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Seasonal Movements and Distribution of Steller's Eiders (*Polysticta stelleri*) Wintering at Kodiak Island, Alaska

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ABSTRACT. We used satellite telemetry in 2004–06 to describe the annual movements and habitat use of a segment of the Pacific population of Steller's Eiders (*Polysticta stelleri*) that winters at Kodiak Island, Alaska. Information about broad-scale patterns of seasonal distribution and links among annual cycle stages is 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 after departure from Kodiak Island of 24 satellite-tagged birds: 16 after-second-year (ASY) age class females, one second-year age class female, and seven ASY males. All birds used the same intercontinental migration corridor during spring, but routes and chronology of spring migration appeared to vary by year and among individuals. Sixteen of the 24 birds that were tracked migrated to breeding areas along the Arctic coast of Russia from the Chukotka Peninsula to the Taymyr Peninsula; five birds, assumed to be non-breeding, spent the summer in nearshore waters of Russia and Alaska; and the remaining three birds either died during spring migration or had failed transmitters. Thirteen birds were tracked to molt sites that were broadly distributed along the coast of Alaska. Molt sites included St. Lawrence Island, the Kuskokwim Shoals, Kamishak Bay, and three sites along the Alaska Peninsula. Twelve of these 13 birds returned to Kodiak Island to winter, and a single male wintered on the Alaska Peninsula. Steller's Eiders marked during winter at Kodiak Island were widely distributed during the breeding season, but a large proportion of marked birds returned to molting and wintering areas in two years of the study.

Key words: Alaska, habitat use, Kodiak Island, migration, *Polysticta stelleri*, Russia, satellite telemetry, sea duck, Steller's Eider, waterfowl

RÉSUMÉ. De 2004 à 2006, nous avons recouru à la télémétrie satellitaire pour décrire l'utilisation de l'habitat et les mouvements annuels d'un segment de la population d'eiders de Steller (*Polysticta stelleri*) dans la région du Pacifique, eiders qui hivernent sur l'île Kodiak, en Alaska. Il est essentiel d'obtenir des données sur les tendances à grande échelle de la répartition saisonnière et des liens entre les divers stades du cycle annuel de ces oiseaux afin d'être en mesure d'interpréter leurs tendances démographiques et d'élaborer des stratégies de conservation. Nous avons capturé des oiseaux dans la baie Chiniak de l'île Kodiak vers la fin février et le début mars. Après notre départ de l'île Kodiak, nous avons surveillé les mouvements de 24 oiseaux pistés par satellite : 16 femelles de plus de deux ans, une femelle de deux ans et sept mâles de plus de deux ans. Tous les oiseaux ont emprunté le même couloir de migration intercontinental au printemps, mais les routes et la chronologie de la migration printanière semblaient varier d'une année à l'autre et d'un individu à l'autre. Seize des 24 oiseaux pistés ont migré vers des aires de reproduction situées le long de la côte arctique de la Russie, depuis la presqu'île de Tchoukotkae jusqu'à la presqu'île de Taïmyr; cinq oiseaux, probablement non reproducteurs, ont passé l'été dans les eaux côtières de la Russie et de l'Alaska, tandis que les trois autres oiseaux sont morts pendant la migration printanière ou étaient dotés de transmetteurs défectueux. Treize oiseaux ont été repérés à des sites de mue largement répartis le long de la côte de l'Alaska. Parmi ces sites, notons ceux de l'île Saint-Laurent, du haut-fond de Kuskokwim, de la baie de Kamishak et de trois autres sites le long de la péninsule de l'Alaska. Douze de ces 13 oiseaux sont retournés à l'île Kodiak pour passer l'hiver, et un seul mâle a hiverné dans la péninsule de l'Alaska. Les eiders de Steller qui ont été marqués à l'île Kodiak pendant l'hiver étaient largement répartis pendant la saison de reproduction, mais une grande proportion d'oiseaux pistés sont retournés aux aires de mue et d'hivernage au cours des deux années visées par l'étude.

Mots clés : Alaska, utilisation de l'habitat, île Kodiak, migration, *Polysticta stelleri*, Russie, télémétrie satellitaire, canard de mer, eider de Steller, sauvagine

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INTRODUCTION

The Steller's Eider (*Polysticta stelleri*) is a species of sea duck (Tribe Mergini) found at higher latitudes in a range that includes Arctic and subarctic regions of northern Europe, Russia, and Alaska. Within the species, two geographically distinct populations are recognized, distinguished by their Atlantic and Pacific distributions (Palmer, 1976; Kertell, 1991; Nygård et al., 1995; Dau et al., 2000; Pihl, 2001; Fredrickson, 2001). The Atlantic population, the smaller of the two populations (~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 uses two breeding areas separated by international boundaries (Fredrickson, 2001). A relatively large segment of the population (> 100 000 breeding birds; Hodges and Eldridge, 2001) breeds along the eastern Arctic coast of Russia. A much smaller number (< 1000 breeding birds; Larned et al., 2009) breeds almost exclusively on the Arctic Coastal Plain of Alaska, concentrated over a relatively small area near the village of Barrow (Pitelka, 1974; Flint and Herzog, 1999; Quakenbush et al., 2004). Both breeding segments of the Pacific population winter together, primarily in marine coastal waters of Alaska, from Cook Inlet and Kodiak Island westward along the Alaska Peninsula to the eastern Aleutian Islands (Fredrickson, 2001).

