

**Latitudinal and Seasonal Variation  
in Non-breeding Survival of  
Surf and White-winged Scoters**

**by  
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Thesis Submitted In Partial Fulfillment of the  
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## **Abstract**

To understand wildlife population dynamics and identify when and where demographic or distributional constraints may exist within the annual cycle, it is important to quantify timing and sources of variation in demographic attributes. I documented survival of surf and white-winged scoters during remigial molt, and surf scoter survival during winter, at multiple sites along the Pacific coast of North America. I detected no mortalities during remigial molt, indicating high survival within this annual cycle stage, irrespective of latitude, species, or age and sex cohort. Winter survival was related to location, period of winter, cohort, and mass. These results highlighted times (mid-winter) and locations (range peripheries) in which mortality was elevated for some cohorts, and that attributes of individuals, specifically mass, was positively related to survival. My findings indicate mechanisms leading to observed population dynamics and distributions, as well as times and places in which conservation action would be most productive.

**Keywords:** remigial molt; sea duck; surf scoter; survival; white-winged scoter; winter

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# 1. General Introduction

## 1.1. Thesis Background

Migratory animals often have very large geographic ranges and occur in a variety of habitats and conditions both among and within annual cycle stages. Different areas can vary in many factors that may influence distribution and abundance of animals including resources (Johnson and Sherry 2001, Lindberg et al. 2007, Norris and Martin 2008), competition (Kelly 2003, Dellinger 2007), climate (Venier et al. 1999, Valiela and Bowen 2003, Ward et al. 2009, Flint 2012), disease (Dobson and May 1991, Rocke et al. 2005), and predation danger (Lank et al. 2003). Geographic variation in demographic traits can indicate factors that affect distribution of animals at a given annual cycle stage (Ozugal et al. 2006, Ciannelli et al. 2007). Understanding the underlying influences on geographic variation in demography is important for identifying causes of population change, trade-offs associated with using one location or another, and locations that warrant conservation attention (Saracco et al. 2010).

Quantification of variation in demographic rates, particularly when generated on a season-specific basis and linked to underlying mechanisms, provides important insights on causes and timing of variation in population dynamics (Lebreton et al. 1992, Alisauskas et al. 2004). In turn, documentation of season-specific survival rates leads to implications for when and where to direct conservation efforts to influence population dynamics. While many studies of demographic variation of northern hemisphere birds have been conducted during the breeding season, other stages of the annual cycle, such as migration, staging, molt, and winter, also can have strong influences on vital rates and population dynamics (Calvert et al. 2009, Bridge 2011). For species whose life histories are characterized by long life spans, delayed reproductive maturity and low annual productivity (Kehoe et al. 1989, Goudie et al. 1994), proportional variation in adult survival has stronger effects on population dynamics than does variation in other factors, such as reproductive performance (Schmutz et al. 1997, Heppel et al. 2000, Saether and

Bakke 2000, Calvert et al. 2009, Flint 2012). Therefore, documentation of variation in season-specific survival, and factors related to that variation, can provide important insight into wildlife population dynamics (Hupp et al. 2008).

There is increasing recognition that factors within the non-breeding period of the annual cycle have important effects on waterfowl population dynamics (Hoekman et al. 2006, Kery et al. 2006, Calvert et al. 2009). The non-breeding period represents the majority of the annual cycle for waterfowl and includes the periods of remigial molt, fall and spring migration, and winter. Further, factors in one season can have effects on fitness and population size in other periods (Norris 2005, Norris & Marra 2007). Understanding conditions during the non-breeding period is important because factors during this period can have carry over effects on population dynamics in other periods of the annual cycle, such as migration survivorship (Sillert and Holmes 2002), and reproduction (Lehikoinen et al. 2006), and have been linked to population declines (Newton 2004, Calvert et al. 2009). Many factors have the potential to influence survival during the non-breeding period including food resources (Sherry et al. 2005), habitat quality (Sherry and Holmes 1996), thermoregulatory costs (Lehikoinen et al. 2006), climate (Saether et al 2000, Kery et al 2006), 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), exposure to contaminants (Esler et al. 2002, Elliot et al. 2007), and harvest (Menu et al. 2002). These factors may have differential effects among individuals, based on age (Krementz et al. 1987), sex (Schmutz and Ely 1999), mass (Mason et al. 2007), condition (Boos et al. 2002), or other attributes. Identifying these influences on demographic rates, and when they operate within the annual cycle, is critical for understanding population dynamics, especially for species of population concern.

