

Trends in Annual Survival of Steller's Eiders Molting at Izembek Lagoon on the Alaska Peninsula, 1993–2006

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ABSTRACT. Izembek Lagoon, located on the Alaska Peninsula, is an important molting area for the Pacific population of Steller's Eiders (*Polysticta stelleri*) and was the site of consistent banding effort during 1993–2006. We used Pradel mark-recapture models to estimate annual survival and population growth rates for adult Steller's Eiders molting at Izembek Lagoon. We designed 32 models that included effects of sex and year on survival, recapture rate, and seniority, as well as potential trends in survival and seniority. The top model incorporated a two-phase trend (1993–98, 1999–2003) in survival and seniority for each sex and fully sex- and year-specific recapture rates. Average annual adult survival was estimated at 0.86 (SE = 0.030) for females and 0.87 (SE = 0.018) for males. Average annual population growth rates since 1998 were estimated to be approximately 1.0 for both sexes. A brief warming event in the Pacific Decadal Oscillation (1997–98) coincided with the lowest estimates of annual survival, while a subsequent return to cooler conditions in the Bering Sea coincided with the highest estimates and an increasing trend in annual survival.

Key words: Alaska, mark-recapture, *Polysticta stelleri*, Pradel, Steller's Eider, survival

RÉSUMÉ. La lagune d'Izembek, située dans la péninsule de l'Alaska, constitue une aire de mue importante pour la population d'eiders de Steller (*Polysticta stelleri*) du Pacifique. Elle a fait l'objet de travaux de baguage soutenus entre 1993 et 2006. Nous nous sommes servis des modèles de marquage et de recapture de Pradel pour estimer les taux de survie et d'accroissement de la population d'eiders de Steller adultes en période de mue à la lagune d'Izembek. Nous avons conçu 32 modèles qui comprenaient les effets du sexe et de l'année sur le taux de survie, le taux de recapture et l'ancienneté. Le meilleur des modèles comprenait une tendance diphasique (de 1993 à 1998, et de 1999 à 2003) en ce qui a trait aux taux de survie et d'ancienneté de chacun des sexes ainsi qu'en ce qui a trait aux taux de recapture entièrement en fonction du sexe et de l'année. Chez les adultes, le taux de survie moyen était estimé à 0,86 (SE = 0,030) pour la femelle et à 0,87 (SE = 0,018) pour le mâle. Depuis 1998, les taux annuels d'accroissement de la population étaient estimés à environ 1,0 dans le cas des deux sexes. Un bref événement de réchauffement dans l'oscillation décadaire du Pacifique (1997-1998) a coïncidé avec les estimations de survie annuelles les plus faibles, tandis que le retour de conditions plus fraîches dans la mer de Béring a coïncidé avec les estimations les plus élevées ainsi qu'à une tendance à la hausse du taux de survie annuel.

Mots clés : Alaska, marquage et recapture, *Polysticta stelleri*, Pradel, eider de Steller, survie

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INTRODUCTION

The Pacific population of Steller's Eiders (*Polysticta stelleri*) breeds, molts, and winters in parts of Alaska and northern Russia. The Alaska breeding population, a small (< 1%) but unknown proportion of the Pacific population, once nested in both northern and western Alaska, but is now limited mainly to the pairs of birds that nest on the Arctic Coastal Plain, concentrated near Barrow, Alaska (Kertell, 1991; Quakenbush et al., 2004). Steller's Eiders breeding in Alaska were listed as threatened under the Endangered Species Act in 1997 (Federal Register, 1997).