The Pacific population includes more than 80% of the world's population of Steller's Eiders, but numbers declined by more than 50%, from ca. 400 000 – 500 000 birds in the 1960s (Palmer, 1976) to an estimated 200 000 birds in the 1990s (Fredrickson, 2001), and a continued decline is suspected (Larned, 2012). Cause(s) of the decline are unknown, and it has generated global conservation concern (BirdLife International, 2013). Steller's Eiders breeding in Russia are classified as a rare species in the Red Book for the Yakutsk Republic (Solomonov, 1987; Kertell, 1991), and the group breeding in Alaska is listed as threatened under terms of the Endangered Species Act in the United States (Federal Register, 1997). Concerns over the long-term decline of Steller's Eiders have increased focus on this sea duck, particularly in Alaska, where most of the Pacific population winters.

Accordingly, efforts have been made to better understand the biology of Steller's Eider and protect the species and its habitats (U.S. Fish and Wildlife Service, 2002). Recently, understanding has improved of basic demographics and distribution (Jones, 1965; Dau et al., 2000; Quakenbush et al., 2004), but many information gaps remain. Data that contribute to knowledge of migration routes and chronology, seasonal habitat use, and links among life-cycle stages provide valuable broad-scale information for identifying population-limiting factors and for developing conservation strategies. Unfortunately, these data are often difficult to obtain, particularly for species with remote Arctic distributions.

Remote-sensing technologies have valuable applications for monitoring the large-scale movements of migratory birds (Fancy et al., 1988). Satellite telemetry has been used to help describe broad-scale patterns in annual movements and habitat use of numerous sea duck species (e.g., Petersen et al., 1995; Oppel et al., 2008; De La Cruz et al., 2009), including the Atlantic population of Steller's Eiders (Petersen et al., 2006).

In this study, we used satellite telemetry to track 24 individuals from the Pacific population of Steller's Eiders (hereinafter Steller's Eiders) that winters at Kodiak Island in Southcentral Alaska and provide additional information on their annual distribution, seasonal habitat use, and migration. Approximately 5000 Steller's Eiders winter at Kodiak Island (Larned and Zwiefelhofer, 2002) near the eastern limit of the Pacific population's winter range. Our specific objectives were 1) to identify staging, breeding, and molting areas of birds wintering at Kodiak Island and 2) to determine migration routes and timing of annual movements. Such information will allow us to determine connectivity between seasonal habitats and discuss our data in relation to other available information on spatial and temporal movements of Steller's Eiders.

METHODS

In late February through early March of 2004 – 06, we captured Steller's Eiders at northeastern bays of Kodiak Island, Alaska, namely Women's Bay and Kalsin Bay, in the larger Chiniak Bay (57˚ 42′ N, 152˚ 21′ W) (Fig. 1). Kodiak Island is approximately 290 km long and 16 – 96 km wide. It is the largest island in the Kodiak Archipelago, which is located in the northwestern Gulf of Alaska, separated from the Alaska Peninsula by Shelikof Strait. The coastline of Kodiak Island is characterized by numerous fjord-like bays and inlets that remain relatively ice-free during the winter.

We used floating mist nets and decoys (Kaiser et al., 1995; Brodeur et al., 2008) to capture flight-capable Steller's Eiders over open water. Captured birds were immediately removed from mist nets, placed in small pet carriers, and transported to a surgical unit, where they were weighed (± 1.0 g), banded with a U.S. Geological Survey metal leg band, and assigned to either a second-year (SY) or after-second-year (ASY) age class on the basis of plumage characteristics (Palmer, 1976; Gustafson et al., 1997).

A satellite transmitter (a platform transmitter terminal, hereinafter PTT; Microwave Telemetry Inc., Columbia, Maryland) was surgically implanted into the coelomic cavity of each captured bird, following protocols developed by Korschgen et al. (1996) with slight modifications for sea ducks (Mulcahy and Esler, 1999; Robert et al., 2000). The PTTs weighed approximately 39 g, equivalent to 5% or less of the average body mass of captured birds.

In 2004, birds were returned to pet carriers immediately after surgery and allowed to recover from anesthesia before being released. However, in response to high rates

