NRC Research Press

ARTICLE

Interacting effects of latitude, mass, age, and sex on winter survival of Surf Scoters (*Melanitta perspicillata*): implications for differential migration

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Abstract: We quantified variation in winter survival of Surf Scoters (*Melanitta perspicillata* (L., 1758)) across nearly 30° of latitude on the Pacific coast of North America to evaluate potential effects on winter distributions, including observed differential distributions of age and sex classes. We monitored fates of 297 radio-marked Surf Scoters at three study sites: (1) near the northern periphery of their wintering range in southeast Alaska, USA, (2) the range core in British Columbia, Canada, and (3) the southern periphery in Baja California, Mexico. We detected 34 mortalities and determined that survival averaged lower at the range peripheries than in the range core, was lower during mid-winter than during late winter at all sites, and was positively correlated with body mass within locations. Although neither age nor sex class had direct effects, mass effects led to differential survival patterns among classes. When simultaneously incorporating these interacting influences, adult males of mean mass for their location had highest survival at the northern range periphery in Alaska, whereas adult females and juveniles had higher survival at the range core and the southern periphery. Our observations help to explain patterns of differential migration and distribution reported for this species and highlight seasonal periods (mid-winter) and locations (range peripheries) of elevated levels of mortality for demographically important age–sex classes (adult females).

Key words: demography, distribution, *Melanitta perspicillata*, sea duck, Surf Scoter.

Résumé : Nous avons quantifié les variations de la survie hivernale des macreuses à front blanc (*Melanitta perspicillata* (L., 1758)) sur 30° de latitude le long de la côte pacifique de l'Amérique du Nord afin d'en évaluer les effets potentiels sur la répartition hivernale, dont différentes répartitions observées selon les classes d'âge et de sexe. Nous avons surveillé le destin de 297 macreuses munies de radioémetteurs dans les trois sites d'étude suivants : (1) près de la bordure nord de leur aire d'hivernage dans le sud-est de l'Alaska (États-Unis), (2) au cœur de leur aire de répartition en Colombie-Britannique (Canada) et (3) à la bordure méridionale de leur aire de répartition, en Basse-Californie (Mexique). Nous avons relevé 34 cas de mortalité et déterminé que la survie moyenne était plus faible en bordure de l'aire de répartition qu'en son centre, qu'elle était plus faible au milieu de l'hiver qu'à la fin de l'hiver dans tous les sites, et qu'elle était possiblement corrélée à la masse du corps à l'intérieur d'un même site. Si ni la classe d'âge, ni la classe de sexe n'avaient d'effet direct, des effets de la masse entraînaient différents motifs de survie au sein des classes. Quand ces influences interactives étaient incluses simultanément, les mâles adultes de masse moyenne pour leur emplacement présentaient le taux de survie le plus élevé à la bordure nord de l'aire de répartition en Alaska, alors que les femelles adultes et les juvéniles présentaient le plus grand taux de survie au centre de l'aire de répartition et à sa bordure méridionale. Nos observations aident à expliquer les motifs de migration et de répartition différentielles signalés pour cette espèce et font ressortir des périodes saisonnières (le milieu de l'hiver) et des lieux (aux bordures de l'aire de répartition) de mortalité élevée pour des classes d'âge et de sexe importantes sur le plan démographique (femelles adultes). [Traduit par la Rédaction]

Mots-clés : démographie, répartition, *Melanitta perspicillata*, canard marin, macreuse à front blanc.

Introduction

Understanding factors affecting animal distributions is a fundamental issue in ecology. Migratory animals often occur in a variety of habitats and conditions both among and within annual cycle stages. Population dynamics may vary across species ranges, with range cores tending to be more stable (Brown et al. 1995; Doherty et al. 2003). At each stage of the annual cycle, factors affecting migratory bird distributions may include resources (Johnson and Sherry 2001), competition (Kelly et al. 2003), climate (Zipkin et al. 2010), disease (Rocke et al. 2005), and predation danger (Lank et al. 2003). These factors may have differential effects among individuals, based on age (Krementz et al. 1987), sex (Schmutz and Ely

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Received 24 June 2015. Accepted 22 December 2015.

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Can. J. Zool. **94**: 233–241 (2016) dx.doi.org/10.1139/cjz-2015-0107

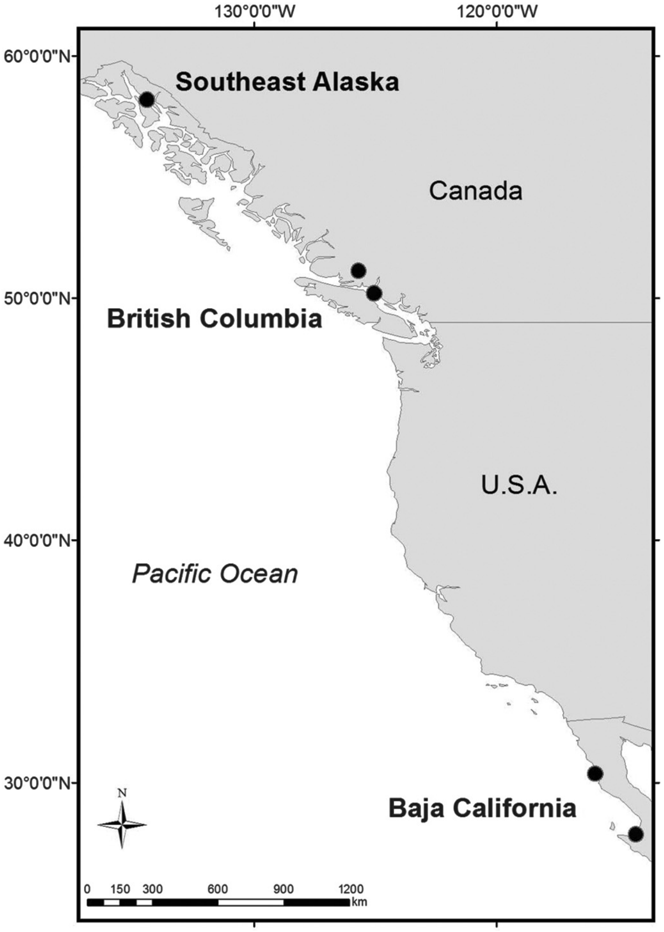
1999), mass (Mason et al. 2006), condition (Boos et al. 2002), or other attributes. In turn, latitudinal variation in influential factors, and their differential effects on individuals with different attributes, may lead to differential migration and latitudinal distributions skewed by age or sex classes or other characteristics (Cristol et al. 1999). Although rarely considered directly, demographic rates, including survival effects, may be a mechanism driving differential distribution of migratory animals (Tilman and Kareiva 1997).

