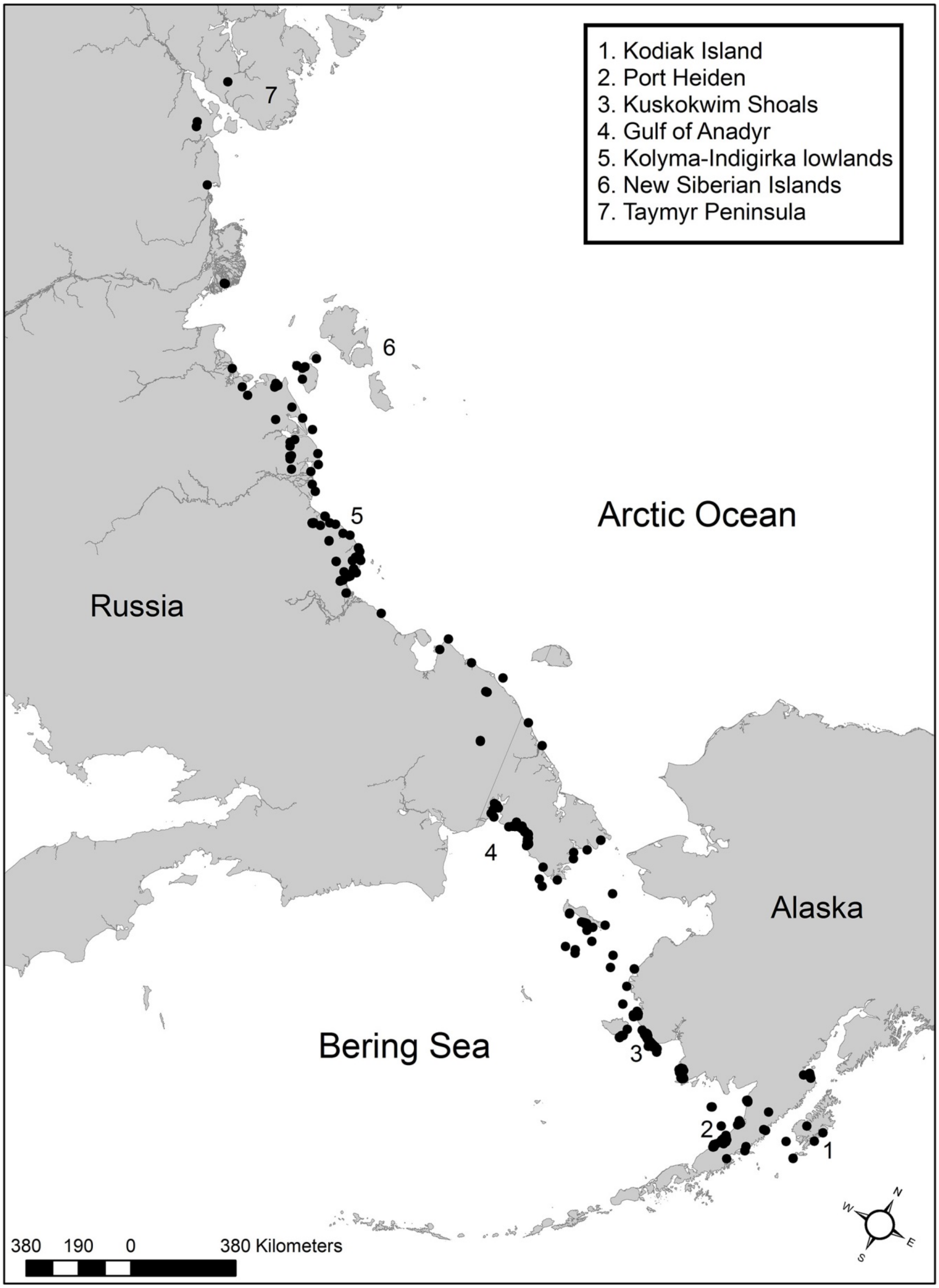

**Figure 4. Satellite telemetry locations of 23 adult and 1 second-year Steller's eiders during migration from Kodiak Island, Alaska to summer sites 2004–2006.**

**Table 2. Region and site of spring staging areas used by satellite-tagged Steller's eiders wintering at Kodiak Island, Alaska 2004–2006. Staging areas were defined as a location where ≥1 bird remained for ≥7 days. Period of use indicates the range of dates transmitted birds were present at a specific site. Spring staging areas were located in nearshore coastal waters until birds reached the Kolyma–Indigirka lowlands, where birds began to stage in freshwater wetlands up to 70 km inland.**

| Year | Region | General location | No. birds: Total birds[a] | Period of use |
|---|---|---|---|---|
| 2004 | Alaska Peninsula | Egegik Bay | 1:5 | 16–22 April |
| | | Port Heiden | 4:5 | 21 April–7 May |
| | Kuskokwim Bay | Goodnews Bay | 1:5 | 14–20 April |
| | | Kuskokwim Shoals | 3:5 | 24 Apr–21 May[b] |
| | Etolin Strait | Nunivak Island | 1:5 | 11–29 May |
| | | Cape Vancouver (Nelson Island) | 1:5 | 8–17 May |
| | Gulf of Anadyr | Val'katlen to Epran | 3:4 | 21 May–9 June |
| | Kolyma–Indigirka lowlands | Kon'kovaya–Alazeya Rivers | 2:4 | 6–16 June |
| 2005 | Cook Inlet | Kamishak Bay | 2:17 | 25 Mar–8 May |
| | Alaska Peninsula | Egegik Bay | 1:17 | 14 April–2 May |
| | | Ugashik Bay | 2:17 | 12–20 April |
| | | Port Heiden | 11:17 | 10 Apr–11 May[c] |
| | | Seal Islands Lagoon | 2:17 | 16–30 April |
| | Bristol Bay | Hagemeister Strait | 1:16 | 10 May–22 July[d] |
| | Kuskokwim Bay | Chagvan Bay | 3:16 | 24 April–23 May |
| | | Goodnews Bay | 5:17 | 21 Apr–24 May[c] |
| | | Kuskokwim Shoals | 10:16 | 25 April–1 June |
| | Etolin Strait | Kinak Bay | 2:16 | 28 April–27 May |
| | | Cape Vancouver (Nelson Island) | 1:16 | 12–23 May |
| | St. Lawrence Island | SE to SW Cape | 4:16 | 13 May–14 June |
| | Gulf of Anadyr | Val'katlen to Epran | 14:16 | 16 May–6 June |
| | Kolyma–Indigirka lowlands | Kon'kovaya–Alazeya Rivers | 13:16 | 31 May–16 June |
| 2006 | Alaska Peninsula | Chignik Lagoon | 1:9 | 28 April–6 May |
| | | Port Heiden | 7:9 | 20 Apr–13 May[e] |
| | | Seal Islands Lagoon | 2:9 | 8 April–2 May |
| | Kuskokwim Bay | Chagvan Bay | 2:7 | 12–30 May |
| | | Goodnews Bay | 3:7 | 4–22 May |
| | | Kuskokwim Shoals | 7:7 | 6 May–7 June |
| | Gulf of Anadyr | Val'katlen to Epran | 6:7 | 9–16 June |

[a] The proportion of satellite-tagged birds that used a site to total number of satellite-tagged birds alive and carrying a functional transmitter. [b] One nonbreeding male remained until 17 July. [c] A male that was tagged in 2004 arrived in Port Heiden on 21 March 2005 and in Goodnews Bay on 14 April 2005 during its second spring migration. [d] One second-year female used this location. [e] One male arrived in Port Heiden by 30 March 2006.