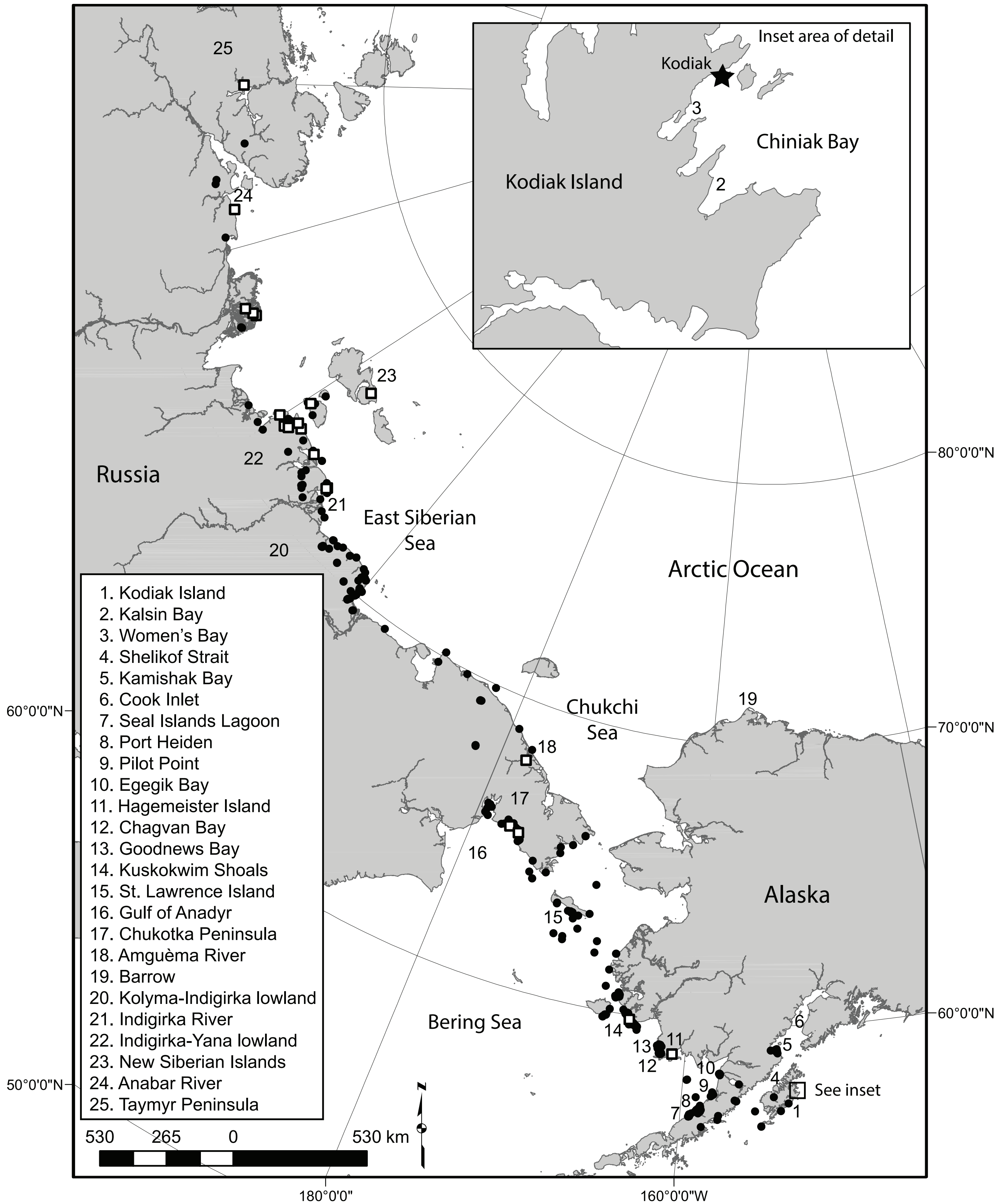

FIG. 1. Spring migration locations (circles) based on the best locations per transmission period and summer locations (open squares) of Steller's Eiders implanted with satellite transmitters during winter at Kodiak Island, Alaska, in 2004–06. Summer locations were calculated as the centroids of minimum convex polygons constructed from the best locations per transmission period.

of post-release mortality in 2004 (see Results), we modified handling procedures in 2005. In that year, we held 12 birds in a captive facility for 6–13 days before surgery and 8–12 days after surgery to alleviate potential effects from capture and facilitate surgical rehabilitation. Nine other birds were held in captivity only after surgery. We released captive birds at their capture sites once they remained dry at the ventral incision site; gained mass; had values within a normal range for hematocrits, total plasma solids, and leukocytes (buffy coat); and exhibited no signs of trauma or lethargy. In 2006, because of the logistical and monetary constraints associated with holding captive birds, we again released birds shortly after allowing them to recover from anesthesia.

We programmed the PTTs with various ON/OFF (duty) cycles based on presumed periods of seasonal bird movements. Specifically, we set duty cycles so that PTTs remained ON for six consecutive hours, during which time they transmitted location data, and OFF for 24 to 120 hours, depending on the life-cycle stage of the birds. For example, ON hours (i.e., data collection) were more frequent during spring migration, when birds were moving long distances, and less frequent during winter, when birds were relatively sedentary.

Satellite telemetry data were acquired using Argos Data Collection and Location Systems (Service Argos, Inc. Landover, Maryland). We filtered data using the PC-SAS Argos-Filter Algorithm v.7.02 (D. Douglas, U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska) for accuracy (Harris et al., 1990), to remove implausible locations, and to retain the best location class per transmission. Filter criteria were based on travel distance, travel rate, and redundancy from previous or subsequent locations (Ely et al., 1997). We plotted filtered locations using ESRI ArcMap™ 10.0 (Environmental Systems Research Institute, Redlands, California). To reduce autocorrelation from consecutive daily locations, we used the best location selected by the filter program from each duty cycle for mapping and distance calculations. To minimize any effects of surgery on bird behavior, data collected within 14 days of release in 2004 and 2006 were excluded from our analyses.

The PTTs were equipped with body temperature and battery-voltage sensors that allowed us to infer the fate of the birds or transmitters (Murray, 2006). For example, ambient body temperature readings indicated that a bird had died, and battery failure was determined by a rapid drop (or sequential drop) in the battery voltage sensor prior to the final signal of a transmitter.

We used the definitions of life-cycle stages (migration, breeding, molting, and wintering) from Petersen et al. (2006), which were based primarily on published information about Steller's Eiders. We defined the start of spring and fall migration as the median date between two sequential locations (e.g., the last date at a site and the first date after departing the site) when birds had moved away from either the wintering or the breeding site and did not return. The duration of spring migration was considered the number of days between the start date of spring migration and the date of first arrival at a confirmed summer location. Spring migration distance was estimated using the sum of distances 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.

A potential breeding area was defined as the last terrestrial location where a bird spent either 10 days or more after its arrival in spring or any 10-day period between 17 June and 10 July before departing to a suspected molting area. This definition is consistent with the timing of nesting observed at the Lena Delta in Russia (Solovieva, 1999; Petersen et al., 2006). Our assignment of breeding areas does not imply breeding status of birds using those areas; however, we refer to birds that use known breeding areas as potential breeding birds and those that use other locations as nonbreeding birds. Molt migration was defined as a series of different locations in the same general direction from the last date a bird was on a potential breeding or summer area until it arrived at a molting area. Molt was considered the period when the rate of movement between locations was less than 0.1 kph for approximately 21 days. We considered the winter period to be a time of relatively sedentary bird movements following molt and fall migration. Staging areas were defined as sites where one or more birds stayed for a minimum of seven days. We did not estimate arrival and departure dates at staging or stopover areas if we did not receive a location for eight or more consecutive days between movements. We calculated the length of stay (residency) at areas as the difference in days between the arrival date and departure date.