Izembek Lagoon, located on the Alaska Peninsula, is one of the most important molting areas for the Pacific population of Steller's Eiders and was the site of consistent banding effort during 1993–2006 (Dau et al., 2000). Previous mark-recapture analyses of selected years of the Izembek banding data have mixed results. Several attempts to quantify annual survival (Flint et al., 2000; Runge, 2004; Reynolds, 2007) have been hindered by small sample sizes and variable banding effort. Flint et al. (2000) used standard Cormack-Jolly-Seber (CJS; Pollock et al., 1990) analyses and multi-state movement models to examine records from 1991–97, a period that included two years (1991 and

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1992) of substantially lower effort. Their work resulted in highly uncertain estimates for those two years and, when coupled with low recapture rates, uninformative and imprecise estimates for 1994, 1995, and 1996. We have therefore omitted 1991 and 1992 from our data analysis (Table 1). Second-order non-Markovian movement models were also used by Flint et al. (2000) and again by Reynolds (2007) for records collected during 1992–2004, but neither study found any differences in survival rates by molting location on the Peninsula. The resulting analyses by Reynolds retained only about 13% of banding records (those with consecutive captures).

Runge (2004) estimated quasi-extinction probabilities using population growth rates (λ) derived through CJS analyses for a period similar to the years studied by Flint et al. (2000). However, because of the range of uncertainty in the input parameters, he was unable to predict a viable long-term population (> 20 years). Estimates of population trajectory are key to determining population viability.

Our objectives were to update survival rates with mark-recapture models that used all of the available banding information obtained during years of consistent effort (1993–2006) and to estimate the approximate rate of population growth (λ) for adult Steller's Eiders molting at Izembek Lagoon. We predicted that annual survival varied by sex and would potentially fluctuate according to observed environmental signals, but would be fairly consistent year to year to support a stable population. The study provides information to support management decisions and planning of future banding efforts.

STUDY AREA

Izembek Lagoon (55°20' N, 162°50' W) is located on the Alaska Peninsula near Cold Bay, Alaska (Fig. 1). The lagoon is a shallow estuary typified by tidal flats, large beds of eelgrass (*Zostera marina*), and vegetated islands (Ward et al., 1997). Steller's Eiders have been captured and banded at Izembek Lagoon since 1961, but banding effort was structured (targeted numbers of birds to be captured) and consistent (no missing years of effort) only during 1993–2006. Birds were rounded up by boat during wing molt (August to October) and marked with U.S. Fish and Wildlife Service metal leg bands (for detailed banding procedure and timing, see Dau et al., 2000).

METHODS

We used the Pradel class of mark-recapture models to estimate adult survival (ϕ), recapture rate (p), and seniority (γ). Seniority is defined as the probability that an individual alive and in the population at time t was also alive and in the population at time $t-1$ (Pradel, 1996). Recruitment can be then estimated by inverting capture histories (reading backward) to determine the probability of a bird being in

TABLE 1. Number of female and male Steller's Eiders (*Polysticta stelleri*) captured and banded at Izembek Lagoon along the Alaska Peninsula, 1993–2006.

Year	Female	Male
1993	4648	1540
1994	2789	2434
1995	5422	2580
1996	1666	2674
1997	1991	2297
1998	1896	717
1999	873	1234
2000	771	1328
2001	895	829
2002	1515	237
2003	1939	671
2004	1485	549
2005	16	222
2006	737	970
Total	26 643	18 282

the population earlier than its current capture year. Population growth rate is derived as:

$$\lambda_t = \frac{\phi_t}{\gamma_{t+1}}$$

Pradel models assume that ϕ , p , γ , and λ all do not vary among individuals of similar capture groups. We found no evidence of variability at the individual level that would violate any of the above assumptions and necessitate using further specified capture groups. We chose the Pradel formulation to extend the analysis of the long-term banding records to obtain estimates of λ and population trajectory that are critical to management of a threatened species. Concurrent estimates of λ and ϕ are particularly useful since small changes in adult female survival have been shown to have large effects on the population dynamics of waterfowl species (Flint et al., 1998). We used median \hat{c} of the CJS variant of the same model structure as a variance inflation factor and measure of goodness-of-fit since the likelihood of the CJS model and lack of fit of the Pradel model are both based on recapture likelihood (Matlock and Skoda, 2009). Values of median $\hat{c} < 3$ indicate adequate fit of the model. We designed and tested 32 models (Appendix 1) in Program MARK (White and Burnham, 1999) that included effects of sex and year and potential trends in survival and seniority based on the capture/recapture of 26 643 female and 18 282 male Steller's Eiders. We tested first- and second-order trends in survival over time, as well as two-phase trends of varying years based on current ecosystem-level research in the Bering Sea region (Grebmeier et al., 2006). Uncommon atmospheric conditions in 1997 produced warmer air temperatures and calmer sea conditions that altered primary phytoplankton production, which in turn affected the entire marine food web (Napp and Hunt, 2001). In some models, we allowed the last three years of the analysis to vary by sex and time (thus not including them in any potential trend in survival rate) in an attempt to remove the potential effect of low recapture rates on estimates of survival in the final years of banding (2004, 2005,