Variation in winter survival is likely to have implications for waterfowl migration strategies, as mortality during winter may be particularly high (Conroy et al. 1989). Potential stresses associated with the overwintering period include increased thermoregulatory costs (Lehikoinen et al. 2006), less time available for foraging due to decreased day length (Systad et al. 2000), prey depletion (Kirk et al. 2008), increased predation (Anderson et al. 2012), habitat degradation (Pettifor et al. 2000), and exposure to contaminants (Esler et al. 2000*a*). These factors can differ across a species wintering range and may have differential survival effects among individuals, based on their age, sex, mass, condition, or other attributes.

Surf Scoters (*Melanitta perspicillata* (L., 1758)) are migratory sea ducks that breed in boreal forest habitats throughout northern Canada and Alaska and winter in nearshore marine habitats along the Pacific and Atlantic coasts of North America. Their winter range on the Pacific Coast extends more than 5000 km over nearly 35° of latitude stretching from the Aleutian Islands in Alaska to the Baja Peninsula in Mexico (Savard et al. 1998). Previous studies have addressed Surf Scoter abundance, movements, foraging behavior, and physiological condition during winter (Kirk et al. 2007, 2008; Lewis et al. 2008; Anderson and Lovvorn 2011; VanStratt 2011). Lacking are estimates that quantify fitness consequences of responses to habitat variation, and that identify when and how distributions are influenced within the annual cycle.

Challenges facing Surf Scoters during the nonbreeding period vary across a latitudinal gradient. Surf Scoters wintering at northern latitudes (e.g., southeast Alaska) or in the core of their range (coastal British Columbia) face very different environmental conditions and less costly migrations compared with Surf Scoters wintering in the southernmost portion of the range (Baja California). Surf Scoters have been shown to exhibit differential migration along the Pacific coast, with higher proportions of males and adults wintering at more northern latitudes and higher proportions of females and juveniles wintering at more southern latitudes (Iverson et al. 2004). However, factors leading to differential migration in Surf Scoters are unknown and we hypothesized that differential survival among age and sex classes may be involved. Few studies have examined variation in winter survival rates at a continental scale or considered trade-offs associated with wintering site selection, despite the implications for population dynamics, distribution, and conservation. We measured Surf Scoter survival over the latitudinal span of their wintering areas, allowing for consideration of geographical variation in survival and influences on Surf Scoter distribution. We tested the hypothesis that winter survival varied by latitude, with the a priori prediction that survival would be lower at range extremes than at the range core. We also evaluated the hypothesis that observed differential migration by Surf Scoters is driven by differential survival of age and sex classes by latitude. Support for this hypothesis would come in the form of survival probabilities that correspond with distributions of age and sex classes, i.e., higher survival of adult males at higher latitudes and higher survival of females and juveniles at lower latitudes.

Fig. 1. Locations of study sites on Surf Scoter (*Melanitta perspicillata*) survival during winter in southeast Alaska (USA; 2009–2010), British Columbia (Canada; 2001–2005), and Baja California (Mexico; 2006–2008). The Surf Scoter wintering range extends from the Aleutian Islands in Alaska (not shown) to the Baja Peninsula in Mexico.



Materials and methods

Study areas

During 2001–2010, we attached very high frequency (VHF) radio transmitters to Surf Scoters during winter in three areas (Fig. 1): southeast Alaska (USA; hereafter SE AK); the Strait of Georgia, British Columbia (Canada; hereafter BC); Baja California, Mexico (hereafter Baja). The SE AK site was near the northern extent of the wintering range of Surf Scoters near Juneau, Alaska, USA (58.4°N, 134.5°W). Hodges et al. (2008) estimated that ca. 77 000 scoters (species of the genus *Melanitta* F. Boie, 1822) winter in SE AK, with Surf Scoters being the most numerous species. Deep channels and fjords are characteristic of the area. Blue mussels (*Mytilus trossulus* Gould, 1850) were common and widespread in rocky intertidal areas and constituted the primary prey of Surf Scoters (J.W. Hupp, unpublished data). Predators of Surf Scoters included Bald Eagles (*Haliaeetus leucocephalus* (L., 1766)) and American mink (*Neovison vison* (Schreber, 1777)) (Anderson et al. 2012).

We collected survival data at the core of the Surf Scoter wintering range in BC at two sites: Malaspina Inlet (50.0°N, 124.7°W) and Baynes Sound (49.5°N, 124.8°W). Malaspina Inlet is located in the northern Strait of Georgia and includes the waters of Malaspina, Okeover, and Lancelot inlets on mainland British Columbia. Approximately 100 000 Surf Scoters winter in the Strait of Georgia (Crewe et al. 2012), which constitutes only a portion of their coastal BC wintering range. Similar to the SE AK site, this area is

Table 1. Numbers of very high frequency (VHF) radio transmitters deployed on wintering Surf Scoters (*Melanitta perspicillata*) and monitored beyond a postcapture censor period by location, year, and age–sex class.