Because sample sizes were small in each year, we were not able to quantify the variation in our data (see Lindberg and Walker, 2007); thus, we offer a qualitative assessment of the timing and patterns of movements of Steller's Eiders. Data are presented as medians with a minimum-maximum range. If there was only a single bird, we reported actual values. Also, we were not able to determine if holding birds captive in 2005 influenced our results beyond a qualitative assessment of post-surgery survival.

RESULTS

We implanted 36 Steller's Eiders (25 females, 11 males) with satellite transmitters during the three study years: 10 in 2004, 21 in 2005, and five in 2006. Of these, one female died from aspiration during surgery in 2005, and seven of 15 birds (46.7%) died during the immediate 14-day post-release period in 2004 and 2006. Further, in 2005 three birds (15.0%) died during the immediate 14-day post-surgical period, two in captivity and one two days after release. Another bird had a PTT fail within a few days after surgery. Our procedure in 2005 of holding birds in captivity appeared to improve post-surgery survival dramatically:

85% survived for more than two weeks. Notably, the combination of both holding and assessing birds before surgery and holding them after surgery seemed to be important, as the only mortality that occurred was in those birds that we held only after surgery.

We monitored the movements and fate of 24 satellite-tagged birds (16 ASY females, one SY female, and seven ASY males) that departed in spring from Kodiak Island. We received 3623 locations from five birds marked in 2004, 12 668 locations from 16 birds marked in 2005, and 1005 locations from three birds marked in 2006. After filtering, we used 13.9% of all location data. In 2004, four birds survived for more than one year, but the transmitter in a fifth bird failed on day 82 of transmission, as indicated by a rapid voltage drop in the battery sensor. In 2005, eight birds survived a full year, five birds died between April and September, and an additional three birds had transmitters fail after 140, 141, and 169 days, respectively. Of the three birds marked in 2006 that departed Kodiak Island, one bird died during spring migration and the other two birds had transmitters that failed after 71 and 181 days, respectively, with no indication of bird mortality or transmitter malfunction.

Spring Migration

The departure dates for spring migration from Kodiak Island appeared to be similar across years in our study, although the range of dates over which birds departed was annually variable (Table 1). After departure from Kodiak Island, most marked birds migrated to areas along the north side of the Alaska Peninsula from Egegik Bay south to Seal Islands Lagoon near Port Heiden (Fig. 1) where the majority of birds (17 of 24) staged. However, two birds appeared to stage at either Pilot Point or Egegik Bay, and two other birds migrated northwest to stage in lower Cook Inlet at Kamishak Bay (Table 2). After leaving the Alaska Peninsula, the majority of satellite-tagged birds (71%) migrated northwesterly across Bristol Bay to stage at Kuskokwim Shoals. The remaining birds staged farther to the southeast of Kuskokwim Shoals for a relatively short period at Chagvan Bay or Goodnews Bay (Table 2), though a portion of these birds later moved to Kuskokwim Shoals. The median arrival date at Kuskokwim Shoals was the same in 2004 and 2005, but was ~9 days later in 2006 (Table 2). With the exception of a single bird that spent a month at Kamishak Bay, median residency at Kuskokwim Shoals was longer than at any other staging area (Table 2).

From Kuskokwim Shoals, 83% (19 of 23) of birds traveled across the Bering Sea south of St. Lawrence Island to stage in the northern Gulf of Anadyr (Fig. 1). The other four birds remained in Alaska waters for the summer. One female migrated northeast of St. Lawrence Island along the east coast of the Chukotka Peninsula to the Chukchi Sea. Median arrival dates at the Gulf of Anadyr were later in 2006 than in 2004 and 2005 (Table 2). In general, residency at the Gulf of Anadyr was shorter than at the Alaska Peninsula or Kuskokwim Shoals sites (Table 2).

From the Gulf of Anadyr, birds proceeded northward across the Chukotka Peninsula (minimum overland distance of ~215 km). Birds arrived on coastal lagoons between the Chukchi Sea and the East Siberian Sea in the general region of the Amguèma River, where they remained briefly and then migrated rapidly westward to the Kolyma – Indigirka lowlands (Fig. 1). Median arrival dates at the Kolyma – Indigirka lowlands were in early June in all years. Residency here was shorter than at the Alaska Peninsula or Kuskokwim Shoals sites (Table 2). The Kolyma-Indigirka lowlands appeared to be the final marine staging area for birds before they traveled along inland routes (up to 70 km from the coast) and coastal routes across the lowlands, moving to more westerly summer areas that ranged from the Indigirka Delta to the Taymyr Peninsula (Fig. 1).

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 approximately eight days earlier in 2006 (6 April, 26 March – 10 April) than in 2005 (14 April, 8 April – 25 April), the year they were marked. In addition, these birds departed 12 days earlier than the three birds satellite-tagged in 2006 (18 April, 5 April – 19 April).

Summer Locations

Birds spent the summer either at inland sites in Russia or in nearshore waters off the coasts of Russia and Alaska. Inland sites included those from the Indigirka River Delta west to the Taymyr Peninsula (a difference in distance of ~1700 km) and north to the New Siberian Islands (Fig. 1). Seven of 17 marked birds, one male and six females, used inland sites along the Indigirka – Yana lowlands. Median arrival at inland locations was near mid-June in each year of the study (Table 1). The number of satellite-tagged females that met our criteria to be classified as potential breeding birds varied across years; two met the criteria in 2004, nine in 2005, and one in 2006. Most inland locations 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 on the Taymyr Peninsula used a potential nesting site located approximately 175 km from the coast, and a pair used a site approximately 40 km from the coast on the Indigirka – Yana lowlands (Fig. 1).