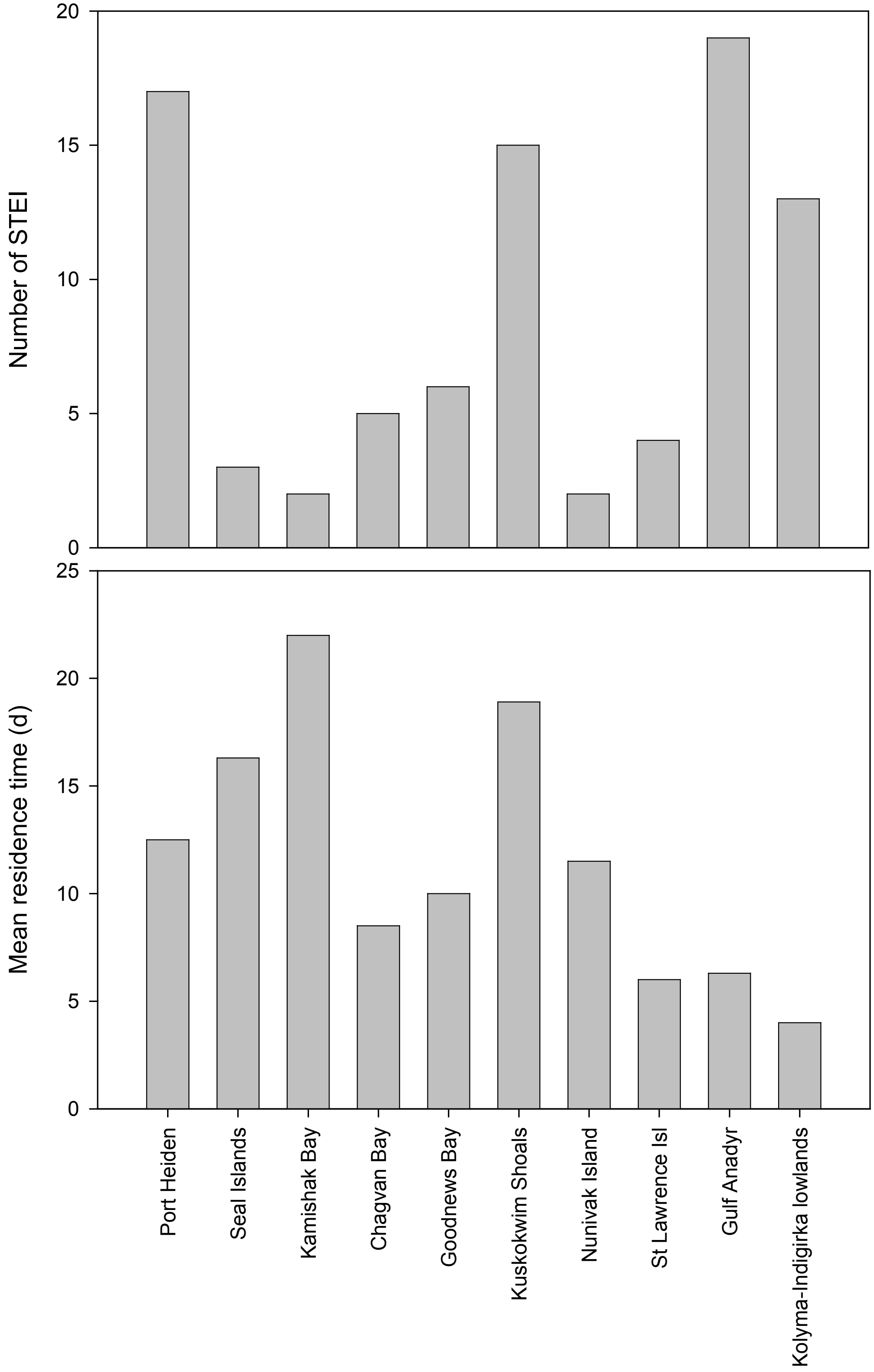

**Figure 5. Number of satellite tagged Steller's eiders and mean residence time at spring staging sites in Alaska and Russia 2004–2006.**

Median arrival dates to the Kolyma–Indigirka lowlands appeared to vary by year:[12] 10 June 2004 (range = 6–14 June, *n* = 2), 2 June 2005 (range = 31 May–14 June, *n* = 14), and 13 June 2006 (range = 12–15 June, *n* = 2). The duration of stay was less than at the Alaska Peninsula or Kuskokwim Shoals sites (Fig. 5). Mean duration of stay was 3.5 days (range = 3–4) in 2004 (*n* = 2), 5 days (range = 1–13) in 2005 (*n* = 14), and 8 days in 2006 (*n* = 2). This area was the final staging area for birds before they used inland (up to 70 km) and coastal routes across the lowlands, moving to more westerly summer areas that ranged from the Indigirka Delta to the Taymyr Peninsula (Fig. 6).

Six birds marked in 2005 had functional transmitters that allowed us to monitor their departure from Kodiak Island for a second spring migration in 2006. These birds departed Kodiak Island ~10 days earlier ($P = 0.03$) in their second spring (5 April ± 5.2 days) than in their first spring (i.e., marking year; 15 April ± 5.6 days). Further, these birds departed 9 days earlier ($P = 0.04$) in their second spring than the 3 birds satellite-tagged in 2006 (14 April ± 7.8 days). Although our sample size is small, the earlier spring departures in the second season may suggest that spring departures in the marking year were delayed due to the satellite transmitter implant procedures.

## Summer

Birds spent the summer at inland sites of Russia or in nearshore waters of Russia or Alaska (Table 3, Fig. 6). Inland sites included those from the Indigirka River Delta west to the Taymyr Peninsula (a distance of 1,700 km) and north to the New Siberian Islands (Table 3, Fig. 6). The earliest bird arrival west of the Indigirka Delta was in 2005, a male (25760) on 2 June. Median arrival appeared to vary by year. The earliest date a bird arrived to an inland site was in 2005, on 6 June (Table 3). Most inland sites used by birds were located on the Russian mainland. However, 2 birds spent the summer on Kotel'nyj Island, part of the New Siberian Islands (Fig. 6); these islands were primarily used as pre- or post-breeding staging areas for birds that spent the summer at mainland sites. The 2 birds arrived at the New Siberian Islands on 19 June in 2004 and 20 June 2005, respectively (Table 3).

The average distance traveled from Kodiak Island to final summer locations during spring migration was significantly different ($P<0.01$) between birds that occupied inland summer sites (3,687 ± 917 km) and those that spent the summer in nearshore waters (1,675 ± 1,165 km). However, among birds that spent the summer at inland sites, spring migration distance, on average, was similar ($P = 0.06$) between males (3,087 ± 1,098 km) and females (3,858 ± 824 km). The average migration period between Kodiak Island and summer locations for those birds that used inland sites was 60.5 ± 7.7 days.

Birds that spent the summer in nearshore waters were classified as nonbreeding birds. The nearshore sites used by these birds included the northern Gulf of Anadyr and the mouth of the Amguema River in Chukotka, Russia, as well as Hagemeister Island and the Kuskokwim Shoals in the eastern Bering Sea of Alaska (Table 3, Fig. 6). The average time spent at these locations was 57.2 ± 25.6 days.

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[12] Small sample sizes and differences in handling procedures precluded use of inferential statistics.

**Figure 6. Centroids for satellite telemetry locations at terminal summer sites of 15 female and 5 male Steller's eiders.**

**Table 3. Summer locations used by satellite-tagged Steller's eiders wintering at Kodiak Island, Alaska 2004–2006. Birds (and potential nesting location) were given a breeding status designation if they used an inland site for ≥10 days after arrival in spring or during any 10-day period during 17 June–10 July (Petersen et al. 2005). Summer locations are reported by region and site within a region. PTTs in bold are birds that had functional transmitters in a consecutive summer. Departure is indicated as censored if during this period it could not be determined due to transmitter failure or mortality.**

| PTT | Sex | Year | Status[a] | Region | General location | Latitude | Longitude | Arrival | Departure |
|---|---|---|---|---|---|---|---|---|---|
| 20376 | F | 2004 | B | Lena River Delta | De-Longa Channel | 73.293°N | 128.284°E | 22 June | 23 August |
| 20377 | M | 2004 | NS | Kuskokwim Bay | Kuskokwim Shoals | 59.698°N | 163.966°W | 2 May | 18 July |
| 23888 | M | 2004 | NS | Northern Chukotka | Amguema River | 67.897°N | 177.559°W | 1 June | 15 June |
| 23889[b] | F | 2004 | NB | New Siberian Islands | Faddeyevskiy Island | 75.690°N | 143.958°E | 19 June | 27 July |
| 23887 | M | 2005 | NS | Gulf of Anadyr | Ruddera Bay | 65.439°N | 176.043°W | 3 June | 28 July |
| 23891 | F | 2005 | NS | Gulf of Anadyr | Ruddera Bay | 65.363°N | 175.975°W | 16 June | 21 August |
| 23893 | F | 2005 | B | Indigirka–Jana Lowlands | Dmitriya Lapteva Strait | 72.675°N | 142.536°E | 12 June | Censored |
| 23894 | F | 2005 | B | Indigirka–Jana Lowlands | Shirokostan Peninsula | 72.276°N | 139.681°E | 11 June | 19 August |
| **24124** | F | 2005 | B | Indigirka–Jana Lowlands | Lopatka Peninsula | 72.076°N | 149.528°E | 17 June | 15 July |
| **24124** | F | 2006 | NB | Lena River Delta | Kynda Island | 73.343°N | 127.778°E | 28 June | 8 August |
| 24126 | F | 2005 | B | Lena River Delta | Macha–Uese Channel | 73.189°N | 127.969°E | 17 June | Censored |
| 25760 | M | 2005 | B | Anabar–Olenek R. Lowlands | Cape Lygyy | 73.702°N | 115.472°E | 8 June | 11 July |
| 25761[c] | F | 2005 | B | Indigirka–Jana Lowlands | Kharstan | 72.213°N | 141.333°E | 6 June | 26 August |
| **25786** | F | 2005 | B | New Siberian Islands | Lyakhovskiye Island | 73.497°N | 140.696°E | 20 June | 2 August |
| **25786** | F | 2006 | NB | Indigirka Delta | Tabor | 71.362°N | 151.107°E | 18 June | 8 August |
| 25813 | M | 2005 | NB | Indigirka–Jana Lowlands | Merkushina Strelka Pen. | 72.490°N | 145.731°E | 20 June | 4 July |
| 27595 | F | 2005 | B | Taymyr Peninsula | Lake Taymyr | 74.368°N | 99.359°E | 16 June | Censored |
| **27597** | M | 2005 | B | Indigirka–Jana Lowlands | Kharstan | 72.213°N | 141.333°E | 6 June | 5 July |
| **27597**[d] | M | 2006 | NB | Anabar–Olenek R. Lowlands | Terpya–Tumsa Peninsula | 73.463°N | 118.730°E | 16 June | 5 July |
| **27598** | F | 2005 | B | Indigirka–Jana Lowlands | Dmitriya Lapteva Strait | 72.699°N | 141.742°E | 12 June | 20 August |
| **27598** | F | 2006 | B | Indigirka–Jana Lowlands | Lopatka Peninsula | 71.962°N | 149.646°E | 20 June | 1 September |
| 27599 | F | 2005 | B | Lena River Delta | Trofimovsk | 72.723°N | 127.531°E | 10 June | Censored |
| 29302 | F | 2005 | NS | Bristol Bay | Hagemeister Island | 58.680°N | 161.085°W | 10 May | 23 July |
| 25816 | F | 2006 | B | Indigirka–Jana Lowlands | Lopatka Peninsula | 72.029°N | 149.618°E | 28 June | 13 August |

[a] Summer status: B=used inland location and suspected of breeding; NB=used inland location and suspected of nonbreeding; NS=used nearshore location, nonbreeder. [b] Resided for ~8 days at the Indigirkga–Jana lowlands where several other marked birds were suspected to have bred. [c] Remained paired with 27597 from capture at Kodiak Island until battery failed 169 days later. [d] NB status uncertain in 2006 because location data were 6 days apart; thus, only a single data point was received between 6 June and 29 June.