	Age–sex class[a]				
Location and year	M AHY	F AHY	M HY	F HY	Total
Southeast Alaska, USA					
2008–2009	12 (1)	7 (0)	11 (4)	8 (3)	38 (8)
2009–2010	12 (1)	15 (2)	9 (1)	9 (2)	45 (6)
Strait of Georgia, B.C., Canada					
2001–2002	17 (1)	8 (1)	5 (2)	3 (1)	33 (5)
2002–2003	24 (4)	10 (0)	1 (0)	2 (0)	37 (4)
2003–2004	16 (3)	7 (1)	1 (0)	2 (0)	26 (4)
2004–2005	26 (1)	14 (1)	14 (1)	19 (0)	73 (3)
Baja California, Mexico					
2006–2007	8 (0)	8 (0)	7 (3)	7 (0)	30 (3)
2007–2008	4 (0)	5 (1)	0 (0)	6 (0)	15 (1)
Total	119 (11)	74 (6)	48 (11)	56 (6)	297 (34)

Note: Numbers in parentheses are confirmed surf scoter mortalities included in the analysis.
[a]Age–sex class abbreviations are as follows: M, male; F, female; AHY, after hatch year; HY, hatch year.

characterized by steep fjords and protected inlets with mostly rocky shores and few soft-sediment beaches. Baynes Sound is located on the east shoreline of Vancouver Island and is a shallow coastal channel with many areas of soft-bottom (mud and sand) flats throughout its small, protected bays. Bald Eagles were abundant at these sites and were confirmed to prey on scoters (Anderson et al. 2012).

Data collected in Baja represented the southern periphery of the Surf Scoter wintering range. Our studies in Baja were conducted in two bays: Bahía San Quintín (30.5°N, 116.0°W) and Laguna Ojo de Liebre (28.0°N, 114.0°W); both were characterized by shallow water and intertidal mud flats. Unlike scoters at more northern latitudes, scoters at these sites primarily fed on infaunal invertebrates such as ghost shrimp (species of the genus *Callianassa* Leach, 1814) (D.H. Ward, unpublished data). In contrast to the SE AK and BC sites, there were virtually no avian or mammalian predators at these southern wintering sites; Bald Eagles were extremely rare at the Baja sites (D.H. Ward, personal communication).

Captures and monitoring

Surf scoters were captured during early winter (November and December) using floating mist nets (Brodeur et al. 2008) at all study sites. We recorded body mass of all captured scoters (±1 g) and each was marked with a uniquely numbered metal tarsal band. We determined sex based on plumage characteristics and age class (hatch year (HY) is <1 year old; after hatch year (AHY) is >1 year old) based on plumage characteristics and bursal depth (Mather and Esler 1999; Iverson et al. 2003). VHF radio transmitters were fitted to 297 individuals, distributed among age and sex classes, as well as year and region (Table 1). Transmitters deployed in SE AK and Baja were attached using subcutaneous prongs and cyanoacrylate adhesive (Lewis and Flint 2008). In BC, deployed transmitters were attached using a variety of methods, including subcutaneous prong and glue, abdominal implants, or subcutaneous implants (Iverson et al. 2006). Iverson et al. (2006) determined that survival rates did not differ among transmitter attachment methods following an acclimation period. Each transmitter was equipped with a mortality sensor that doubled the signal pulse rate if the transmitter did not move for >12 h. Monitoring frequency differed among study areas; however, transmitter status was checked at least once every 10 days throughout the monitoring period. Fates and bird locations were obtained using handheld Yagi antennas or antennas mounted on vehicles or boats, and in some instances, aerial telemetry flights were used to locate marked individuals that had moved out of the immediate study area (Kirk et al. 2008). For each transmitter that displayed a mortality signal, we conducted a search to confirm the status and attempt to determine cause of death (Anderson et al. 2012). If transmitters disappeared without detection of a mortality signal, we assumed this was due to radio failure, or a shed radio, and included these in the analysis up to the point when we did not detect their transmitter.

Captures of Surf Scoters and deployment of VHF radios occurred during four winters in the Strait of Georgia, BC, three winters in Baynes Sound (2001–2002, 2002–2003, and 2003–2004), and one winter in Malaspina Inlet (2004–2005), and two winters each in SE AK (2008–2009 and 2009–2010) and Baja (2006–2007 and 2007–2008). Some abdominally implanted transmitters deployed in Baynes Sound during winter 2002–2003 were still active during winter 2003–2004 ($n = 12$) and were used to generate survival data in both winters. The deployment date for these transmitters in 2003–2004 was considered to be the first day any birds were captured during the 2003–2004 field season (2 December 2003) and these individuals were not subject to a postcapture censor period (see below). This research was conducted under Federal Bird Banding Permits and the Animal Care Protocol was authorized by the Simon Fraser University Animal Care Committee (UACC).

Analysis

We used a modified Mayfield method of nest survival analysis procedures in program MARK version 6.2 to generate daily survival rates (DSR) and cumulative survival rates (CSR) during the overwintering period for Surf Scoters (Dinsmore et al. 2002; Rotella et al. 2004). The nest survival function is recommended for “ragged” telemetry data because it does not require that animals be monitored in discrete intervals or that an exact date of death be known (White and Burnham 1999). We generated encounter histories from the signal monitoring data by classifying the fate of radio-marked individuals as alive, dead, or not detected at each monitoring session. Encounter histories for each individual included the following: the day of capture (i), the last day the bird was detected alive (j), the last day the transmitter was monitored (k), and the fate of the bird (0 = alive, 1 = dead). To avoid potential biases associated with deleterious effects of capture, handling, and transmitter attachment, we applied a censor period of 7 day post capture for externally mounted transmitters and 14 day for implanted transmitters (Esler et al. 2000*b*; Iverson et al. 2006). Mortalities of Surf Scoters that occurred after these censor periods were assumed to be unrelated to effects of capture, handling, or radio attachment, which could have reduced survivorship during the censor period but likely not beyond (Esler et al. 2000*b*). Birds that died during the censor period or were never heard alive after the censor period were excluded from analyses. The date

17 November was the earliest a transmitter was deployed during any of the years at any of our study areas and, with a 7-day post-capture censor period, 24 November became day 1 (*i*) in our analysis. This date was used to calibrate the other information needed for the encounter history (*j*, *k*) for each individual. The last day that we monitored for survival was 1 April, giving us a 129-day study period (24 November to 1 April).