Birds that spent the summer in nearshore waters (three males and two females) were considered to be nonbreeding birds. Nearshore sites used by these birds included the northern Gulf of Anadyr, the mouth of the Amguèma River in Chukotka, Russia, and Hagemeister Island and the Kuskokwim Shoals, in the eastern Bering Sea of Alaska (Fig. 1). Median residency at these nearshore locations was 66 days (range: 14 – 77 days). Median distance traveled from Kodiak Island to final summer locations during spring migration appeared to be greater for birds that occupied inland summer sites (3615.1 km, 1779.5 – 4804.4 km; n = 15) than for those that spent the summer in nearshore waters (1694.2 km, 590.5 – 3550.2 km; n = 5). The median

TABLE 1. Median dates of arrival at and departure from seasonal life-cycle stages of Steller's Eiders marked with satellite transmitters at Kodiak Island, Alaska in winters of 2004–06. Also reported are the date ranges (in parentheses) and sample sizes (*n*). In some instances, single dates are reported if the sample size was *n* = 1.

	2004	2005	2006
Departures:			
Spring migration	18 Apr (14–24 Apr) *n* = 5	13 Apr (22 Mar–26 Apr) *n* = 16	18 Apr (4–19 Apr) *n* = 3
Molt migration	20 Aug (16 Jun–24 Aug) *n* = 3	28 Jul (5 Jul–22 Aug) *n* = 9	8 Aug (12 Jul–1 Sep) *n* = 5
Autumn migration	23 Nov (19 Nov–16 Dec) *n* = 4	18 Nov (4 Oct–26 Nov) *n* = 9	16 Nov *n* = 1
Arrivals:			
Inland summer sites	11 Jun (1–22 Jun) *n* = 3	11 Jun (6–20 Jun) *n* = 11	18 Jun (11–28 Jun) *n* = 4
Offshore sites	2 May *n* = 1	9 Jun (10 May–20 Jun) *n* = 4	23 Jun (18–28 Jun) *n* = 2
Molt sites	25 Aug (19 Jul–9 Sep) *n* = 4	24 Aug (24 Jul–1 Sep) *n* = 9	3 Sep (24 Aug–15 Sep) *n* = 4
Winter sites	1 Dec (23 Nov–25 Jan) *n* = 3	21 Nov (18–29 Nov) *n* = 9	22 Nov *n* = 1

TABLE 2. Median dates of arrival at and residency in areas used during spring migration by Steller's Eiders marked with satellite transmitters at Kodiak Island in winters of 2004–06. Also reported are the date ranges (in parentheses) and sample sizes (*n*). In some instances, single dates are reported if the sample size was *n* = 1.

	2004	2005	2006
Kamishak Bay[1]		9 Apr (22 Mar–27 Apr) *n* = 2 22 d (12–32 d)	
Port Heiden	24 Apr (20–24 Apr) *n* = 4 11.5 d (5–13 d)	14 Apr (11–29 Apr) *n* = 10 14.5 d (11–29 d)	29 Apr (20 Apr–9 May) *n* = 2 17 d
Seal Islands Lagoon[1]		18 Apr (14–22 Apr) *n* = 2 11 d (8–14 d)	8 Apr *n* = 1 27 d
Chagvan Bay[1]		25 Apr (24 Apr–1 May) *n* = 4 7 d (1–12 d)	
Goodnews Bay[1]		2 May (21 Apr–4 May) *n* = 5 4 d (1–21 d)	12 May *n* = 1 5 d
Kuskokwim Shoals	30 Apr (20 Apr–7 May) *n* = 3 14.5 d (11–18 d)	30 Apr (29 Apr–13 May) *n* = 10 27.5 d (15–30 d)	8 May (6–9 May) *n* = 2 15.5 d (1–30 d)
Gulf of Anadyr	21 May (20–31 May) *n* = 3 10 d (8–13 d)	29 May (16 May–16 Jun) *n* = 14 4 d (1–13 d)	12 June *n* = 1 3 d
Kolyma–Indigirka lowlands	10 Jun (6–14 Jun) *n* = 2 3.5 d (3–4 d)	2 Jun (31 May–14 Jun) *n* = 12 5 d (1–13 d)	13 Jun *n* = 1 8 d

[1] Blank spaces signify that marked birds were not detected using the area in a given year.

duration of migration between Kodiak Island and summer locations for those birds that used inland sites was 59.0 days (range: 47–80 days; n = 15).

We received location data for four birds that had functional transmitters in a second summer period. All of these birds had been classified as potential breeding birds the previous summer; however, only one of them was classified as a potential breeder in the second summer. This female used an inland site on the Indigirka River Delta approximately 290 km from the site used in the previous summer at the Indigirka–Yana lowlands. Two of the four birds returned to inland sites different from those they had used the previous summer, one at the Lena River Delta (~750 km from previous site) and the other near the Taymyr Peninsula (~1100 km from previous site). However, they did not settle in a single location, so we did not classify them as potential breeders. Another female spent the second summer in nearshore waters of the Indigirka River Delta.