A high percentage of satellite-tagged females in each year met our criteria to be classified as potential breeding birds: 100% (*n* = 2) in 2004, 82% (*n* = 11) in 2005, and 75% (*n* = 4) in 2006 (Table 3). In all years, only one female (#24124) that migrated to the Russian Arctic Coastal Plain did not meet our criteria for classification as a potential breeding bird. This female may have nested on the Indigirka–Jana lowlands in 2005. However, in 2006 this bird migrated to the Lena River Delta, ~725 km west of the location used in 2005, but did not settle in a single location; thus we did not classify this bird as a breeder in that year (Table 3).

Most potential nesting sites used by satellite-tagged birds were within 15 km of the coast, but a few birds used sites that were located farther inland. A female (#27595) on the Taymyr Peninsula used a potential nest site located ~175 km from the coast and a pair (male #27597 and female #25761) used a site ~40 km from the coast on the Indigirka–Jana lowlands (Fig. 6).

We received location data for 4 birds that had functional transmitters in a second summer period; all of these birds were classified as potential breeding birds the previous summer. Of those 4, only 1 bird (female #27598) was classified as a potential breeding bird in the second summer according to our criteria (Table 3). This female used an inland site on the Indigirka River Delta ~290 km from the site used in the previous summer at the Indigirka–Jana lowlands. Two (male #27597 and female #24124) of the 4 birds returned to inland sites (Lena River Delta and near Taymyr Peninsula), but did not settle in a single location; thus, we did not classify them as potential breeding individuals. A female (#25786) spent the second summer in nearshore waters of the Indigirka River Delta. In the second summer, the 3 females settled at locations 300–720 km from the previous summer while the male's location was more than 1,000 km from the previous summer.

## Molt Migration

We report the molt migration separately for birds that were classified as potential breeding birds (*n* = 15) and those that were classified as nonbreeding birds (*n* = 5) because our definition of the start of molt migration was different for each class. However, the start of molt migration, on average, was not significantly different ($P = 0.40$) between birds classified as potential breeders (31 July ± 24.2 days) and those classified as nonbreeders (28 July ± 24.0 days). In general, all birds migrated to molting areas in Alaska, a considerable distance away from summer sites and closer to their winter location of Kodiak Island.

### *Potential breeders*

We considered that molt migration began for potential breeding birds once they traveled east of the Indigirka River, because prior to migration some post-breeding movements occurred within the general breeding area west of the Indigirka River and many birds remained within the breeding area for up to 3 weeks after leaving an inland summer location. Post-breeding movements included those from the mainland to the New Siberian Islands, as well as movements from more westerly to easterly locations within breeding areas. Thus, for some birds we may have underestimated the start of molt migration.

Males began a molt migration from suspected breeding areas significantly earlier than females (1 July ± 12.6 days and 13 August ± 14.2 days, respectively; $P<0.01$). After departing breeding areas, birds traveled east along the Arctic coast of Russia. We identified 6 staging areas used for

≥7 days by birds traveling from breeding to molting areas (Table 4); birds also made brief stops at several other areas (Fig. 7). The most important staging area appeared to be a region with a series of lagoons and river mouths between Chaun Bay and Kolyuchin Bay (a distance of ~890 km) along the Arctic coast of Chukotka. Birds staged here 2–22 days[13] ($\bar{x}$ = 10.7 ± 5.7) between 5 July and 6 September (Table 4). Within this region, most use occurred over ~269 km of coastline from Cape Yakan (69.6°N, 177.4°E) to 20 km south of the Amguema River (Ekvgvaam River Lagoon, 68.2°N, -177.1°W; Fig. 7). Here, birds were heavily concentrated at Amguema and Tynkurgin lagoons.

After departing this region, birds traveled rapidly to molting areas on the north side of the Alaska Peninsula and Cook Inlet (Fig. 7). We received insufficient data to delineate a migration route due to a seeming rapid pace of migration; birds completed the migration within 1–2 duty cycles. The few locations we received indicated birds traveled in an easterly direction to East Cape (Mys Dezhneva) and proceeded south across the Bering Strait, passing St. Lawrence Island to western Alaska (Fig. 7). Contrary to the route used in spring migration it appeared that birds did not travel across the "isthmus" of the Chukotka Peninsula to the Gulf of Anadyr during molt migration but confined their movements to the Russian Arctic coastline; although the frequency we received data during this period was insufficient to describe migration routes with certainty. Mean travel time for males and females from breeding to molting areas was 40 days (±0.8, range = 40–41, *n* = 3) and 18 days (±7.5, range = 11–33, *n* = 10), respectively. The distance that birds traveled from the Indigirka River to Port Heiden, a common molt site, was ~3,200 km (Fig. 7).

*Nonbreeders*

We defined the onset of molt migration for nonbreeding birds as the date of the first long movement in an easterly direction followed by successive movements in the same direction. We identified 3 staging areas used for ≥7 days (each by a single bird) during molt migration (Table 4). Birds used these areas 13–33 days ($\bar{x}$ = 24.0 ± 10.14) during 3 July–16 September.

One bird spent the summer near the Indigirka River and followed a molt migration route that included multiple stops along the Arctic coast of Russia, similar to the route described for potential breeding birds. Two birds spent the summer in the Gulf of Anadyr and another bird spent the summer at the Kuskokwim Shoals; all birds ostensibly flew direct to molt locations. The SY female (#29302) spent the summer at Togiak Bay, primarily at Hagemeister Island. This bird staged briefly on the Kuskokwim Shoals and then moved north to Etolin Strait and the Kolavinarak River mouth.

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[13] A male remained in this area for 38 days from 5 July until we stopped receiving data on 11 August 2005. We do not know if the bird's physical condition prohibited migration.