To investigate variation in DSR through winter, we evaluated a candidate set of 48 multiple linear logistic regression models. We examined five variables that potentially influenced survival, including (1) study area location (Location), (2) period of winter (Period), (3) age (Age), (4) sex (Sex), and (5) location-adjusted residual mass (MASSLOC). We considered candidate models with individual main effects, and all additive combinations of main effects, and in some models included interactions between Location and other predictor variables.

We treated our three Location variables (SE AK, BC, and Baja) as grouping variables and ran an exploratory analysis to determine if there was variation in survival among years at each location by adding individual covariates for a year effect into the data set. We found that between-year differences in survival were quite small within sites (range 0.01–0.08). Because none of the years in which survival data were collected were consistent among study areas, multiple winters at each site were pooled for analysis, under the assumption that site differences compiled over years were representative of each site, and because our research questions were directed at spatial, not temporal, variation. Study duration was also only 2–4 years at each site, making it difficult to quantify annual variation with such short time series.

To evaluate survival variation in relation to age, two Age classes (AHY and HY) and two Sex classes (male and female) were considered in models as categorical variables. Our Period variable was designed to test the hypothesis that Surf Scoter survival varied between mid-winter (late November to late January) and late winter (early February to early April), representing 64 and 65 days, respectively (i.e., Esler et al. 2000*a*).

We also considered effects of body mass at time of capture on variation in survival, comparing two measures of deviation from mean mass, and hypothesized that there could be survival variation associated with mass (Haramis et al. 1986; Lima 1986; Conroy et al. 1989). We calculated residual mass (deviation from mean mass) in two ways: by location irrespective of age–sex class (MASSLOC) and by age–sex class and location (MASSCLA). MASSLOC was calculated by subtracting mean mass of individuals captured at a specific location from observed mass of each individual outfitted with a VHF radio at a specific site. This mass metric was designed to consider whether there was an effect of mass, irrespective of age–sex class, i.e., whether overall lighter or heavier birds were at higher or lower mortality risk. MASSCLA was calculated by subtracting mean mass of individuals within a specific age–sex class at a certain location from mass of each radio-marked individual within that age–sex class; this metric was used to consider whether deviation from a cohort-specific mass optimum had survival implications. In a preliminary analysis, we compared the influence of MASSLOC and MASSCLA on survival and incorporated them into program MARK as individual covariates. We found that MASSLOC ($w_i = 0.01$, $\Sigma w_i = 0.77$) was better supported than MASSCLA ($w_i = 0.00$, $\Sigma w_i = 0.11$), suggesting that mass relative to the overall mean within a location, irrespective of age–sex class, had a stronger influence on survival than mass relative to the mean within an age–sex class at each location. Thus, MASSLOC was the only mass variable included in the final candidate model set. The effects of mass were held constant between the mid-winter and the late-winter periods.

Because our research questions were focused on spatial differences in survival, we focused on location and interacting effects of location with other main effects. To determine if the effect of location differed between the periods of winter, age–sex classes, and with body mass, we included four models with Location, one of the main effects, and a two-way interaction term with Location (e.g., Location + Period + Location × Period), and four models that included all main effects and a Location two-way interaction term with each of the other main effects (e.g., Location + Period + Age + Sex + MASSLOC + Location × Period). We also added an Age × Sex interaction to each of the 30 models of main effects that included both Age and Sex together, resulting in 7 models evaluating the four individual age–sex class (e.g., AHY male) influences on survival instead of effects of age and sex independently. A constant model was included to allow survival to be consistent over the variables that we considered. One global model was included that considered all main effects and relevant two-way interactions with Location. We structured models in program MARK using design matrices and a logit-link function was used to bound parameter estimates.

An information–theoretic approach was used to quantify and interpret effects of location, period, age, sex, and mass at time of capture on probability of survival (Burnham and Anderson 2002). Using Akaike's information criterion adjusted for small sample size ($\mathrm{AIC_c}$), multiple a priori hypotheses, expressed as candidate models, were ranked by comparing models using $\Delta\mathrm{AIC_c}$ scores and Akaike weights (w_i) (Burnham and Anderson 2002). The $\Delta\mathrm{AIC_c}$ scores were calculated as the difference between each model and the most parsimonious model. To determine the relative support for each model, $\mathrm{AIC_c}$ weights were used. Parameter-likelihood values were calculated to evaluate the level of support for the variables within the candidate model set and were estimated by summing model-specific Akaike weights (Σw_i) across all models in the candidate set containing the particular variable of interest. All variables were included in a similar number of models (Location: 29; Period: 26; Age: 29; Sex: 29; MASSLOC: 25). A model-averaged estimate of DSR (with unconditional 95% confidence intervals) was generated, and using DSR to seven significant digits, a CSR was calculated for the overwintering period (129 days) as DSR^n, where n is the number of days in the period. Confidence intervals for CSR were calculated using the delta method (Powell 2007). Survival estimates are reported with 95% confidence intervals.

Results

We detected 34 mortalities among 297 Surf Scoters monitored after the censor periods ended (Table 1). Ten Surf Scoters died within the censor periods and were not included in the analyses. Of the 48 models that examined factors explaining variation in Surf Scoter winter survival rates, the Period + Sex + MASSLOC model was most parsimonious ($w_i = 0.24$; Table 2). Two other models had high degrees of support relative to the best-supported model (i.e., $\Delta\mathrm{AIC_c} < 2.0$; Table 2), including the Location + Period + Sex + MASSLOC ($w_i = 0.16$, $\Delta\mathrm{AIC_c} = 0.86$), and Period + Age + Sex + MASSLOC ($w_i = 0.12$, $\Delta\mathrm{AIC_c} = 1.35$) models. In contrast, our null model, which assumed constant survival irrespective of period, sex, age, mass, or location received essentially no support ($w_i = 0.00$, $\Delta\mathrm{AIC_c} = 8.75$), indicating that at least some of the variables included in our candidate models explained important variation in survival. We estimated an overall, model-averaged DSR of 0.9985 (95% CI: 0.9979–0.9989) for Surf Scoters of all age–sex classes at all locations, corresponding to a CSR of 0.82 (0.76–0.87) over the 129-day wintering period.