Molt Migration and Molt Locations

In general, all birds migrated to molting areas in Alaska located between 800 and 4500 km away from summer sites, which positioned them closer to their winter location of Kodiak Island (Fig. 2). For potential breeding birds, we considered that molt migration began 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, where many birds remained for up to three weeks after leaving an inland summer location. Post-breeding movements included those from the mainland to the New Siberian Islands and

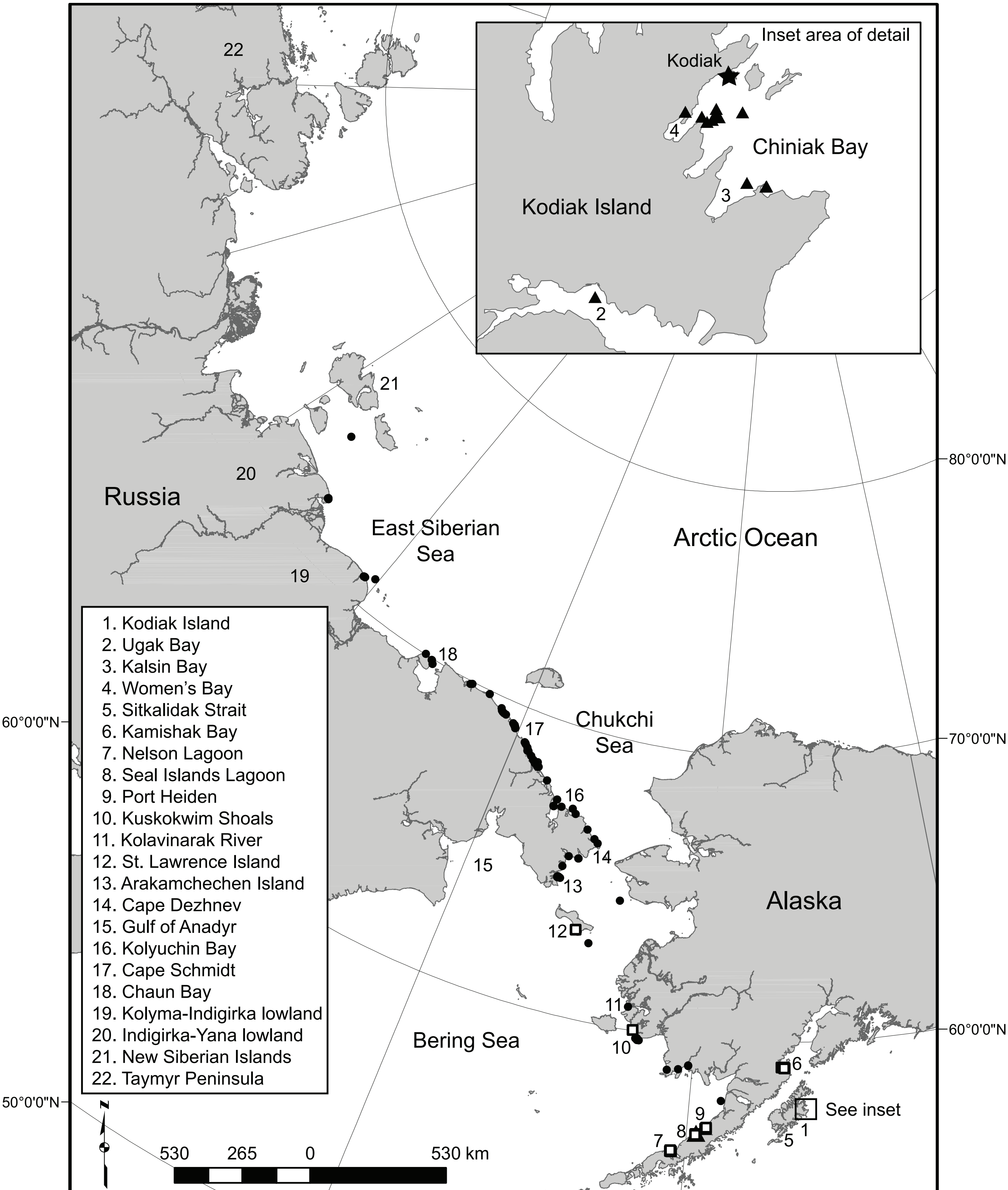

FIG. 2. Molt migration locations (circles) based on the best locations per transmission period, molt areas (open squares), and second-winter locations (triangles) of Steller's Eiders implanted with satellite transmitters during winter at Kodiak Island, Alaska in 2004–06. Molt and second-winter locations were calculated as the centroids of minimum convex polygons constructed from the best locations per transmission period.

movements from more westerly to easterly locations within breeding areas. Thus, for some birds we may have miscalculated the start of molt migration.

Molt migration from suspected breeding areas began significantly earlier for males (6 July, 17 June – 11 July; n = 3) than for females (20 August, 16 July – 25 August; n = 5). After departing breeding areas, birds traveled east along the Arctic coast of Russia. We identified five staging areas used for seven or more days by birds traveling from breeding to molting areas: Arakamchechen Island, the New Siberian Islands, Cape Schmidt, the Kolyma – Indigirka lowlands, and Chaun Bay (Fig. 2). The most important staging area appeared to be a region with a series of lagoons and river mouths between Chaun Bay and Kolyuchin Bay (~890 km apart) along the Arctic coast of Chukotka (Fig. 2). Birds staged here for 2 – 22 days between 5 July and 6 September. After departing this region, birds traveled rapidly to molting areas on the north side of the Alaska Peninsula and Cook Inlet (Fig. 2). Because of the rapid pace of migration, the data we received were insufficient to delineate a migration route: birds completed the migration within one to two duty cycles. The few locations we received indicated that birds traveled in an easterly direction to East Cape and proceeded south across the Bering Strait, passing St. Lawrence Island, to western Alaska (Fig. 2). In contrast 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. However, the frequency at which we received data during this period was insufficient to describe migration routes with certainty.

For nonbreeding birds, we considered the onset of molt migration as the date of the first long movement in an easterly direction followed by successive movements in the same direction. We identified three staging areas used for seven or more days (each by a single bird) during molt migration: Arakamchechen Island in the eastern Bering Strait region, the Kolavinarak River on the Yukon – Kuskokwim Delta, and the Kuskokwim Shoals in western Alaska (Fig. 2). Birds used these areas from 13 to 33 days during 3 July – 16 September. All birds ostensibly flew directly to molt locations after departing summer areas.