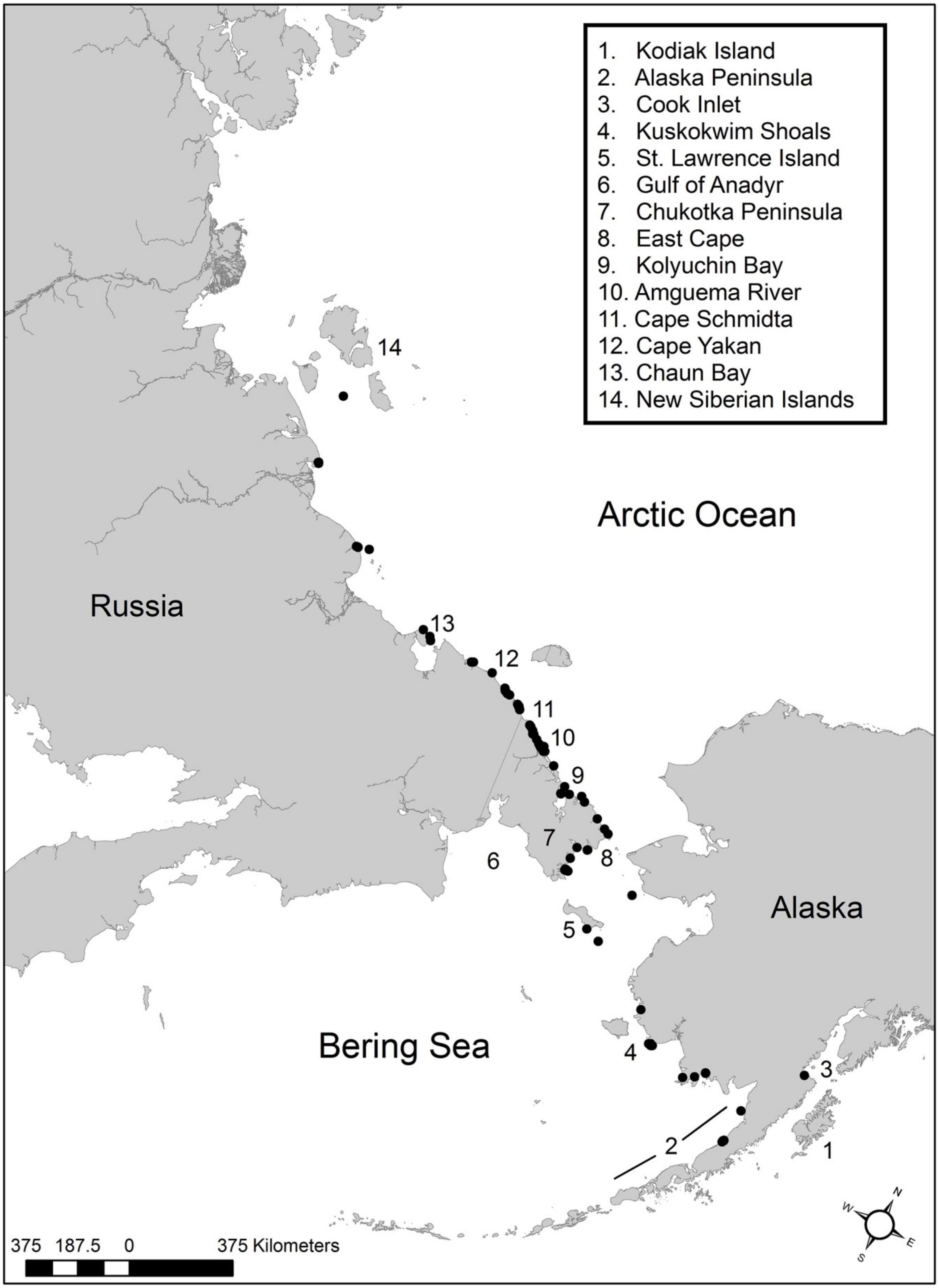

**Figure 7. Satellite telemetry locations of 15 adult and 1 second-year Steller's eiders during molt migration from summer sites to Alaska molt locations in 2004–2006.**

**Table 4. Staging areas used during molt migration by satellite-tagged Steller's eiders wintering at Kodiak Island 2004–2006. Staging areas were defined as locations where one or more individuals spent ≥7 days between departing a summer area and arriving at a molt site (Petersen et al. 2005). Birds that were classified as breeding birds (B) and those classified as nonbreeding birds (NB) are noted. Birds briefly used many additional stopover areas that are not included in this table.**

| Year | Region | General staging area | Latitude | Longitude | Status | No. birds: total birds | Period of use |
|---|---|---|---|---|---|---|---|
| 2004 | North Chukotka | Cape Shmidta–Vankarem [a] | 68.573 | -178.493 | B | 2:4 | 23 August–6 September |
| 2005 | East Yakutia | Kolyma–Indigirka lowlands | 70.920 | -158.587 | B | 2:13 | 13–21 July |
| | Northeast Chukotka | Chaun Bay | 69.942 | -169.193 | B | 1:13 | 5–13 July |
| | North Chukotka | Cape Shmidta–Vankarem [a] | 68.295 | -177.566 | B | 9:13 | 16 July–1 September |
| | Northwest Chukotka | Kolyuchin Bay | 67.023 | -174.533 | B | 1:11 | 5–11 August |
| | East Chukotka, Bering Strait | Arakamchechen Island | 64.700 | -172.478 | NB | 1:4 | 3–29 July |
| | North Yakutia | New Siberian Islands | | | B | 2:11 | 6–26 August |
| | East Bering Sea | Yukon–Kuskokwim Delta[b] | 60.293 | -164.691 | NB | 1:11 | 14 August–21 September |
| | East Bering Sea | Kuskokwim Shoals | 59.695 | -164.001 | B,NB | 3:13 | 25 July–28 September |
| 2006 | North Chukotka | Cape Shmidta–Vankarem [a] | 68.573 | -178.493 | B | 4:5 | 1 August–4 September |

[a] Primarily includes coastal waters from Laguna Tenkergynpil'gyn to Laguna Ukougepil'gyn, east and west of the Amguema River.

[b] Includes a second–year female that may have molted at Kuskokwim Shoals or Kamishak Bay.

### Molt

We identified molt locations for 12 birds that had functional transmitters. Most birds molted at 3 locations on the Alaska Peninsula (Port Heiden, $n = 3$; Seal Islands Lagoon, $n = 2$; and Nelson Lagoon, $n = 3$). Three birds molted at Kamishak Bay in Cook Inlet and one bird molted at St. Lawrence Island (Sekinak Lagoon, Table 5, Fig. 8). Females and males did not differ in the locations used for molt ($\delta_{13} = -1.53$, $P = 0.08$). However, females (28 August ± 8.9 days; $P = 0.01$) arrived to molt locations later, on average, than did males (9 August ± 14.0 days); but residence times at molt locations were not significantly different ($P = 0.19$) between the sexes (81.8 ± 7.6 days [females] and 95.0 ± 39.4 days [males]).

We could not determine a definitive molt site for the SY female (#29302) because the bird was stationary for extended periods of time (>3 weeks) at NW Hagemeister Island, the Kolavinarak River, and in Kamishak Bay. Although we suspect that the bird molted at the mouth of the Kolavinarak River, it possibly molted at Kamishak Bay; however, this would have occurred in early October. The following year (2006) we recaptured this molting bird on 12 September in Kamishak Bay.

Four birds had transmitters that lasted through a second molt period; 3 of 4 birds molted at the same location as in the previous year. One bird (#27597) molted at Port Heiden in the second year, ~155 km from the previous year's location of Nelson Lagoon (Table 5). While the sample size is very small, 75% of birds returned to previous molt locations.

### Winter

Of the 24 birds that departed Kodiak Island on spring migration, 13[14] birds had functional transmitters the following winter (Table 1); and all but one (92%) returned to Kodiak Island, suggesting that fidelity to winter location may be high. The exception, a single male (#23888) departed Kamishak Bay (molt location) and migrated southwest along the Alaska Peninsula, first to Chignik Lagoon on the south side and then to the final winter location of Seal Island Lagoon on the north side of the Alaska Peninsula.

Of the 12 birds that returned to Kodiak Island all but one female (#23894) returned to their capture site. It returned to Ugak Bay,[15] ~30 km southwest of the capture site in Women's Bay.

The timing of returns to capture sites was relatively synchronous. Median arrivals were on 20 November 2005 (range = 18–29 November, $n = 9$) and 25 November 2006 (range = 22–28 November, $n = 2$). One exception was a male that arrived on 22 January after spending ~1 month in Sitkalidak Strait, southeast Kodiak Island. All birds remained in the same bays until either their transmitter failed or they departed Kodiak Island the following spring.

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[14] Female '24124' was included in 2005 and 2006; thus, we monitored a total of 12 individual birds.

[15] This bird remained in Ugak Bay until the last transmission on 16 January 2005.

**Table 5. Duration of stay at molt areas by year and sex of satellite-tagged Steller's eiders wintering at Kodiak Island 2004–2006. Departure is indicated as censored if during this period it could not be determined due to transmitter failure or mortality. PTTs in bold are birds that had functional transmitters in a consecutive year during molt.**

| Year | Sex | PTT | Region | General location | Latitude | Longitude | Arrival | Departure | Duration (days) |
|---|---|---|---|---|---|---|---|---|---|
| 2004 | M | 20377 | Alaska Peninsula | Nelson Lagoon | 56.014°N | 160.804°W | 18 July | 16 December | 150.5 |
| | | 23888 | Cook Inlet | Kamishak Bay | 59.129°N | 153.937°W | 11 August | 30 January | 172.5 |
| 2004 | F | 20376 | Alaska Peninsula | Port Heiden | 56.894°N | 158.816°W | 8 September | 25 November | 77.5 |
| | | 23889 | Alaska Peninsula | Port Heiden | 56.876°N | 158.801°W | 31 August | 22 November | 82.5 |
| 2005 | M | 23887 | Alaska Peninsula | Nelson Lagoon | 56.023°N | 160.817°W | 3 August | 19 November | 108 |
| | | 25813 | Alaska Peninsula | Seal Isl. Lagoon | 56.671°N | 159.386°W | 13 August | 16 October | 64 |
| | | **27597** | Alaska Peninsula | Nelson Lagoon | 56.024°N | 160.852°W | 23 August | 16 October | 53.5 |
| 2005 | F | 23891 | St Lawrence Island | Sekinak Lagoon | 63.040°N | 169.766°W | 21 August | 11 November | 81.5 |
| | | 23894 | Cook Inlet | Kamishak Bay | 59.094°N | 153.749°W | 31 August | 19 November | 80 |
| | | **24124** | Alaska Peninsula | Port Heiden | 56.886°N | 158.818°W | 12 August | 18 November | 97.5 |
| | | **25786** | Cook Inlet | Kamishak Bay | 59.097°N | 153.722°W | 23 August | 20 November | 88.5 |
| | | **27598** | Alaska Peninsula | Seal Isl. Lagoon | 56.659°N | 159.425°W | 31 August | 21 November | 82 |
| | | 29302[a] | Kuskokwim Shoals | Kolavinarak R. | 60.293°N | 164.691°W | 4 October | 19 November | 46 |
| 2006 | M | **27597** | Alaska Peninsula | Port Heiden | 56.024°N | 160.852°W | 24 August | Censored | 86[b] |
| 2006 | F | **24124** | Alaska Peninsula | Port Heiden | 56.892°N | 158.797°W | 27 August | 16 November | 80.5 |
| | | **25786** | Cook Inlet | Kamishak Bay | 59.088°N | 153.699°W | 9 September | Censored | 55[b] |
| | | 25816 | Alaska Peninsula | Port Heiden | 56.890°N | 158.824°W | 26 August | Censored | 5[b] |
| | | **27598** | Alaska Peninsula | Seal Isl. Lagoon | 56.667°N | 159.406°W | 14 September | Censored | 22[b] |

[a] Molt location uncertain, but see Results; in 2006 this bird was recaptured with a nonfunctional transmitter, while flightless in Kamishak Bay.