and 2006). We used Akaike's Information Criterion for small samples (AICc) to rank models by ΔAICc values and used AICc weights (w_i) to determine support for a given model against competing models (Burnham and Anderson, 2002).

RESULTS

The top model— $\phi (s^*T_2) p (s^*t) \gamma (s^*T_2)$ —incorporated a two-phase trend ($T_2 = 1993\text{--}98$, then $1999\text{--}2003$) in survival for each sex (s), fully sex- and time-specific recapture rates (s^*t), and the same two-phase trend in seniority. The AICc weight for this model was 1.0, with all other models more than 500 AICc units away. The estimate of the median for the top model was 2.081 (SE = 0.009), indicating no lack of fit.

Annual survival of female Steller's Eiders increased slightly during 1993–98, dropped sharply from 1998 to 1999, and then increased sharply during 1999–2003 (Fig. 2). Average annual survival (1993–2003) for females was 0.86 (SE = 0.030), average annual recapture rate was 0.16 (SE = 0.022), and average seniority was 0.87 (SE = 0.0013). Estimates of annual survival for females were between the 0.90 reported by Flint et al. (2000) and the 0.81 reported by Reynolds (2007).

Annual survival of male Steller's Eiders decreased during 1993–98, then increased during 1999–2003 (Fig. 2). Average annual survival for males was 0.87 (SE = 0.018), average annual recapture rate was 0.23 (SE = 0.080), and average seniority was 0.89 (SE = 0.028). Estimates of annual survival for males were much higher than the 0.77 reported by Flint et al. (2000) and the 0.76 reported by Reynolds (2007).

Derived estimates of population growth followed the same trends as those for survival of each sex (Table 2), and mean annual growth rates (1993–2003) of the two sexes were approximately equal: 1.00 (SE = 0.036) for females and 0.99 (SE = 0.052) for males.

DISCUSSION

Our estimates demonstrate increases since 1998 in annual survival rates for both sexes of Steller's Eiders molting along the Alaska Peninsula. One notable finding of our analysis was that the difference between mean annual survival for females (0.86, SE = 0.030) and males (0.87, SE = 0.018) was not statistically significant. This finding differs from previous estimates derived from subsets of the full data set (Flint et al., 2000, analyzed early in the long-term effort) and estimates using movement memory restrictions (Reynolds, 2007). Movement memory refers to the birds' ability to "remember" which side of the lagoon they visited the previous year and return to it. The survival of such birds differs from that of birds that do not "remember," but since testing this "memory" requires following the bird for three

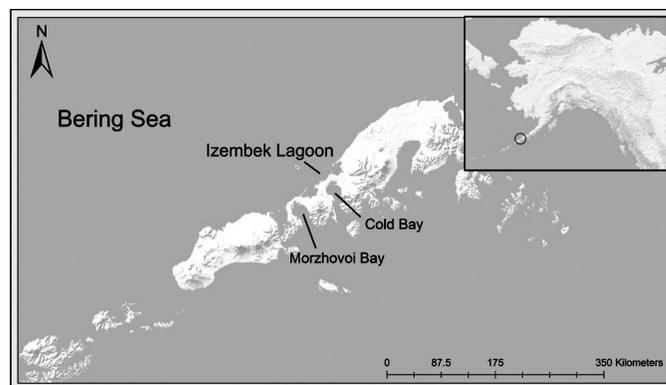


FIG. 1. Izembek Lagoon along the southern Alaska Peninsula near Cold Bay, Alaska.