### **1.1.1. Study Species**

Surf scoters and white-wing scoters are migratory sea ducks that breed in boreal forest habitats throughout northern Canada and Alaska. Scoters undergo remigial molt primarily in near-shore coastal waters and winter along the Pacific and Atlantic coasts of North America (Brown & Fredrickson 1997, Savard et al. 1998). On the Pacific Coast the surf scoter wintering range extends more than 5000 km over nearly 35 degrees of

latitude stretching from the Aleutian Islands in Alaska to the Baja Peninsula in Mexico (Savard et al. 1998). Scoter numbers have declined by roughly 60% over the past 50 years (Hodges et al. 1996, Dickson and Gilchrist 2002) and wintering scoter numbers in the Puget Sound region declined by 56% since the late 1970's (Nysewander et al. 2005). Factors driving these declines are not well understood, however it has been suggested that declines may have resulted from changes in adult survivorship during the non-breeding period (Anderson et al. 2012). Population dynamics of surf scoters are sensitive to variation in adult survival (Goudie et al. 1994), and alterations have occurred to marine habitats they use during the non-breeding period (Kappel 2005). Many previous studies of scoters have addressed the role of food availability on distribution, abundance, movements, foraging behavior, and physiological condition (Žydelis et al. 2006, Lewis et al. 2007a,b, Anderson & Lovvorn 2008, Kirk et al. 2008, Anderson et al. 2009, VanStratt 2011). However, estimates of survival are needed to quantify fitness consequences of responses to variation in habitats, as well as to understand when and where demographic constraints may exist within the annual cycle. While scoter survival rates have rarely been quantified, sea ducks tend to have some of the higher annual survival rates among waterfowl (Krementz et al. 1997b). Annual survival of nesting adult female white-winged scoters was estimated to be 78.2% (Kehoe et al. 1989), while adult surf scoter annual survival has never been documented, and season-specific survival rates have not been quantified for either species.

### **1.1.2. Remigial Molt**

Molt timing and duration varies among bird families, with waterfowl undergoing a flightless period as they simultaneously molt remiges (flight feathers). The remigial molt stage is a discrete period in the annual cycle of waterfowl, usually occurring shortly after breeding, during which they select habitats and employ behavioral strategies that may be different from the remainder of the year (Rowher 1999). Waterfowl and the few other bird families that undergo simultaneous remigial molt are generally aquatic and have some capacity to feed and avoid predators without flying.

Although remigial molt for waterfowl constitutes a relatively short portion of the annual cycle, energy and nutrient demands are high, due to potential costs associated with feather regrowth (Murphy 1996). Being flightless may lead to a reduction in ability

to escape predators and increased predation risk (Dopfner et al. 2009). Sea ducks also may experience higher foraging costs, due to a decrease in dive efficiency (Bridge 2004). Also, sea ducks molt in large aggregations, and thus could be susceptible to catastrophic events, such as oil spills, pollution, heavy metal contamination, and harmful biotoxins associated with algal blooms (Henny 1995, Esler and Iverson 2010, Phillips et al. 2011). Most species of waterfowl exhibit male biased sex ratios, and population dynamics are particularly sensitive to changes in breeding age female survival (Johnson et al. 1992). Breeding age individuals, who may already be poor condition due to costs associated with breeding (Pehrsson 1987), may initiate remigial molt later than failed and non-breeders and may be under a greater temporal constraint to complete remigial molt (Savard et al. 2007). Despite potential for temporal and energetic constraints, and elevated mortality risk during simultaneous remigial molt (Guillemette et al. 2007), relatively few studies have quantified waterfowl survival during this annual cycle stage.

These factors suggest that mortality during remigial molt could be high. Related studies on surf scoter (*Melanitta perspicillata*) and white-wing scoter (*M. fusca*)(hereafter “scoters”) remigial molt ecology found a lack of temporal, energetic or nutritional constraints on scoters during remigial molt (Dickson 2011, Dickson et al. 2012). The few studies of sea duck survival during remigial molt have found survival to be high (Iverson & Esler 2007, Hogan et al. 2013). However all three scoter species experienced large die offs during remigial molt in 1990-1992 in Southeast Alaska (Henny 1995), and survival for other waterfowl species during remigial molt was considerable lower than that for sea ducks (Kirby and Cowardin 1986, Bowman and Longcore 1989, Miller et al. 1992, Fleskes et al. 2010). Survival of scoters during remigial molt has never been previously documented, which leaves a gap in our understanding of how variation in vital rates during remigial molt may affect population dynamics.