[b] Duration of stay at molt location when signal from satellite transmitter was lost.

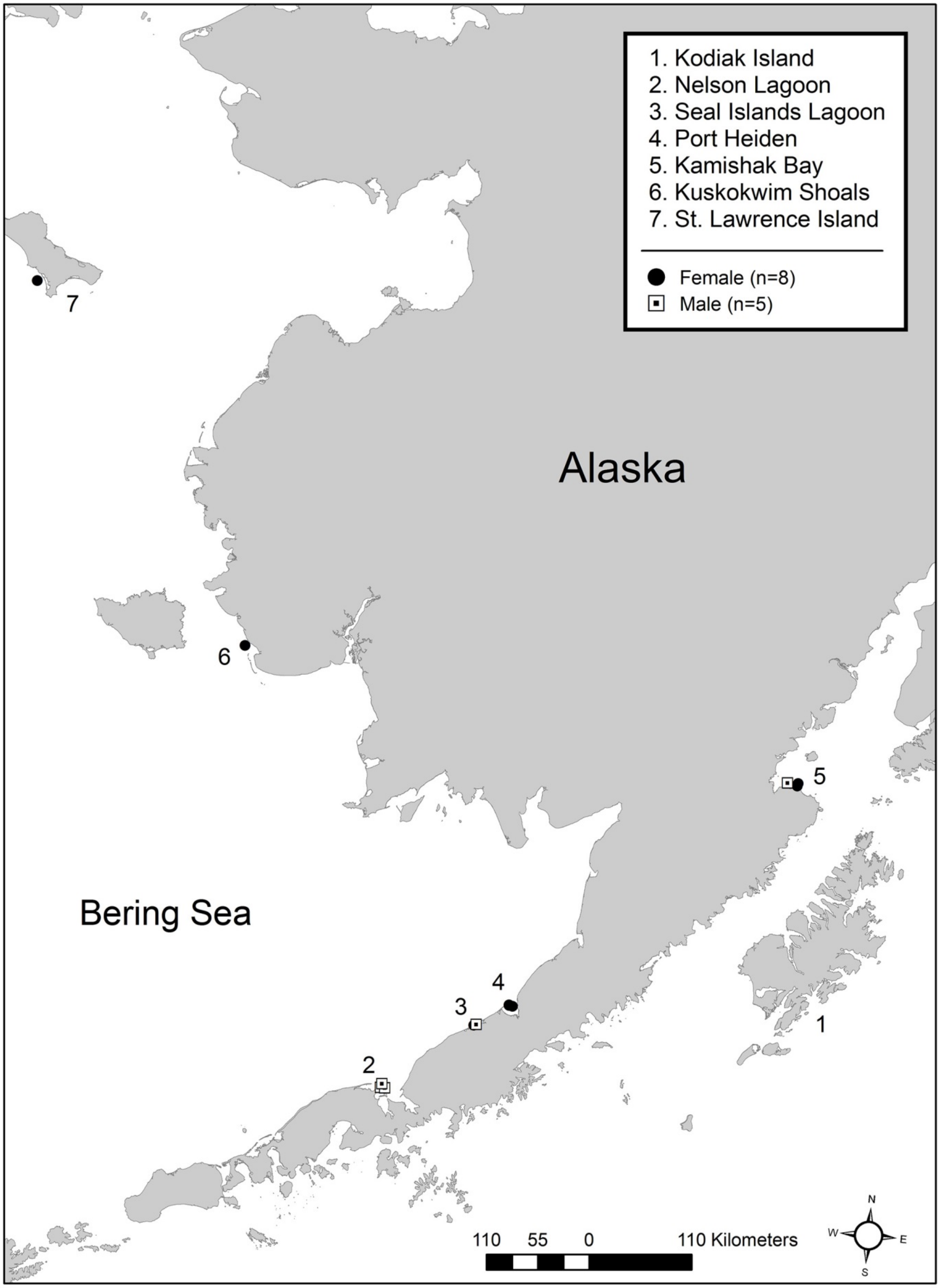

**Figure 8. Centroids of satellite telemetry locations of 12 adults and 1 second-year Steller's eiders at molt sites 2004–2006.**

### SURGERY-RELATED MORTALITY AND ANNUAL SURVIVAL

Of the 36 Steller's eiders (25 females, 11 males) that we implanted during the 3 years of the study, 1 female died during surgery from aspiration in 2005 and we confirmed mortality (based on temperature sensor) in 7 of 15 birds during the immediate 14-day post-release period in 2004 and 2006 (46.7%). In 2005, when birds were held in captivity rather than released following surgery we confirmed mortality (body temperature) in 3 of 20 birds during the immediate 14-day post-surgical period (15.0%); 2 of these birds died in captivity and 1 died 2 days after release. We excluded these 11 birds and 1 bird that had a PTT fail within a few days after surgery from analysis of annual survival.

We estimated monthly and annual survival for 24 birds that departed Kodiak Island 2004–2006. In 2004, 4 birds survived for a year; we censored a fifth bird at 82 days because the battery sensor indicated failure by a rapid voltage drop (Fig. 3). Ten of 16 birds survived a full year in 2005. An additional 4 birds were censored that had transmitters fail at 140, 141, 169, and 306 days (Fig. 3). In 2006, of 3 birds that departed Kodiak 1 bird died during spring migration and the other 2 birds had transmitters that failed to transmit after 71 and 181 days with no indication of bird mortality or transmitter malfunction[16] (Fig. 3). We censored these 2 birds because the internal temperature sensor indicated that the birds were alive at the time of the last transmission.

The model of time-invariant monthly survival rates was supported as the best model for our data ($w_i = 0.73$); a model of sex-specific monthly survival rates was less supported ($w_i = 0.27$). Estimated monthly survival predicted by the time-invariant model was 0.96 (95% CI: 0.93–0.98). A derived estimate of annual survival from this model was 0.64 (95% CI: 0.42–0.82).

## Discussion

Data gathered in this study provide some of the first detailed descriptions of the annual cycle of Pacific Steller's eiders. Although these data originated from a small group of birds wintering at Kodiak Island, the annual distribution we observed corresponds with the known historical range of Pacific Steller's eiders (Fredrickson 2001) and was similar to the distribution reported by Dau et al. (2000) based on band recovery data from molting Steller's eiders marked at Izembek Lagoon (1961–1998) and Nelson Lagoon (1995–1997) on the Alaska Peninsula (Fig. 9). Moreover, the pattern and timing of movements of satellite-tagged birds in this study generally coincided with those described in annual surveys of Pacific Steller's eiders during spring migration (Larned and Bollinger 2009). Inference drawn from our data may be relevant to a large portion of the Pacific population of Steller's eiders. Data from previous satellite-tagging of Steller's eiders at Barrow (Alaska breeding population) indicated that habitat use and timing of movements was similar to our data for a portion of the nonbreeding period (Fig. 10; Martin et al. 2015).

We were unable to quantify much of the apparent variability in our data as sample size (number of transmitted birds) was small (Lindberg and Walker 2007); this often necessitated a qualitative

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[16] In 2006, other researchers reported 'drop-out' of Microwave Telemetry PTT100 transmitters, likely associated with faulty batteries.