seasons, the use of this criterion severely restricts the sample population. In waterfowl, survival of females is often found to be lower than that of males because of the energetic cost and predation risk associated with nesting and brood-rearing (Kertell, 1991; Dau et al., 2000; Flint et al., 2000). The difference between our estimates and those of previous studies is likely the product of our inclusion of more years of banding records and exclusion of movement memory restrictions, which allowed us to include 100% of records as opposed to 13% and reduced the potential bias a small sample size could introduce into grouped estimates. Annual survival rates of female Spectacled Eiders (*Somateria fischeri*, 0.78; Grand et al., 1998) and nesting female Common Eiders (*Somateria mollissima*, 0.89; Wilson et al., 2007), two related and sympatrically nesting eider species in Alaska, were both comparable to our estimate of 0.86.

Derived estimates of approximately 1.0 for population growth indicate recent stability in the population molting at Izembek Lagoon. Recent stability in growth rates for Steller's Eiders has also been demonstrated by annual flock surveys during spring staging in the Bering Sea and by nesting surveys near Barrow, Alaska (Obritschkewitsch and Ritchie, 2008; Larned, 2011). Obritschkewitsch and Ritchie (2008) compiled results of ground and aerial surveys between 1999 and 2008 on nesting habitat near Barrow, Alaska, while Larned (2011) conducted aerial counts on pre-breeding eiders along the Bering Sea coast during 1992–2011. Although these two surveys differed in their timing and effort, both produced estimates of population growth rates that are similar to ours and indicate relative stability since 2003, though ambiguity in the reference populations (Pacific, Russian-breeding, Alaska-breeding) persists. Some potential causes of the decline in the years prior to federal listing include loss of historical nesting habitat, periodic and episodic nesting, incidental take by hunting, lower nest success due to increased predation on eggs and ducklings, and low survival rates due to lack of available food or lead poisoning (Kertell, 1991; Franson et al., 1995; Grand et al., 1998; Flint and Herzog, 1999; Flint et al., 2000; Quakenbush et al., 2004). Recent stability could be due to a variety of factors, including the elimination of lead shot