### **1.1.3. Winter**

After the remigial molt period, scoters may remain near their molting areas to winter or may migrate to a different wintering site. Waterfowl mortality during winter may be particularly high (Conroy et al. 1989, Gauthier et al. 2001) as decreased temperatures may lead to increased thermoregulatory costs (Blums et al. 2002, Mason et al. 2006). Winter severity has been found to have an effect on survival probability and

population dynamics (Bergan and Smith 1993, Blums et al. 2002, Ronka et al. 2005, Kery et al. 2006) as waterfowl that winter at northern latitudes are subject to increased energy costs associated with increased wind and wave action, and lower air and water temperatures (Owen and Reinecke 1979, Prince 1979). These costs may be compounded by individual characteristics, such as sex and age class, or mass, with young birds having lower survival than adults (Johnson et al. 1992, Blums et al. 1996, Mittelhauser 2008, Oppel and Powell 2010), and males having higher survival than females (Johnson et al. 1992, De La Cruz et al. 2012). For sea ducks there is often a positive relationship between mass and survival (Krementz et al. 1997a), however carrying larger nutrient reserves may have associated costs, such as higher risk of predation (Lima 1986). For many waterfowl, individuals with higher mass tend to have higher winter survival and may be better suited to meet energetic costs associated with winter thermoregulation (Haramis et al. 1986, Hepp et al. 1986, Conroy et al. 1989, Bergan and Smith 1993, Krementz et al. 1997a, Jamieson et al. 2006).

Mortality risk can vary across latitudes, and animals may trade-off the risk of starvation against predation risk or exposure to severe weather (McNamara and Houston 1987, Ardia 2005, Nebel and Ydenberg 2005, Ouellett et al. 2008, VanStratt 2011). Challenges facing scoters during the non-breeding period vary across a latitudinal gradient. For example, scoters wintering at northern latitudes (e.g., Southeast Alaska) or in the core of their range (coastal British Columbia) face different environmental conditions and a less energetically costly migration when compared to scoters wintering in the southernmost portion of the range (Baja California). Variation in survival due to individual characteristics such as age, sex, or mass, along with environmental factors, may lead to differential migration and latitudinal distributions skewed by age and sex classes (Cristol et al. 1999, Iverson et al. 2004, O'Hara 2006). Few studies have examined variation in winter survival rates of migratory species at a continental scale or have considered the trade-offs associated with wintering site selection, despite the implications for population dynamics, distribution, and conservation.

Previous studies of winter ecology of surf scoters found that high quality foraging habitat exists at the range core in the Strait of Georgia, British Columbia, Canada (Lewis 2005, Kirk 2007, Kirk et al. 2007, Lewis et al. 2008). Related studies found that scoter

foraging efforts were comparable between the molt and winter periods (VanStratt 2011, Dickson 2011, Dickson et al. 2012). VanStratt (2011) compared winter surf scoter foraging behaviour at the range core to sites at the northern (Southeast Alaska) and southern (Baja California) peripheries of the surf scoter wintering range. Foraging effort was lowest at the northern periphery, and highest at the southern periphery, with intermediate levels at the range core. This suggests that differences in foraging conditions may be limiting surf scoter winter distribution at the southern periphery, while other factors are limiting distribution at the northern periphery. I measured scoter survival over the latitudinal span of their wintering areas, allowing for consideration of geographical variation in survival and influences on surf scoter demography and distribution.

## **1.2. Thesis Objective**

The purpose of this study was to determine influences on survival rates of scoters during the non-breeding period of the annual cycle. To identify spatial and temporal variation in survival rates, I documented fates of scoters marked with VHF transmitters during the non-breeding period of the annual cycle along the Pacific coast of North America. Further, I evaluated whether scoter survival during remigial molt varied by scoter species, sex, and age, as well as latitude. I also quantified variation in winter survival of surf scoters in relation to latitude, age and sex class, and body mass, in an effort to understand potential influences on population dynamics.

## **1.3. Thesis Outline**

My thesis consists of four chapters, including two data chapters, which describe remigial molt and winter survival of scoters, and a concluding chapter that summarizes my findings.