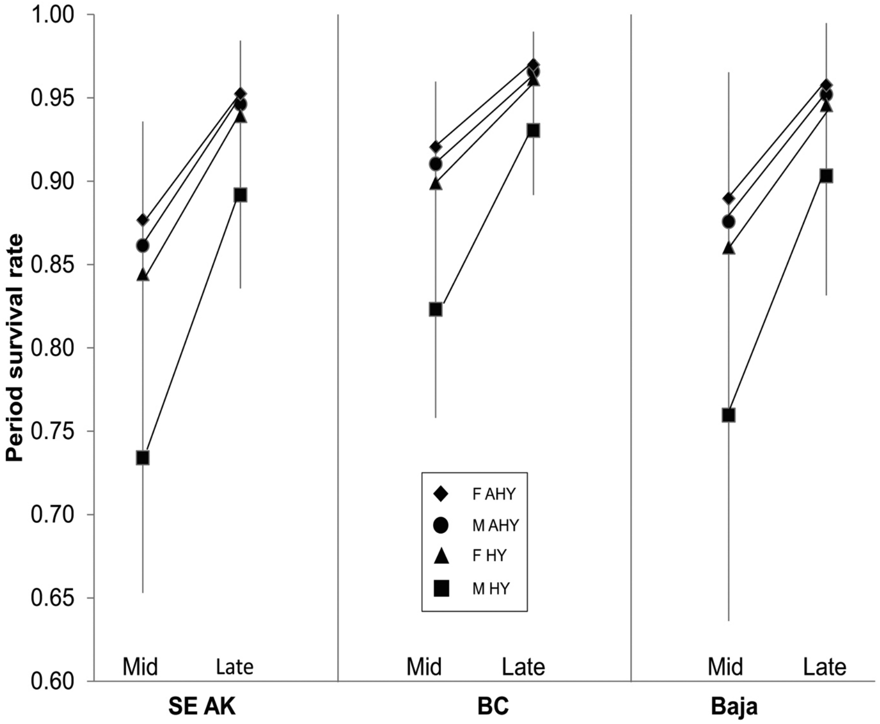
The variable Location received modest support from the data, based on parameter likelihoods ($\Sigma w_i = 0.38$), and was included in the second best-supported model (Location + Period + Sex + MASSLOC) and two other models within the top 10 (Table 2). Overwintering Surf Scoter survival averaged highest in the range core of BC and lower at the peripheries, based on model-averaged estimates. Scoters in SE AK had the lowest mean wintering CSR among locations, 0.75 (0.62–0.85; Fig. 2). Scoters in BC, the range core for Surf Scoters, had the highest CSR, 0.86 (0.79–0.91). Scoters

Table 2. Model selection results for the 10 best-supported models from analyses of variation in winter survival of Surf Scoters (*Melanitta perspicillata*) at three locations along the Pacific coast of North America (southeast Alaska (USA), British Columbia (Canada), Baja California (Mexico)).

Model	K	Deviance	AIC_c	ΔAIC_c	w_i
Period + Sex + MASSLOC	5	381.82	391.83	0.00	0.24
Location + Period + Sex + MASSLOC	7	378.68	392.68	0.86	0.16
Period + Age + Sex + MASSLOC	6	381.17	393.17	1.35	0.12
Location + Period + Age + Sex + MASSLOC	8	378.60	394.61	2.78	0.06
Sex + MASSLOC	3	389.05	395.06	3.23	0.05
Location + Sex + MASSLOC	5	385.09	395.10	3.23	0.05
Period + MASSLOC	4	387.76	395.76	3.94	0.03
Age + Sex + MASSLOC	4	387.97	395.97	4.14	0.03
Period + Age	4	388.20	396.20	4.37	0.03
Period + Age + MASSLOC	5	386.46	396.46	4.64	0.02

Note: Winter was delineated into two periods: mid- (late November to late January) and late (early February to early April). MASSLOC is residual mass of individuals calculated as the difference between mass at capture and mean mass of all individuals captured at each study area. Four sex and age cohorts were included (males and females; after hatch year and hatch year). K, number of parameters; AIC_c, Akaike's information criterion adjusted for small sample size; w_i, Akaike weight.

Fig. 2. Model-averaged (±SE) period survival rate of wintering Surf Scoters (*Melanitta perspicillata*) assuming mean mass (irrespective of age–sex class) at three locations along the Pacific Coast of North America (SE AK: southeast Alaska, USA; BC: British Columbia, Canada; Baja: Baja California, Mexico) contrasted between mid-winter (64 days; end November to end January) and late winter (65 days; end January to early April) and among age–sex classes (F: female; M: male; AHY: after hatch year; HY: hatch year).



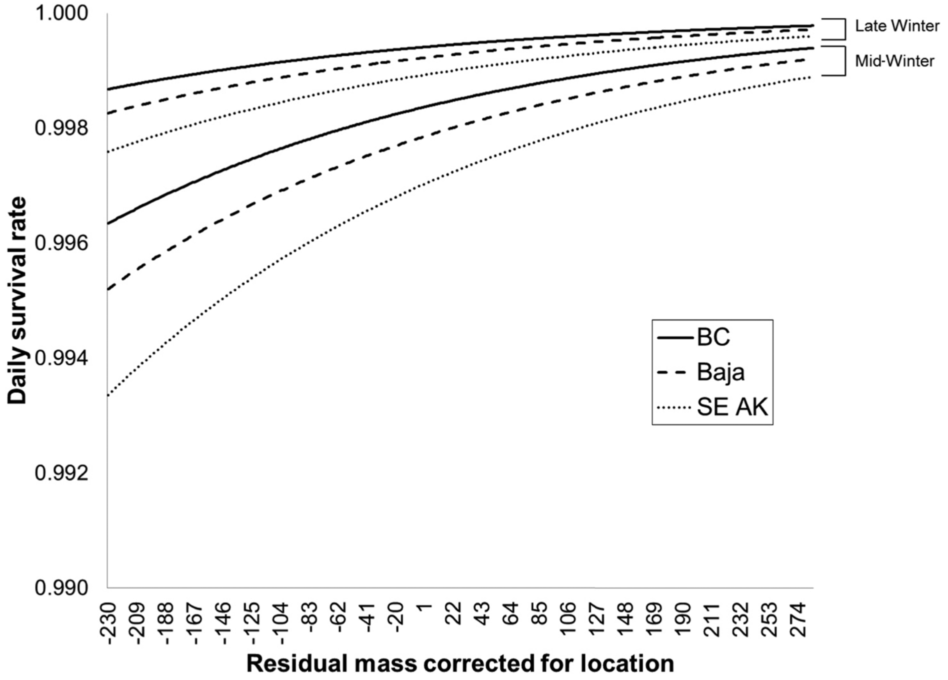
in Baja at the southern periphery of their wintering range had a mean CSR of 0.80 (0.58–0.93).