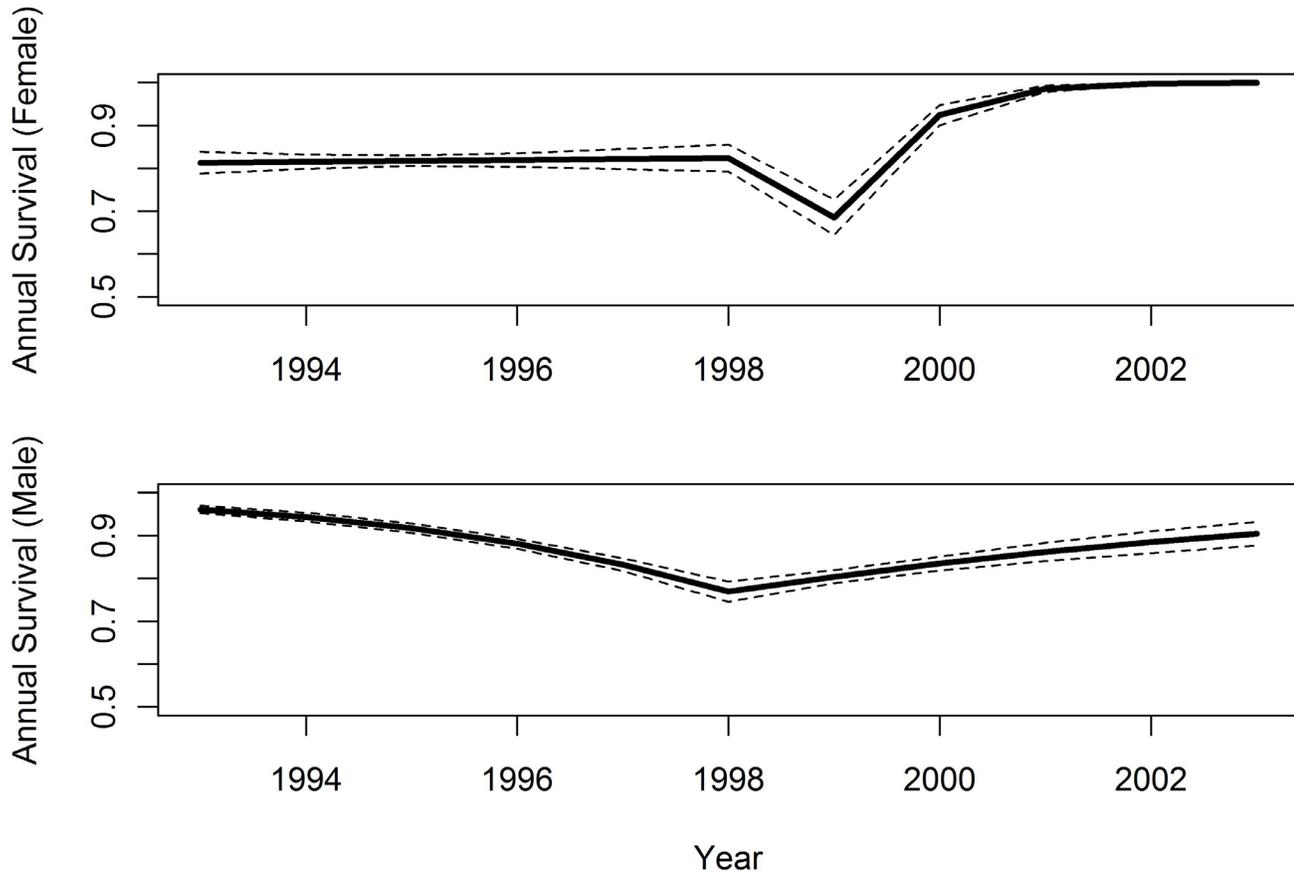


FIG. 2. Annual survival estimates (solid line) with 95% confidence intervals (dashed line) for female and male Steller's Eiders (*Polysticta stelleri*) molting at Izembek Lagoon, Alaska, 1993–2003.

use in breeding, molting, and wintering habitat, predator control efforts, and other protections since the 1997 listing under the Endangered Species Act. Estimates of λ indicative of a stable population of Steller's Eiders molting along the Alaska Peninsula are encouraging, but continued banding and survey effort are necessary to confirm the trend.

The lowest estimate of female survival was that for 1999, immediately after a brief warming event in the Pacific Decadal Oscillation in 1997–98 before it reversed to a slightly colder trend in 1999 and beyond (Napp and Hunt, 2001; Bond et al., 2003; Peterson and Schwing, 2003). In contrast, male survival declined between 1993 and 1998, after which survival increased. The difference between sexes in the magnitude of the changes in survival could be due to the unique and complex breeding biology observed in Steller's Eiders and is not necessarily directly attributable to climate conditions (Quakenbush et al., 2004). The observed deviations in sea surface temperature, wind velocity, and other components of climate indices were not as severe as in previously documented regime shifts (Rodionov and Overland, 2005), but were substantial enough to alter zooplankton bloom timing, which in turn affected fish, seabird, and benthic communities (Napp and Hunt, 2001; Hamazaki et al., 2005; Grebmeier et al., 2006). Steller's Eiders depend on benthic biomass while in the Bering Sea region during molting and pre-breeding (Petersen, 1981). Substantial

TABLE 2. Estimates of growth rate (with standard error) for female and male Steller's Eiders (*Polysticta stelleri*) molting at Izembek Lagoon, Alaska, in 1993–2003.