In my second chapter, I quantify survival rates of surf and white-winged scoters during the period of remigial molt at two major molting areas (Southeast Alaska and British Columbia) along the Pacific Coast of North America. I evaluate whether scoter

survival during remigial molt varies by species, sex and age, and latitude, and then compare these findings to other periods of the annual cycle to determine if the remigial molt period was potentially constraining scoter populations.

In my third chapter, I measure surf scoter survival at three sites throughout their winter distribution along the Pacific coast of North America to consider how temporal and geographical variation in survival may influence surf scoter distributions and population dynamics. I quantify variation in winter survival of surf scoters in relation to latitude, age and sex class, and body mass and identify when and where management efforts would be most effective.

In the final chapter I highlight the major findings of my research, present general conclusions from each of my data chapters, and suggest future directions to expand upon this research.

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## **2. Survival of surf scoters and white-winged scoters during remigial molt**

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### **2.1. Abstract**

Surf scoters (*Melanitta perspicillata*) and white-winged scoters (*M. fusca*) undergo simultaneous remigial molt (in June through September) during which they are flightless for >1 month. Molt could result in reduced survival due to increased predation risk or increased energetic demands associated with regrowing flight feathers. However, survival during remigial molt rarely has been assessed for waterfowl, generally, and particularly for sea ducks. To quantify survival during remigial molt, we deployed VHF transmitters on surf scoters (n=110) and white-winged scoters (n=57) in Southeast Alaska and the Salish Sea (British Columbia and Washington) in 2008 and 2009. After censoring mortalities potentially related to capture and handling effects, we detected no mortalities during remigial molt; thus estimates of daily and period survival for both scoter species during molt were 1.00. We performed sensitivity analyses in which mortalities were added to the dataset to simulate potential mortality rates and then estimated the probability of obtaining a dataset with zero mortalities. We found that only with very high levels of survival was there a high probability of obtaining our results of zero observed mortalities. We conclude that remigial molt is a period of low mortality in the annual cycle of scoters, although note that rare, catastrophic mortality events may be important. Factors during other annual cycle stages are likely responsible for observed, persistent declines in scoter populations and thus should be targeted by research and management efforts.

## 2.2. Introduction

Quantification of variation in demographic rates, particularly when generated on a season-specific basis and linked to underlying mechanisms, provides important insights on causes and timing of variation in population dynamics (Alisauskas et al. 2004, Holmes 2007). In turn, documentation of season-specific survival rates leads to implications for when and where to direct conservation efforts to influence population dynamics. While many studies of demographic variation of northern hemisphere birds have been conducted during the breeding season, other stages of the annual cycle, such as migration, staging, molt, and winter, can have important influences on vital rates and population dynamics (Calvert et al. 2009).

Molt timing and duration varies among bird families, with waterfowl undergoing a period of flightlessness as they simultaneously molt remiges (flight feathers). The remigial molt stage is a discrete period in the annual cycle of waterfowl, usually occurring shortly after breeding, during which they select habitats and employ behavioral strategies that may be different from the remainder of the year (Rohwer 1999). Waterfowl and the few other bird families that undergo simultaneous remigial molt are generally aquatic and have some capacity to feed and avoid predators without flying. Despite potential for energetic constraints (Guillemette et al. 2007) and elevated mortality risk during simultaneous remigial molt, relatively few studies have quantified waterfowl survival during this stage of the annual cycle.

Surf scoters (*Melanitta perspicillata*) and white-winged scoters (*M. fusca*)(hereafter “scoters”) are migratory sea ducks that winter along the Pacific and Atlantic coasts of North America, breed throughout northern Canada and Alaska, and undergo remigial molt primarily in nearshore coastal areas (Brown and Fredrickson 1997, Savard et al. 1998). Scoter numbers in North America have declined by about 60% over the past 50 years (Hodges et al. 1996, Dickson and Gilchrist 2002). Because of these declines, it is important to understand sources and timing of variation in demographic rates. Observed surf scoter population declines may have resulted from changes in adult survivorship during the non-breeding period as population dynamics of surf scoters are sensitive to variation in adult survival (Goudie et al. 1994), and alterations have occurred to marine habitats they use during the non-breeding period

(Kappel 2005). However, estimates of survival are needed to quantify fitness consequences of variation in habitats, as well as to understand when and where demographic constraints may exist within the annual cycle. Documenting such patterns is critical for directing effective conservation efforts (Lebreton et al. 1992). Scoter survival rates have rarely been quantified. Annual survival of nesting adult female white-winged scoters was estimated to be 78.2% (Kehoe et al. 1989), while adult surf scoter annual survival has never been documented, and season-specific survival rates have not been quantified for either species.