The explanatory variable Period was included in the four highest ranked models and had the third highest parameter likelihood (Σw_i = 0.81), indicating that Surf Scoter survival varied over the course of the winter. In all cases, late-winter survival was higher than mid-winter survival (Fig. 2). The mean period survival rate (PSR) for the 64-day mid-winter period (late November to late January), 0.87 (0.81–0.91), was markedly lower than the PSR for late winter (65 days; early February to early April), 0.95 (0.91–0.98).

The MASSLOC variable had the highest parameter likelihood (Σw_i = 0.86) and was included in 9 of the 10 best-supported models (Table 2). Birds with higher MASSLOC had higher winter survival rates, particularly at the peripheries of the range and during mid-winter (Fig. 3).

We observed differences in model-averaged CSR across age–sex classes, with adult birds having higher survival rates than young birds and females having higher survival than males (Fig. 2). Juvenile males (MHY; for sample sizes see Table 1) had the lowest overall mean winter CSR, 0.69 (0.52–0.82). Juvenile females (FHY) had higher CSR, 0.82 (0.65–0.92), than MHY, but lower than that for adults—MAHY CSR, 0.86 (0.77–0.92), and FAHY CSR, 0.87 (0.73–0.94). The variable Sex had the second highest parameter likelihood (Σw_i = 0.82) and received more support than Age (Σw_i = 0.40), suggesting that differences between sexes had a greater influence on Surf Scoter survival than age. Models that addressed age–sex class influences on survival through an Age × Sex interaction were not well supported by the data (i.e., Age + Sex + Age × Sex; w_i = 0.00, ΔAIC_c = 11.47).

Fig. 3. Daily survival rates of Surf Scoters (*Melanitta perspicillata*) during mid-winter (64 days; late November to late January) and late winter (65 days; early February to early April) in southeast Alaska (USA; SE AK), British Columbia (Canada; BC), and Baja California (Mexico; Baja), in relation to residual mass corrected for location. Residual mass of individuals corrected for location was calculated as the difference between mass at capture and mean mass of all individuals captured at each study area, irrespective of age–sex class.



We recognize that although there was a high degree of variation in body mass within age–sex classes (Fig. 4), effects of body mass at time of capture and effects of age–sex class on survival are best calculated and interpreted simultaneously, given covariation between class and mass. Mean mass of males was higher than that of females and AHY age classes of both sexes had higher mean mass than the corresponding HY age class (Fig. 4); these patterns are consistent with those of most waterfowl. We also found that Surf Scoters captured at more northerly latitudes generally had higher body masses, both within and across age–sex class, with birds in SE AK generally being heaviest, followed by birds from BC, while scoters in Baja were lightest (Fig. 4). When we combined categorical effects of period, location, age, and sex (Fig. 2) with the continuous effect of body mass variation (Fig. 3), we found that important patterns emerged in the survival estimates (Fig. 5). By virtue of their higher mass, AHY males of mean mass in SE AK had slightly higher survival than AHY males of mean mass at other locations (Fig. 5). In contrast, AHY female survival for individuals of mean mass within locations was highest in the range core of BC (Fig. 5). For HY Surf Scoters of both sexes, survival rates of individuals of mean, location-specific mass were highest in the range core and (or) the southern periphery relative to the northern periphery of SE AK (Fig. 5).