Year	Females		Males	
	Growth rate	SE	Growth rate	SE
1993	0.93	0.012	1.36	0.029
1994	0.94	0.0083	1.23	0.01
1995	0.94	0.0061	1.12	0.008
1996	0.94	0.0065	1.02	0.0047
1997	0.95	0.0092	0.93	0.005
1998	0.95	0.013	0.83	0.0085
1999	0.79	0.017	0.85	0.005
2000	1.07	0.01	0.87	0.0056
2001	1.14	0.0058	0.89	0.0075
2002	1.16	0.0065	0.90	0.0091
2003	1.16	0.0081	0.92	0.01

decreases in benthic biomass or shifts in its species composition could account for lower survival during years of anomalous climate conditions. Similar decreases in survival and recruitment, as well as increased mortality due to prey base shifts caused by sea conditions, have been reported for other avian species in the Bering Sea (Kitaysky et al., 2006; Lovvorn et al., 2009). A return to cooler trends in oceanic conditions after 1998 coincided with the highest estimates of annual survival for female Steller's Eiders and increasing trends in survival for both males and females. If the

population of Steller's Eiders molting at Izembek Lagoon is sensitive to even minor changes in overall marine conditions in the Bering Sea, then we would predict decreasing estimates of annual survival in the event of future warming events indicated by the Pacific Decadal Oscillation. We hesitate, however, to base any conclusions on a single environmental event that occurred coincidentally during the banding period. The trends we observed also illustrate the importance of committing to long-term data collection, as the anomalous environmental conditions and subsequent biological response in 1998 could easily have been missed with a shorter banding regime.

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APPENDIX 1. Candidate models used to estimate adult survival (ϕ), recapture rate (p), and seniority (γ) of Steller's Eiders molting at Izembek Lagoon, Alaska, 1993–2003, by sex (s), year (t), temporal trend (T), quadratic temporal trend (T^2), or constant (\cdot). Temporal trends were defined as: $T_1 = 1993\text{--}2003$, $T_2 = 1993\text{--}98$ and $1999\text{--}2003$, $T_3 = 1993\text{--}97$ and $1998\text{--}2003$, and $T_4 = 1993\text{--}99$ and $2000\text{--}03$.

- $\phi (s^*T_1) p (s^*t) \gamma (s^*T_1)$
- $\phi (s^*T_2) p (s^*t) \gamma (s^*T_2)$
- $\phi (s^*T_3) p (s^*t) \gamma (s^*T_3)$
- $\phi (s^*T_4) p (s^*t) \gamma (s^*T_4)$
- $\phi (s^*T_1) p (s^*t) \gamma (s)$
- $\phi (s^*T_2) p (s^*t) \gamma (s)$
- $\phi (s^*T_3) p (s^*t) \gamma (s)$
- $\phi (s^*T_4) p (s^*t) \gamma (s)$
- $\phi (T_1) p (s^*t) \gamma (T_1)$
- $\phi (T_2) p (s^*t) \gamma (T_2)$
- $\phi (T_3) p (s^*t) \gamma (T_3)$
- $\phi (T_4) p (s^*t) \gamma (T_4)$
- $\phi (s^*T_2) p (s^*t) \gamma (T_1)$
- $\phi (s^*T_3) p (s^*t) \gamma (T_1)$
- $\phi (s^*T_4) p (s^*t) \gamma (T_1)$
- $\phi (s+T_1) p (s^*t) \gamma (s+T_1)$
- $\phi (s+T_2) p (s^*t) \gamma (s+T_2)$
- $\phi (s+T_3) p (s^*t) \gamma (s+T_3)$
- $\phi (s+t) p (s^*t) \gamma (s+t)$
- $\phi (s) p (s^*t) \gamma (s)$
- $\phi (s+T_1) p (s^*t) \gamma (s)$
- $\phi (s+T_2) p (s^*t) \gamma (s)$
- $\phi (s+T_3) p (s^*t) \gamma (s)$
- $\phi (s+t) p (s^*t) \gamma (s)$
- $\phi (s) p (s) \gamma (s)$
- $\phi (t) p (s^*t) \gamma (t)$
- $\phi (t) p (t) \gamma (t)$
- $\phi (s^*T_1^2) p (s^*t) \gamma (t)$
- $\phi (s^*T_2^2) p (s^*t) \gamma (t)$
- $\phi (s^*T_3^2) p (s^*t) \gamma (t)$
- $\phi (s^*T_4^2) p (s^*t) \gamma (t)$
- $\phi (\cdot) p (\cdot) \gamma (\cdot)$