For scoters, remigial growth requires over 40 days (Dickson et al. 2012). Due to costs associated with feather regrowth, energy and nutrient demands may be elevated during this time (Murphy 1996). Also, flightlessness may lead to increased predation risk and wing-propelled divers, like scoters, may experience decreased dive efficiency and thus incur higher foraging costs (Bridge 2004). Scoters also molt in large aggregations and thus are susceptible to catastrophic events, such as oil spills, pollution, heavy metal contamination, and harmful biotoxins associated with algal blooms (Henny 1995, Esler and Iverson 2010, Phillips et al. 2011). These factors all suggest that the molting period could be a time of potential population constraint. The few previous studies of sea duck survival during remigial molt documented high survival rates (Iverson and Esler 2007, Hogan et al. 2013). Because survival of scoters during remigial molt has never been documented, it is unknown if they follow the same pattern or how variation in vital rates during remigial molt might affect population trajectories.

We quantified survival of surf and white-winged scoters during remigial molt at two major molting areas along the Pacific coast of North America. We specifically assessed whether the remigial molt period might constitute a demographic constraint within the annual cycle of scoters. Further, we evaluated if scoter survival during remigial molt was influenced by scoter species, sex, age, mass, or location.

## **2.3. Methods**

### **2.3.1. Study Sites**

We studied survival of surf and white-winged scoters during remigial molt in Seymour Canal on Admiralty Island near Juneau, Alaska (AK) and in the Salish Sea of British Columbia (BC) and Washington (WA) (Fig. 2.1). Approximately 20% of North American surf and white-winged scoters undergo remigial molt in Southeast AK (Hodges *et al.* 2008), with at least 16,000 scoters observed in the northern half of Seymour Canal during August 2008 (Dickson 2011). More than 20,000 scoters molt in the Salish Sea, which constitutes the main molting sites for scoters south of Alaska (J. Evenson, Washington Department of Fish and Wildlife, unpublished data).

Seymour Canal (58.0°N, 134.3°W) is a sheltered inlet, about 65 km long and 8 km wide. Study sites in the Salish Sea included the Fraser River Delta (49.2°N, 123.3°W) and Boundary Bay (49.0°N, 123.0°W) in BC and Padilla Bay (48.5°N, 122.5°W) and Forbes Point (48.3°N, 122.6°W) in WA. The Fraser River Delta and Boundary Bay are composed of intertidal mudflats, seagrass beds, and occasional rocky outcrops. Padilla Bay is almost entirely intertidal and contains one of the largest contiguous seagrass beds on the Pacific coast of North America (Bulthuis 1995). Intertidal flats in Padilla Bay are drained by many tidal channels that are mainly <5 m deep. Forbes Point is largely unvegetated, with intertidal substrates ranging from coarse sand to cobble, and subtidal substrates are mainly fine sands. In contrast to Seymour Canal, the Salish Sea is bordered by large urban centers with industrial development and high volumes of commercial and recreational boat traffic.

### **2.3.2. Captures and Radio-transmitter Monitoring**

We captured surf and white-winged scoters undergoing remigial molt in late July through mid-September of 2008 and 2009 at both study areas. We used floating gill net methods similar to those described by Breault and Cheng (1990) and Dickson *et al.* (2012). Capture and radio-marking were conducted throughout the molt period to allow examination of temporal variation in survival by both molt stage and molt initiation date. All captured scoters were marked with a uniquely numbered metal tarsal band, and

identified to species and sex using plumage characteristics. Age class was determined by measuring bursal depth; birds with bursal depths of >15 mm were considered second-year (SY; i.e., hatched the previous summer) and those with bursa <15 mm were classified as after-second-year (ASY) (Mather and Esler 1999). A subset of individuals received very high frequency (VHF) radio transmitters within each of the four age-sex classes of each species (ASY males and females and SY males and females). Morphometric features were measured, including 9<sup>th</sup> primary length as an indication of stage of remigial molt. Because 9<sup>th</sup> primary length was measured when captured, molt initiation and completion dates could be estimated based on average 9<sup>th</sup> primary growth rates (Dickson et al. 2012). We also measured body mass ( $\pm$  1 g) to evaluate relationships with variation in survival.