Discussion

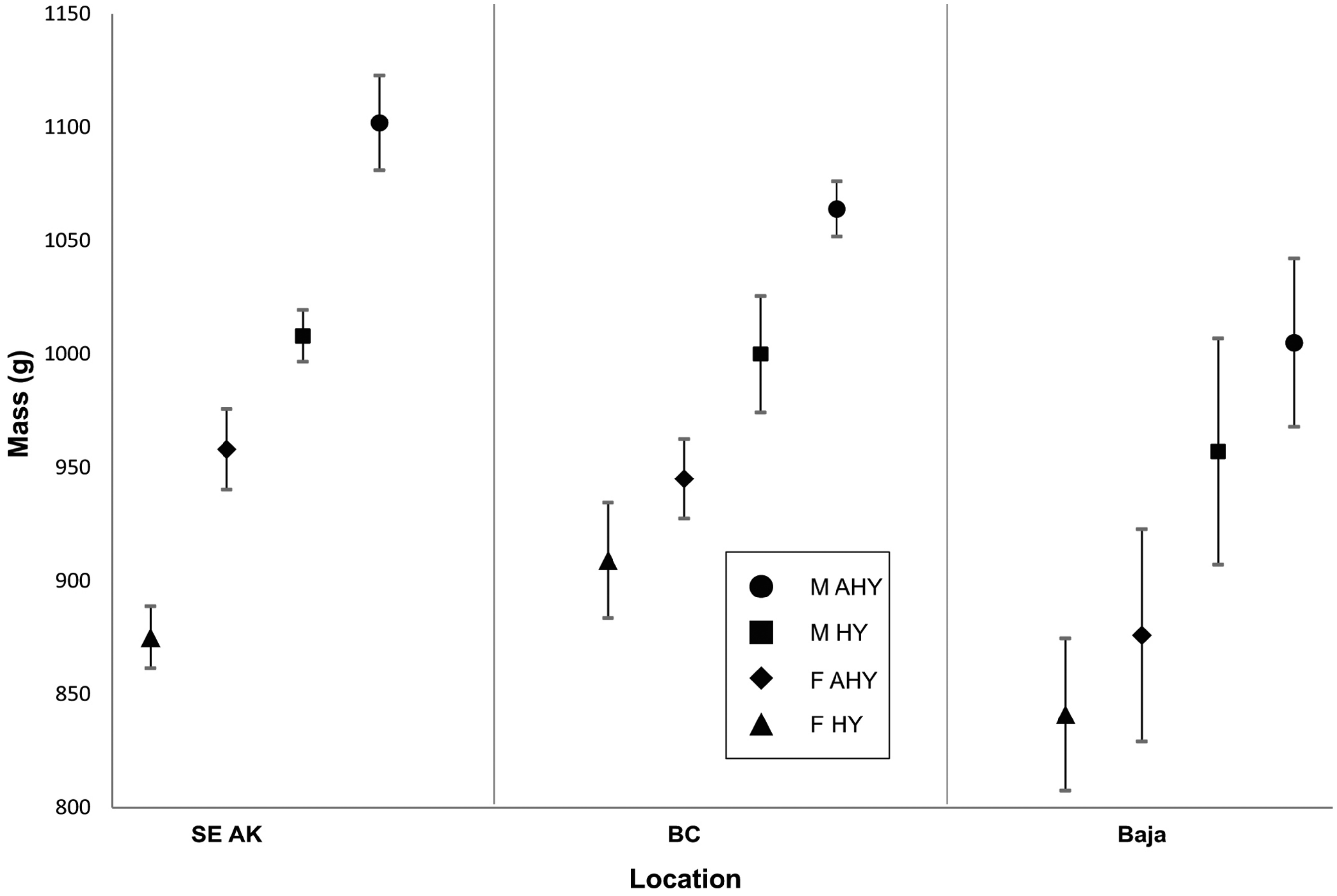
Our results indicate interacting effects of age, sex, and body mass at capture on winter survival of Surf Scoters at a continental scale, which may be an underlying mechanism leading to differential migration in this species. Higher proportions of male and adult Surf Scoters winter at more northern latitudes, whereas higher proportions of females and juveniles winter at more southern latitudes (Iverson et al. 2004). These distribution patterns correspond to our findings that, after accounting for mass effects, adult male survival was highest at the northern range extent, while survival of adult females was highest at the range core and juveniles had higher survival at the range core and southern periphery than at the northern periphery. Very few survival studies have been conducted at the geographic scale necessary to detect these relationships and quantify factors that influence winter site use in a migratory bird.

Patterns in both distribution and survival were not absolute, i.e., all age and sex classes were represented at all study sites and survival of individuals was not perfectly predicted by location, age, sex, or mass. Aspects other than survival must certainly factor into optimization of site choice by individuals. In this case, at the same study sites, associated research (VanStratt 2011) determined that foraging effort (amount of time spent feeding) varied by latitude, with effort lowest in SE AK, highest in Baja, and intermediate effort in BC. These findings indicated that foraging conditions improved with increasing latitude and, also, that poor foraging conditions may be limiting distribution at the southern periphery. Varying foraging conditions, and the potential influences of body size and body mass on birds' abilities to accommodate poor foraging conditions (Anderson and Lovvorn 2011; Palm et al. 2013), may also have played a role in the cost–benefit optimization process of individuals and the resultant distributional patterns.

Our finding that mass was related to survival is consistent with previous findings for other waterfowl species, as individuals with higher mass tend to have higher winter survival (Haramis et al. 1986; Conroy et al. 1989; Krementz et al. 1997). However, there are clear indications of costs of carrying mass (e.g., Lima 1986) and our data are consistent with patterns from other waterfowl that optimal mass varies by habitat (Palm et al. 2013) and, in this case, by latitude. Further consideration of trade-offs that dictate optimal mass is warranted.

Age class has been related to waterfowl survival in other studies at smaller geographic scales, with young birds having lower survival than adults (Mittelhauser 2008; Oppel and Powell 2010). For young inexperienced individuals, there may be costs associated with experiencing marine environments for the first time (i.e., lack of experience in what and where to eat, predator aversion,

Fig. 4. Body mass (mean ± 95% confidence intervals) of radio-marked Surf Scoters (*Melanitta perspicillata*) at three locations along the Pacific Coast of North America (SE AK: southeast Alaska, USA; BC: British Columbia, Canada; Baja: Baja California, Mexico) and among age–sex classes (M: male; F: female; AHY: after hatch year; HY: hatch year). Sample sizes are presented in Table 1.



how to avoid dangerous areas and times). Adults may also exclude juveniles from optimal wintering habitats (Cooke et al. 2000).