We identified molt locations for 13 birds that had functional transmitters. Most birds molted at three 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, one bird likely molted at St. Lawrence Island, and the SY female likely molted at the Kolavinarak River near the Kuskokwim Shoals (Fig. 2). Median arrival date at molt areas was similar in 2004 and 2005, but was later in 2006 (Table 1). Further, females arrived at molt locations later (1 September, 13 August – 10 September; n = 8) than did males (13 August, 20 July – 25 August; n = 5), but residency at molt locations appeared not to differ between the sexes (females: 80.0 days; 72 – 97 days; males: 94.0 days, 52 – 150 days).

Four birds had transmitters that lasted through a second molt period, and three of these birds molted at the same location as in the previous year. One bird molted at Port Heiden in the second year, approximately 155 km from the previous year's location of Nelson Lagoon.

Autumn Migration and Winter Locations

Median departure dates from molting areas were similar across years and were not different for males (20 November, 16 October – 16 December; n = 5) and females (19 November, 4 October – 25 November; n = 8). Most birds appeared to fly directly without stopovers from molt sites to wintering areas. Other birds used stopover locations that included Kamishak Bay, Seal Islands Lagoon, and Port Heiden for short periods before moving to wintering areas.

Of the 13 birds that had functional transmitters in the winters following capture, all but one (92%) returned to within 20 km of their capture sites at Kodiak Island, which suggests a high rate of return to winter locations. One male wintered at Seal Islands Lagoon on the north side of the Alaska Peninsula (Fig. 2). Of the 12 birds that returned to Kodiak Island, all but one female returned to their capture bays. That female returned to Ugak Bay, approximately 30 km southwest of the capture site in Women's Bay (Fig. 2). The timing of returns to capture sites was relatively synchronous across the years of the study (Table 1). One exception was a male that arrived on 22 January in 2005 after spending approximately one month in Sitkalidak Strait at southeast Kodiak Island. All birds remained in the same bays until either their transmitter failed or they departed Kodiak Island the following spring.

DISCUSSION

Our data provide some of the first detailed descriptions of the annual cycle for a wintering segment of Pacific Steller's Eiders. Although these data originated from a small group of birds wintering at the eastern edge of their range, the annual distribution we observed corresponds with the known historical range of Pacific Steller's Eiders (Fredrickson, 2001) and was similar to the distribution of band recoveries from a much larger group of molting Steller's Eiders marked at Izembek Lagoon (1961 – 98) and Nelson Lagoon (1995 – 97) on the Alaska Peninsula (Dau et al, 2000). 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) and on Russian breeding areas (Solovieva, 1999; Hodges and Eldridge, 2001).

However, we recognize that surgical procedures or carrying internal transmitters, or both, possibly influenced some behaviors (e.g., spring departure dates; Wilson and McMahon, 2006; Oppel et al., 2008) of birds in our study.

Spring Migration

Most birds departed Kodiak Island in early to mid-April, but the range between first and last departures was 35 days from late March to late April. Protracted spring departures likely were strongly influenced by physiological condition or environmental cues (Weber et al., 1998) such as regional weather patterns (Alerstam et al., 2006) and appeared to result in asynchronous movements throughout spring migration. However, the apparent large-scale pattern and chronology of migratory movements of satellite-tagged birds were similar. Spring migration was completed in a series of rapid movements punctuated by frequent stopovers at coastal locations, which was comparable to migration patterns found in other Pacific sea duck populations (Phillips et al., 2006; Petersen, 2009; De la Cruz et al., 2009). Between Kodiak Island and their respective summer locations, most birds used the same intercontinental migration corridor that included overland crossings and offshore routes. This was the first study to verify an overland route across the Chukotka Peninsula from the Gulf of Anadyr, and the use of coastal tundra wetlands in spring contrasted with the pattern found for the Atlantic population of Steller's Eiders, which migrated primarily along coastal nearshore waters (Petersen et al., 2006).

At a finer spatial scale, the selection of stopover sites and residency at each site appeared to vary among satellite-tagged birds, but their migration route varied little across years. Individual body condition or predation risks were factors found to contribute to the selection of stopover habitat (Alerstam and Lindstrom, 1990; Lindstrom, 2003), and ice cover of stopover habitats also may have influenced their use by birds in our study. We identified a few critical spring migration stopovers (e.g., Port Heiden and the Kuskokwim Shoals) that most birds (≥ 71%) used for nearly 50% of their total migration time across years. The repeated use of these habitats may be profitable to individuals that are knowledgeable about ecological conditions along the migration route (Bauer et al., 2008) and may indicate the availability of abundant food resources (Piersma, 1987), which are necessary to build nutrient reserves for continued migration or reproductive investment (Gauthier et al., 2003).

Birds we classified as breeders stopped at coastal wetlands in Russia prior to arrival at breeding areas, perhaps to replenish or add to energy stores. Prop et al. (2003) emphasized the importance of final stopover areas to acquire nutrients for reproduction, and this interpretation is consistent with evidence that Steller's Eiders arrived at Russian breeding sites with greater mass than was recorded at wintering areas (Solovieva, 1999; D. Rosenberg, pers. obs.). However, the origin of nutrients (i.e., marine vs. freshwater) used in reproduction of Steller's Eiders is unknown.

Summer Locations

Most study birds that used inland areas were dispersed throughout the known core breeding range of Steller's Eiders (Solovieva, 1999), from the Indigirka River to the Anabar River; however, half of our birds were located on the Indigirka–Yana lowlands. Hodges and Eldridge (2001) also estimated a higher proportion of birds in this region than elsewhere on the eastern Arctic coast of Russia. These studies suggest relatively high-density nesting in this area.