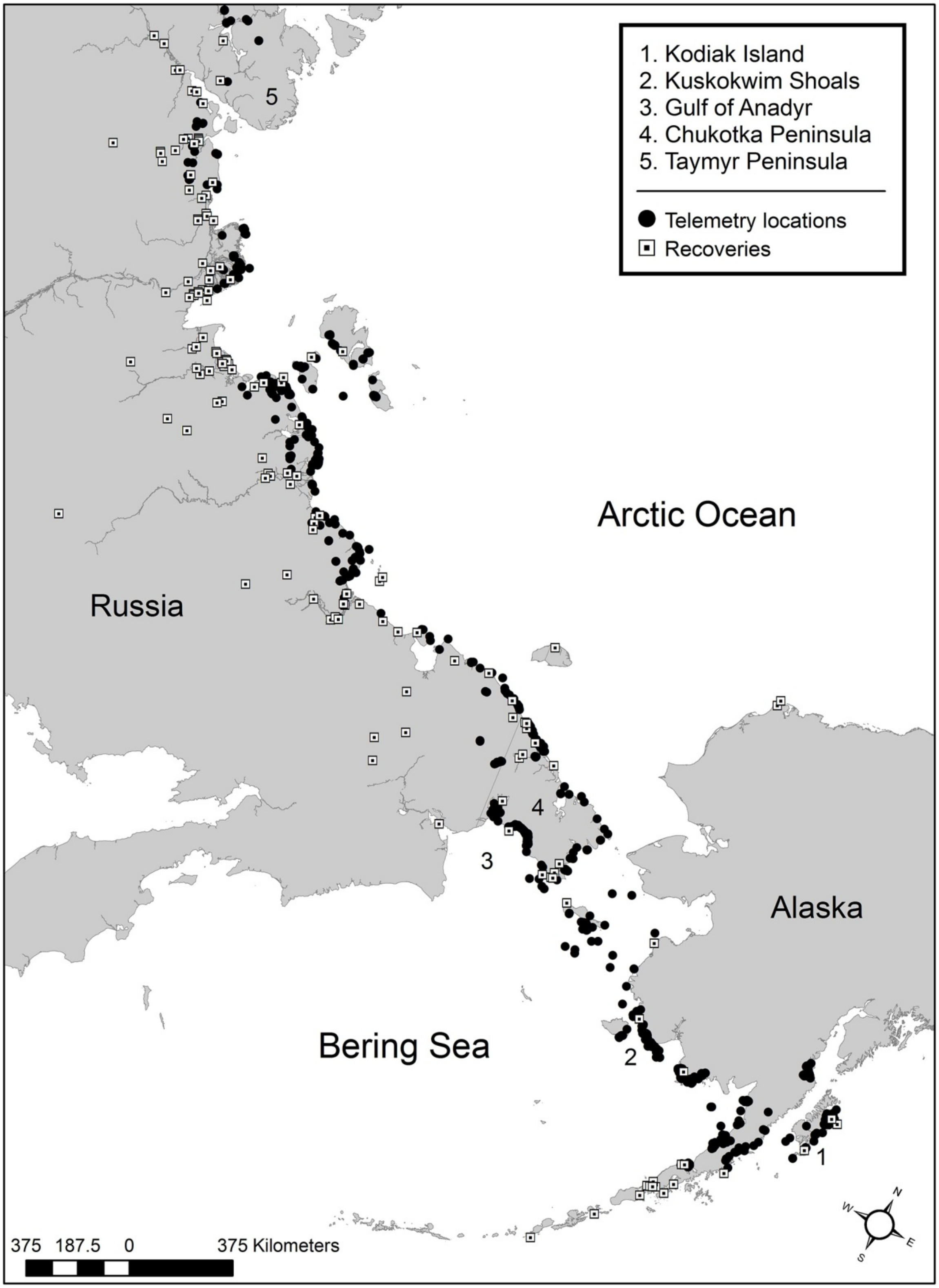

**Figure 9. Distribution of recoveries of Steller's eiders banded on the Alaska Peninsula (Dau et al. 2000) versus satellite telemetry locations from Steller's eiders implanted at Kodiak Island 2004–2006 (this study).**

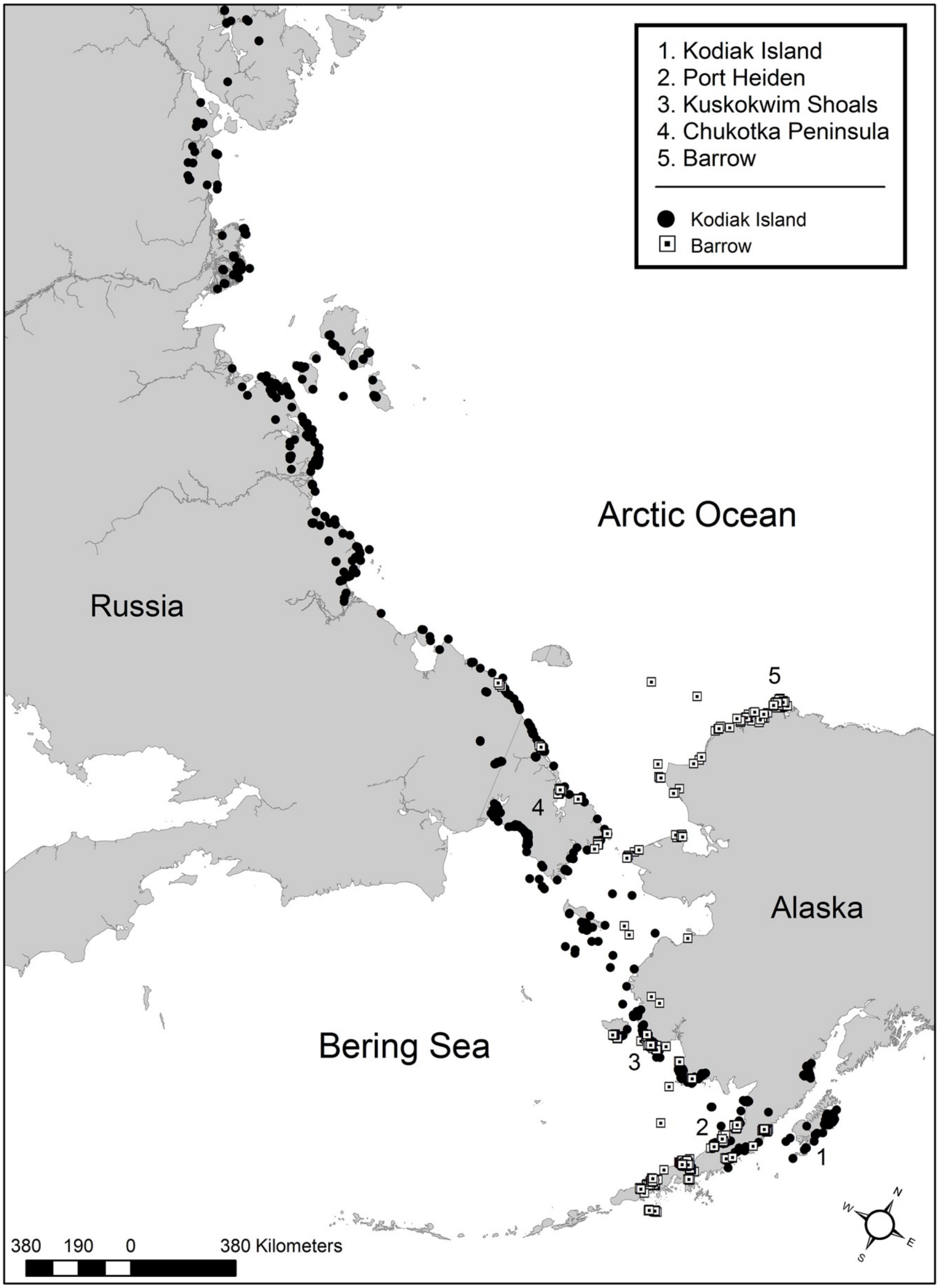

**Figure 10. Satellite telemetry locations of Steller's eiders implanted at Barrow, Alaska 2000–2001, and at Kodiak Island, Alaska 2004–2006.**

assessment of migration patterns and habitat use. The short duration of the study did not allow us to assess variation over the natural life span of individuals. Surgical procedures and/or internal transmitters likely influenced the behavior of some birds in our study (e.g., arrival or departure times; Wilson and McMahon 2006, Oppel et al. 2008). However, the general pattern and timing of migration and habitat use we observed is supported by past data from aerial surveys, satellite telemetry, capture-mark-recapture methods and field observations.

## MOVEMENTS AND DISTRIBUTION

### Spring Migration

Individually marked birds migrated from Kodiak Island to summer locations along the Arctic coast of Russia from the Chukotka Peninsula to the Taymyr Peninsula, as well as nearshore waters of Russia and Alaska. Most birds made long-distance migrations. Birds completed spring migration in a series of rapid movements punctuated by frequent stopovers at coastal locations, similar to the migration pattern found in other Pacific sea duck populations (Petersen et al. 2009, Phillips et al. 2006, De la Cruz et al. 2009). Most birds appeared to use the same intercontinental migration corridor between Kodiak Island and their respective summer locations. Birds followed the Alaska coastline, but also used overland crossings of the Alaska Peninsula and offshore pathways across Bristol Bay and the Bering Sea south of Saint Lawrence Island. In Russia, the migration corridor included an overland route from the Gulf of Anadyr, across the Chukotka Peninsula to the Russian Arctic coast, where birds' final movements were over coastal tundra wetlands; this is consistent with the observations of Solovieva (1999). The use of tundra habitat in spring was contrary to that found for the Atlantic population of Steller's eiders, which primarily migrated along coastal nearshore waters (Petersen et al. 2006).

At finer spatial scales, the pattern and chronology of migratory movements of birds in this study were individually variable and suggestive of dissimilar migration strategies. Individuals varied in their selection of stopover sites and length of stay at each site, but altered their migration route little across years. Factors such as body condition or predation risk likely influenced selection of stopover habitat (Lindström 2003, Alerstam and Lindstrom 1990). Repeated use of specific stopover sites may improve individuals' knowledge of ecological conditions along migration routes (Bauer et al. 2008).