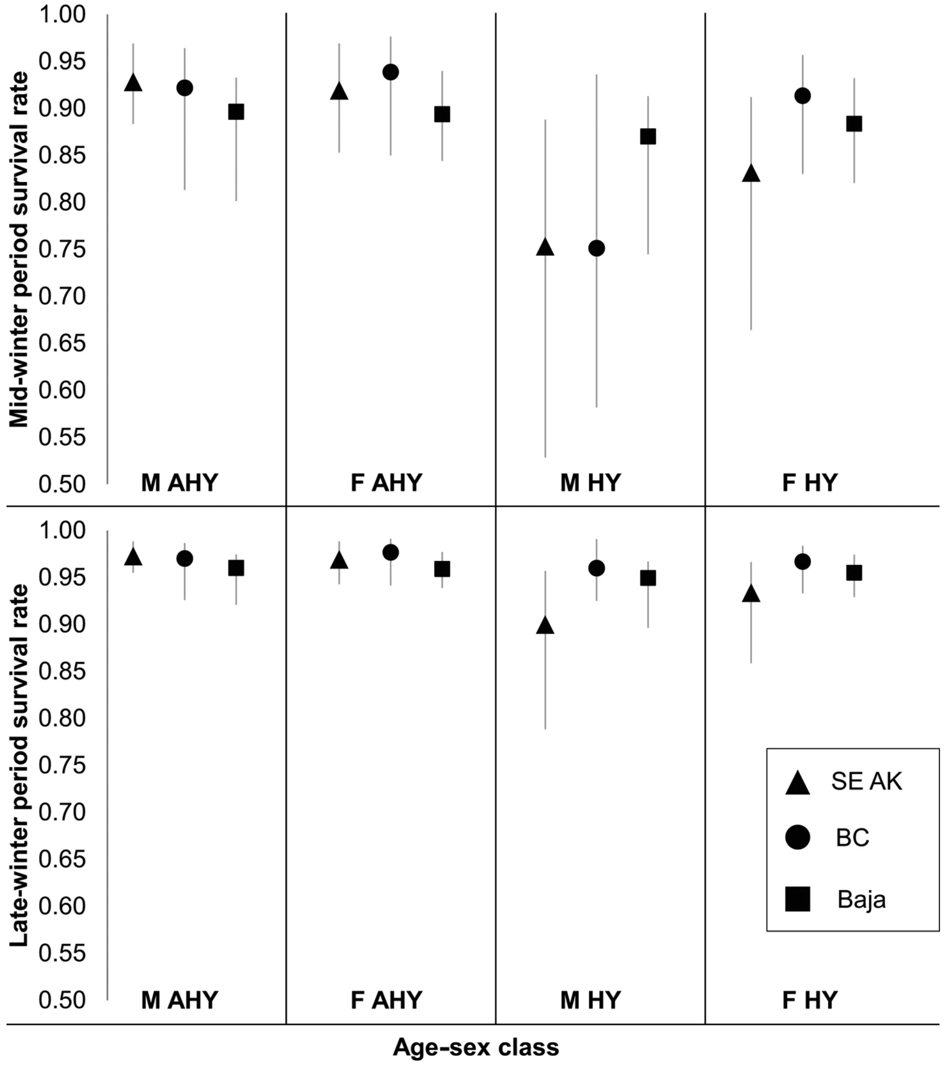
Most species of waterfowl, including Surf Scoters, exhibit male-biased sex ratios. We found that although spatial patterns of survival varied between sexes, overall adult survival rates were similar between sexes, suggesting that differential survival during other annual cycle stages may be driving these male-biased sex ratios (e.g., decreased adult female survival during incubation; Devries et al. 2003).

Period was strongly supported as a factor influencing winter survival of Surf Scoters, with estimates for mid-winter consistently lower than those for late winter. Model-averaged estimates of survival for each winter period differed between sex and age classes and were more pronounced for young birds. Winter survival of other sea ducks has been found to be low during mid-winter, suggesting that this particular portion of the annual cycle may serve as a population constraint (Esler et al. 2000*a*). Mid-winter generally has the harshest weather conditions and shortest day length, particularly at more northerly latitudes (Systad et al. 2000). Sea ducks can influence prey abundance and exhaust their resources over the course of the winter, including Surf Scoters in our study areas (Kirk et al. 2007; Lewis et al. 2007). Our result of high late-winter survival suggests that prey depletion at our study locations was not adversely affecting winter survival rates. At the range core and northern periphery, Surf Scoters shift their diet in late winter from mussels to herring spawn (Anderson and Lovvorn 2011). Surf Scoters in BC gained mass while consuming spawn during late winter (Anderson et al. 2009) and this abundant resource may contribute to high late-winter survival rates.

Radio transmitters can have a negative impact on survival of waterfowl (Paquette et al. 1997), although no impacts have been found for certain taxa and transmitter types (e.g., Esler et al. 2000*b*; Hepp et al. 2002). We acknowledge that radio transmitters may have had an influence on wintering Surf Scoter survival in our study, but we used censor periods to both minimize bias associated with captures and account for short-term effects of radio transmitter attachment. Additionally, the type of radio transmitter was not found to be an important predictor of winter Surf Scoter survival probability (Iverson et al. 2006). Even if radio-transmitter deployment had a negative impact on survival in our study, the effects would likely be the same for all locations thus supporting our observed survival differences among locations.

De La Cruz et al. (2013) found rates of winter survival for Surf Scoters near San Francisco, California, similar to those in this study. Our overall winter survival estimates were also similar for other species of waterfowl (e.g., Dugger et al. 1994), including other sea duck species (Cooke et al. 2000; Esler et al. 2000*a*; Mittelhauser 2008; Esler and Iverson 2010). These winter survival estimates for sea ducks are much lower than survival rates estimated during other stages of the nonbreeding period. An associated study (Uher-Koch et al. 2014) estimated that Surf Scoter survival during remigial molt was 1.000. Remigial molt constitutes a relatively short part of the annual cycle of scoters (approximately 47 flightless days for Surf Scoters; Dickson et al. 2012) and, given the high survival rates, likely does not result in a demographic constraint on scoter populations (Dickson et al. 2012; Uher-Koch et al. 2014). To fully understand Surf Scoter population dynamics, age, sex, and stage-specific estimates, such as adult

Fig. 5. Period survival rates (95% CI) of Surf Scoters (*Melanitta perspicillata*) of mean mass for each age–sex class (M: male; F: female; AHY: after hatch year; HY: hatch year) during mid-winter (64 days; late November to late January) and late winter (65 days; early February to early April) in southeast Alaska (USA; SE AK), British Columbia (Canada; BC), and Baja California (Mexico; Baja).



female survival during the breeding period, need to be addressed further. The combination of our results of low survival rates during winter and the sensitivity of sea duck population dynamics to variation in adult survival relative to other demographic parameters suggests that winter survival may be an important driver of population trends, in addition to the influence on distributions described here.

Acknowledgements

This work was supported financially and logistically by the Sea Duck Joint Venture, the U.S. Geological Survey Alaska Science Center, Simon Fraser University, Environment Canada, the U.S. Fish and Wildlife Service, and the U.S.D.A. Forest Service. The National Oceanic and Atmospheric Administration (NOAA) Auke Bay Laboratories provided additional logistical support in Juneau. We thank the numerous individuals who provided assistance in the field. We also thank T. Bowman, D. Green, J. Pearce, B. Sandercock, B. Smith, R. Ydenberg, and two anonymous reviewers for their helpful comments on the manuscript. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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