Two birds used inland sites at the fringes of the known breeding range (Dau et al., 2000). The Taymyr Peninsula at the western edge of the range, where one female possibly nested, is hypothesized to be a geographic boundary between the Pacific and Atlantic populations where breeding birds from the two populations overlap (Petersen et al., 2006). Evidence of interchange between these populations has been found (Pearce et al., 2005), but the rate of exchange is unknown. At the eastern edge of the range, a single male briefly used an inland area near the Amguèma River on the Chukotka Peninsula. However, nests have not been located in this region (Solovieva, 1999). If Steller's Eiders nest there, it is likely at very low densities.

In general, birds arrived at breeding areas within 10 days of each other despite the considerably longer distances that some birds traveled. Arrival dates appeared to vary annually, likely because timing of nesting in Steller's Eiders is thought to be highly correlated with annual variability in snowmelt (Solovieva, 1999; Quakenbush et al., 2004). Staging for short periods at multiple locations before arrival at nesting areas may allow Steller's Eiders to assess local conditions in order to optimize nest initiation relative to habitat availability.

Nearly 35% of the birds in our study were classified as nonbreeders. This high proportion might be attributed to altered breeding behavior caused by carrying a PTT. However, non-instrumented females are known to forgo breeding in some years (Ankney and Alisauskas, 1991). For example, Steller's Eiders observed on some localized breeding areas in Arctic Russia and Alaska appear to nest primarily in years of high microtine abundance when nomadic breeding species like jaegers and Snowy Owls are also nesting, which results in an irregular pattern that includes some nesting years and some non-nesting years (Solovieva, 1999; Quakenbush et al., 2004). Steller's Eiders may increase individual fitness by limiting reproductive effort to years when conditions are favorable (Quakenbush et al., 2004). However, it is unknown whether birds forfeit nesting in years when they do not breed at these localized areas or simply attempt to breed elsewhere in Alaska or in Russia. Additional studies are needed that focus on patterns of breeding and site fidelity in Steller's Eiders.

Molt Migration and Molt

Steller's Eiders migrated up to 4500 km from breeding areas in Russia to molting areas in Alaska—locations that were much closer to wintering areas than to breeding areas. A long-distance migration to molt areas close to winter grounds was also observed in the Atlantic population of Steller's Eiders (Petersen et al., 2006). Among our breeding birds, males began molt migration much earlier (~42 days on average) than females, but arrived to molting areas only 18 days (on average) before females. Males spent a longer time migrating (average 55 days) than females (average 15 days), spending much of the additional time at coastal staging areas in Russia. This pattern was expected, as male sea ducks typically depart nesting areas at the onset of incubation, but female departure is delayed by nesting, brood rearing, or both; thus, females likely expedite molt migration to regain flight prior to winter (Oppel et al., 2008).

The pattern of habitat use during molt migration differed from that of spring migration. Birds primarily followed the northern coastline of Russia, making several short stops, with heaviest use of sites between Chaun Bay and Kolyuchin Bay, where most birds spent more than seven days. From there, birds moved to molting areas fairly rapidly, possibly within one to two days (within a PTT duty cycle). In contrast to their spring route, birds appeared to follow a coastal route to the Bering Sea and did not cross overland to the Gulf of Anadyr; however, we received too few locations to identify exact routes.

Most birds in our study used known molting areas. However, three of 13 birds molted in Kamishak Bay, an area in lower Cook Inlet not previously described as a molting area. Birds molted in Kamishak Bay in all three years of our study, and two birds molted there in two consecutive years, which suggests some degree of fidelity to the area. From aerial photographs taken in 2005 and 2006, we estimated that a minimum of 2500 Steller's Eiders molt in Kamishak Bay annually. Most birds were in the vicinity of Douglas Reef, a large reef situated along the southern end of Kamishak Bay (D. Rosenberg, unpubl. data). Larned (2006) estimated that approximately 1700 Steller's Eiders used the area during winter.

Males and females used the same molt areas regardless of breeding classification, but the timing of use differed by sex. Males arrived earlier than females, but sexes departed almost simultaneously. In general, males arrived from late July to mid-August and females from late August to early September, a timing consistent with patterns of arrival at molting areas observed in studies at Izembek Lagoon and Nelson Lagoon, Alaska (Petersen, 1981; Laubhan and Metzner, 1999).

Use of molt sites was independent of breeding area, which supports earlier observations of no substructuring in molting areas (Dau et al., 2000). However, three of four birds in our study returned to the same molting location in two consecutive years, suggesting high return rates. This finding is consistent with an estimate of 95% or greater fidelity to molting areas on the Alaska Peninsula (Flint et al., 2000).

Winter Locations

Our data indicate high return rates to winter areas. With one exception, all birds (n = 12) that carried a functional PTT and survived to the subsequent winter returned to Kodiak Island. A high rate of return to winter locations appears to be a life-history attribute found in many species of sea ducks (Robertson and Cooke, 1999). This practice may allow pairs to reunite and thus maintain the fitness associated with long-term pair bonds, and it may also confer selective advantages associated with site familiarity (knowledge of food resources and predators) that may increase overwinter survival (Robertson et al., 2000). However, high return rates also predispose the small and relatively solitary winter aggregation at Kodiak Island to localized perturbations that may adversely affect these birds, either directly through increased mortality or indirectly through effects on habitat quality and quantity.

CONCLUSIONS

Steller's Eiders were dispersed widely in coastal habitats along a well-defined intercontinental pathway between Alaska and Arctic Russia, and they appear to concentrate at and be faithful to migration and winter habitats. Many of these coastal habitats have been or have the potential to be affected by factors such as mineral extraction (BOEM, 2013), urban development (Dickson and Gilchrist, 2002), or climate-related changes (Grebmeier et al., 2006). The information we present on the timing and distribution of Steller's Eiders in coastal habitats throughout the annual cycle can help managers predict and mitigate possible future impacts of habitat changes on the Pacific population of Steller's Eiders, with the ultimate goal of developing action plans that protect important habitat resources and the birds using those regions.

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