Among multiple stopover sites, we identified Port Heiden, the Kuskokwim Shoals, and the Gulf of Anadyr as most critical during spring migration. Most birds (≥71%) used these areas and spent nearly 50% of their total migration time, on average, at these sites. At each of these sites, birds were located primarily (i.e., 95% contours) in proximity to shore and core use areas (i.e., 50% contours) and were concentrated at specific locales, suggesting that these areas provided features important to migrants (Fig. 11). The Kuskokwim Shoals and locations on the Alaska Peninsula, including Port Heiden, also were found to be important stopover areas to spring migrants in the Alaska breeding population (Martin et al. 2015). Heavy use of these stopover sites may indicate the availability of good food resources (Piersma 1987), particularly in core use areas. Abundant food resources are required to build capital nutrient reserves for continued migration or reproductive investment (Gauthier et al. 2003). Other sites, such as Kamishak Bay, Seal Islands Lagoon, Goodnews Bay, Chagvan Bay, Nunivak Island, and St. Lawrence Island

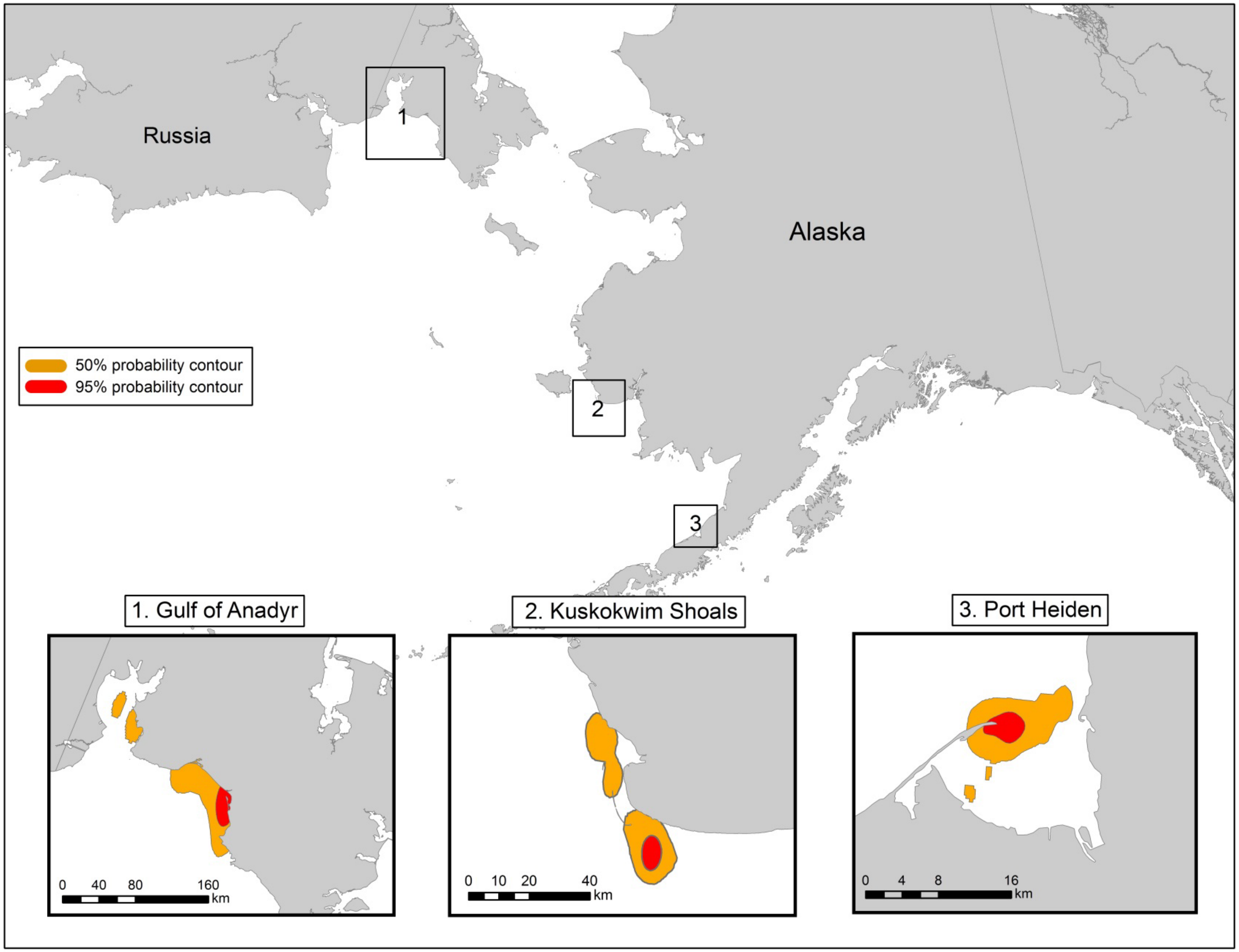

**Figure 11. Map of primary spring staging areas depicting 95% and 50% probability contours based on kernel home range analyses.**

also were important stopovers but these sites were visited by fewer individuals and in some cases for shorter duration. Birds classified as breeders made stops at coastal wetlands in Russia prior to arrival at breeding areas. Final stopover sites may provide nutrients necessary for reproduction (Prop et al. 2003). Nutrient allocation in Steller's eiders has been little studied; thus, the importance of nutrient origin (i.e., marine vs. freshwater) to reproduction is unknown. The timing of migration appeared to vary by year and among individuals; we were unable to quantify this variability. However, we detected no difference in spring departure dates from Kodiak Island between males and females, suggesting that mate-pairs likely migrated together; sea ducks are thought to form pair bonds during winter. Most birds departed Kodiak Island in early to mid-April, but the range between first and last departures was 10 to 35 days from late-March to late-April. Spring departures likely were strongly influenced by individuals' physiological condition or environmental cues (Weber et al. 1998) such as weather patterns or availability of ice-free habitat (Larned and Bollinger 2009). Protracted spring departures appeared to result in asynchronous movements throughout spring migration, which included variation in timing of stopovers. Birds in this study seem to have the ability to adjust individual migration timing within and among years, which may signify migratory flexibility to respond to changing ecological conditions.

### Summer

We classified most birds as breeding if they visited inland areas of Russia and nonbreeding if they spent the summer in nearshore waters of Russia and Alaska. Although we lacked data to verify nesting, a high proportion of birds were classified as breeding because they were associated with known breeding areas and their timing of arrival was consistent with other arrival data from Russia (Solovieva 1999). Most birds using inland sites were dispersed throughout the known core breeding range of Steller's eiders (Solovieva 1999) from the Indigirka River to the Anabar River. Half of our birds within this region were located on the Indigirka–Yana lowlands, suggesting this may be a relatively high-density nesting area. Hodges and Eldridge (2001) also estimated a higher proportion of birds in this region than elsewhere on the eastern Arctic coast of Russia. A few birds used inland sites outside of the core areas, but within the extent of the known breeding range (Dau et al. 2000). One female settled farther west at the Taymyr Peninsula, the hypothetical boundary separating the Pacific and Atlantic populations. Here, breeding birds from the 2 populations overlap (Petersen et al. 2006). The level of interchange between these populations is unknown, but separation is likely maintained through fidelity to nonbreeding areas (i.e., molting, wintering; Petersen et al. 2006). One male used an inland site near the Amguema River on the Chukotka Peninsula. Nests have not been located in this region (Solovieva 1999). If nesting occurs here, it may be irregular and in very low densities.

In general, birds arrived to breeding areas within a range of 10 days, despite the considerably longer travel distances of some birds. Arrival dates appeared to vary annually, likely because timing of nesting in Steller's eiders is highly correlated with annual variability in snowmelt (Solovieva 1999, Quakenbush et al. 2004). Staging for short periods at multiple locations prior to arrival at nesting locations may allow Steller's eiders to optimize nest initiation relative to habitat availability.

### Molt Migration

Steller's eiders migrated long distances from breeding areas to molting areas which were closer to Kodiak Island. A long-distance migration to molt areas closer to winter grounds also was observed in the Atlantic population of Steller's eiders (Petersen et al. 2006). Among birds that used inland sites, males began molt migration much earlier (~42 days on average) than females, but arrived to molting areas only 18 days prior to females. Males spent a much longer time migrating, on average, than did females (55 and 15 days, respectively). Male sea ducks typically depart nesting areas at the onset of incubation, but female departure is constrained by nesting and/or raising young to fledging; thus, females likely expedite molt migration and molt to regain flight prior to winter (Oppel et al. 2008). With one exception, all females that used inland sites in this study resided 43–81days before initiating molt migration, timing consistent with a breeding attempt.

Patterns of habitat use during molt migration differed from spring migration. Birds primarily followed the northern coastline of Russia making short stops of 1–7 days at several coastal locations, with heaviest use occurring at sites between Chaun Bay and Kolyuchin Bay where most birds spent >7 days. In contrast to the spring route, birds appeared to follow the coast of the Chukotka Peninsula and did not fly overland to the Gulf of Anadyr. From here, birds seemingly moved to molting areas fairly rapidly, possibly within 1–2 days. Once leaving Russian staging areas, we received too few location data to distinguish routes to molting locations with certainty.

### Molt

Most birds used known molting locations that included sites along the Alaska Peninsula (Port Heiden, Seal Islands Lagoon, or Nelson Lagoon), St Lawrence Island and the Kuskokwim Shoals (Martin et al. 2015, Jones 1965, Petersen 1981, Fredrickson 2001). However, ~20% of birds used Kamishak Bay, which had not been previously described as a molt location. Birds molted in this area in all years of our study. Further, 2 birds molted at Kamishak Bay in 2 consecutive years, suggesting some degree of fidelity to this area. From aerial photographs in 2005 and 2006 we estimated a minimum of 2,500 molting birds in each year. Most birds were associated with a large reef (Douglas Reef) situated along the southern end of Kamishak Bay (D. Rosenberg, Waterfowl Program Coordinator, ADF&G, Anchorage, personal communication). Kamishak Bay is a known wintering site for Steller's eiders; Larned (2006) estimated ~1,700 birds used the area during winter.

Males and females used the same molt locations regardless of breeding status. However, the timing of molt was different between sexes. Males arrived at molt locations ~3 weeks prior to females, but because females' length of stay was shorter, sexes departed almost simultaneously. In general, males arrived between late-July to mid-August and females arrived in late-August to early September. Most birds departed molting areas in mid- to late-November, but 2 males departed as early as 16 October and another male departed as late as 16 December.

Birds visited molt sites independent of breeding location in support of an earlier finding (using band recoveries) of no substructuring within molting areas (Dau et al. 2000). However, 3 of 4 birds in our study returned to the same molting location in a consecutive year, suggesting fidelity to molt locations. Flint et al. (2000; >95%) used capture-mark-recapture analyses to show high rates of fidelity to molt sites on the Alaska Peninsula.

Winter

High fidelity to winter location appears to be a life-history attribute found in many species of sea ducks (Robertson and Cooke 1999); and our data support a high degree of winter site fidelity in Steller's eiders. With one exception, all birds in our study returned to Kodiak Island in a consecutive winter. Winter-site fidelity may allow mate-pairs to reunite during winter to maintain fitness benefits of a long-term pair bond. As well, fidelity to winter site may confer selective advantages associated with site familiarity such as knowledge of food resources and predators that may increase overwinter survival (Robertson et al. 2000). Most birds in our study returned to their respective capture site at a specific bay and remained there throughout the duration of the transmitter's life or until departing the following spring.

### SURGERY-RELATED MORTALITY AND ANNUAL SURVIVAL

In 2004 and 2006 we encountered nearly 50% mortality within 2 weeks of post-surgery release. Most mortality was likely additive and associated with transmitter implantation; thus, much greater than naturally occurring mortality. High post-surgical mortality also occurred in other sea duck species implanted during late winter (D. Rosenberg, Waterfowl Program Coordinator, ADF&G, unpublished data; T. Bowman, Sea Duck Joint Venture Coordinator, USFWS, unpublished data). Such high mortality may be related in large part to the winter period, given that other satellite-transmitter implant studies conducted at breeding areas observed much lower post-surgical mortality (Petersen et al. 1995, Dickson et al. 1998, Oppel and Powell 2010; D. Rosenberg, Waterfowl Program Coordinator, ADF&G, unpublished data).

Sea ducks incur high energetic costs during winter in high latitude marine habitats, and therefore, must consume large amounts of food to sustain positive physiologic condition (Goudie & Ankney 1986). However, factors such as shortened day length (Systad et al. 2000), weather events (Finney et al. 1999), and increased predator vigilance (Squires et al. 2007) may place constraints on foraging opportunities, making winter a particularly stressful period of the annual cycle. Accordingly, the effects of surgery or carrying internal transmitters may exacerbate winter stressors such that some individuals may be unable to compensate and self maintain. Some evidence suggests that implanted devices may alter dive performance of sea ducks (Latty et al. 2010), which likely affects foraging dynamics and may ultimately influence individual energy balance. In other studies, some implanted birds were isolated from flocks, failed to maintain waterproofing and showed signs of lethargy, or possible infection at the incision site (Rosenberg et al. 2006 a, b). As a result, altered behavior following implantation may cause individual birds to be highly vulnerable to predation.

Kodiak Island has an abundant population of bald eagles (*Haliaeetus leucocephalus*), which prey on sea ducks Todd et al. 1982). We recovered a number of transmitters from under eagle roosts. However, these eiders associated with the transmitters may have been scavenged rather than directly depredated by eagles. Hence, we don't know with certainty the proximate or ultimate causes of mortality in our study, but the difficulty of meeting energy demands in late winter combined with the stresses of capture and surgical implantation were likely the major contributors to the high mortality we observed.

Holding birds in captivity in 2005 appeared to dramatically improve post-surgery survival (85% survived >2 weeks). Notably, both holding and assessing birds pre-surgery and holding post-surgery (recovery period) seemed to be important, as the only mortality that occurred was in birds held post-surgery only. The monetary costs of building and maintaining a captive facility were appreciable and may preclude using this method. We don’t believe it is appropriate to draw inference from our model of time-invariant annual survival because of our small sample size and inability to fit a model of temporal heterogeneity to the data; however, similar patterns of time-invariant survival have been reported for other sea ducks (Grand et al., 1998; Wilson et al. 2007).

# Conclusions

Conservation and management of Steller’s eiders requires a detailed understanding of their annual movements and habitat use. Steller’s eiders are dispersed widely in remote areas throughout the annual cycle, particularly during the nonbreeding season when they are at sea (Fredrickson 2001) and little is known about connectivity among life-history stages. Although previous studies offered a fundamental description of annual distribution (Dau et al. 2000) and characterized movements of a small segment of the Pacific population for part of the annual cycle (Martin et al. 2015), this study provides the first complete description of the annual cycle of Pacific Steller’s eiders.

Steller’s eiders used a linear spring migration corridor between wintering and breeding areas, with some individual variability in regional habitat use along the route and appeared to alter annual timing of movements throughout spring migration. Such variation may indicate birds’ ability to adjust in response to changes in food resources (Catry et al. 2004) or weather conditions (Alerstam et al. 2006). Further, our study underscored the importance of areas such as the Kuskokwim Shoals, Gulf of Anadyr, and others to spring migrants, presumably because of predictable and abundant food resources to build nutrient capital (Prop et al. 2003) for migration or reproduction (Gauthier et al. 2003). Little is known about food resources in these areas.

In summer, nearly 35% of the birds in our study were classified as nonbreeders, consistent with the annual periodicity in nonnesting observed on breeding areas in Russia and Alaska (Solovieva 1999, Quakenbush et al. 2004). Steller’s eiders appear to nest primarily in years of high microtine abundance when jaegers and snowy owls also are nesting (Quakenbush et al. 2004). While it’s possible Steller’s eiders use this strategy to increase individual fitness by limiting reproductive effort to years when conditions are favorable (Quakenbush et al. 2004), it is unknown whether birds forfeit nesting in some years or attempt to breed elsewhere (Alaska or Russia). Of the 4 birds that returned to breeding areas in consecutive years, all moved to locations that were from 300–1,000 km from the previous summer. Suspected breeders in our study were widely distributed across their known range in Russia, but appeared to exhibit fidelity to molt sites and winter location.

Dau et al. (2000) also found a broadly dispersed breeding distribution among birds from different molting locations (and presumably multiple winter locations) and concluded a lack of substructuring in molting areas of the Pacific population. Diffuse connectivity between breeding and nonbreeding areas suggests a lack of subpopulation structure throughout the Pacific population and supports a pattern of genetic homogeneity among birds at multiple life-history stages (Pearce et al. 2005). Nonetheless, high fidelity to discrete molting areas (this study, Flint et al. 2000) and winter sites may suggest the potential for demographic independence among birds using these areas.

Many coastal habitats important to sea ducks have been or have potential to be impacted by factors such as mineral extraction (BOEM 2013), urban development (Dixon and Gilchrist 2002), or climate-related changes (Grebmeier et al. 2006). Alteration of marine habitats may evoke strong demographic responses in Steller's eiders because they appear to concentrate at and show high fidelity to discrete nearshore areas during nonbreeding periods. Direct (e.g., reduced survival) or indirect responses (i.e., carryover effects) may influence demographic attributes at multiple breeding locations, including the small number of birds breeding on the North Slope of Alaska where slight perturbations to demography could have dramatic impacts on population dynamics. Our study provides fundamental information, including timing and patterns of use of critical habitat throughout the annual cycle and affiliations among seasonal habitats. Such information is an initial step toward understanding population-limiting factors and helping managers predict and mitigate possible future impacts of habitat changes on the Pacific population of Steller's eider, with the ultimate goal of developing action plans to protect important habitat resources and the birds using those regions.

# Acknowledgments

We thank Leslie Kerr, William Pyle, Jeff Lewis, and Paul Banyas of the Kodiak National Wildlife Refuge for their many invaluable contributions to all aspects of the project. Brad Stevens and Rich MacIntosh, National Marine Fisheries Service, Kodiak Fisheries Research Center provided their facilities, field support and local knowledge. Loren Buck of the University of Alaska graciously provided holding facilities for the eiders and lab space. Exceptional veterinary care and animal husbandry were provided by Dr. Pam Tuomi, Heidi Cline, and Tasha DiMarzio of the Alaska SeaLife Center; Dr. Corrine Brown and Joanne Luebbert of the Alaska Wildlife and Wildfowl Conservation; and Dr. Vicki Vanek of the Alaska Department of Fish and Game (ADF&G). We owe many thanks to Captain Robert L. Lachowsky, Commanding Officer of the U.S. Coast Guard Integrated Support Command Kodiak for use of the Base, and Tom Demi of the Coast Guard Fire Department. We thank the NOAA Fisheries Office for Enforcement for use of their facilities. Also, we thank Tom Rothe, John Crye, Larry Van Daele, Doris Mensch, Celia Rozen, Denby Lloyd, Jim McCullough, and Patty Nelson of the ADF&G for their many contributions. We thank Declan Troy of Troy Ecological Research Associates; Tim Bowman, Nora Rojek and Chris Latty of the USFWS; and Dave Simmers of the USCG for their dedicated assistance in capture operations. Finally, we extend many thanks to Mike Roy, Judy Jacobs, and Sue Detweiler of the USFWS Endangered Species Program and the USFWS for their financial and administrative support.

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Alaska Department of Fish and Game Division of Wildlife Conservation