We deployed 105 VHF transmitters in Southeast Alaska and 62 in the Salish Sea on scoters that had recently initiated molt (Table 2.1). Transmitters were mounted externally and dorsally and were affixed using either one or two subcutaneous prongs and then were glued to a few feathers (Iverson et al. 2006, Lewis and Flint 2008). Transmitters were equipped with a mortality sensor, which doubled the signal pulse rate when a transmitter did not move for  $\geq$  12 hr. After transmitters were deployed we regularly monitored signal strength, approximate location, and scoter fate (alive, dead, or not heard). Monitoring schedules varied by location but we attempted to locate all birds every few days using a combination of land based hand-held yagi-antennas, a skiff specially outfitted for radio-tracking, and occasional aerial telemetry flights in Southeast Alaska. When a mortality signal was detected, we attempted to confirm the fate of the bird by locating the transmitter. We considered location of a transmitter in terrestrial habitats as a confirmed mortality, as scoters do not otherwise occur in upland habitats during remigial molt. Additionally, presence of a carcass or scoter parts (feathers, bill, feet) in the vicinity of a transmitter was considered mortality confirmation. For confirmed mortalities, we documented circumstantial evidence of the marked individual's fate in an attempt to identify cause of death. We assumed that transmitters found within the intertidal zone had been shed and these were censored from the survival analysis from the point that the transmitter was shed. If transmitters disappeared without detection of a mortality signal, we assumed this was due to radio failure, a shed radio, or the individual leaving the study area after regaining flight (i.e., these were assumed to not be

mortalities). These marked individuals were included in the analysis up to the point when their transmitter was not detected. We performed all activities in accordance with the requirements of the Simon Fraser University Animal Care Committee (Permit No. 868B).

### **2.3.3. Analysis**

We estimated survival using a modified Mayfield method of nest survival analysis in Program MARK (White and Burnham 1999, Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). This nest survival model accommodates data in which animals are marked and monitored at irregular time intervals. To estimate survival we used the following data: the day of capture when the individual received the transmitter (i), the last day the individual was heard alive within its estimated remigial molt period or the day it regained its ability to fly (j), the last day on which we attempted to monitor an individual or when it had completed molt (k), and the fate of the bird (0=alive, 1=dead). For birds that survived the entire monitoring period, j=k. Dates on which flight was regained were calculated using information from an associated study (Dickson et al. 2012) that estimated 9<sup>th</sup> primary lengths required for scoters to fly (surf scoter (SUSC) male (M): 158mm, SUSC female (F): 139mm, white-winged scoter (WWSC) M: 179mm, WWSC F: 164mm) and mean 9<sup>th</sup> primary growth rates for scoters during remigial molt (SUSC: 3.39mm/day, WWSC: 4.26mm/day). To limit survival estimates to the flightless period, we estimated the stage (day) for each individual at capture using its 9<sup>th</sup> primary length and the mean 9<sup>th</sup> primary growth rates (molt stage or day of molt = 9<sup>th</sup> primary length at captures / 9<sup>th</sup> primary growth rate). We used the flightless period instead of the 9<sup>th</sup> primary growth period because we speculated that scoters might have lower mortality risk once they regained flight. A 7-day post-capture censor period was then included to account for effects of captures and handling and acclimatization to the transmitters (Esler et al. 2000, Iverson et al. 2006). Birds that died during the censor period, or were found dead upon first observation following the censor period, were not included in the analyses (n=8; Table 2.1). Individuals that were heard alive during the censor period but not thereafter and individuals for which the mortality status was unknown were not included in the analyses (n=10). The first piece of information used to create the encounter history to generate survival estimates became the molt stage of the individual

on the day of capture plus the 7-day censor period ( $i$ ). All other numbers used in the encounter history were based on these. For example, birds captured with 0 mm 9<sup>th</sup> primaries had  $i=7$ , due to the censor period. Transmitters deployed on individuals that had yet to undergo remigial molt and retained old primaries were assumed to be at day 0 ( $i=7$ ,  $n=5$ ).

We estimated daily survival rates (DSR) for scoters during the molting stage of the annual cycle. We also estimated a period survival rate (PSR) that reflected survival across the duration of the molting period within the non-breeding season. The PSR is the product of all DSRs within the molting period, which is calculated as  $DSR^n$ , where  $n$  is the number of days scoters are flightless (48 days SUSC M, 43 days SUSC F, 49 days WWSC M, 46 days WWSC F; Dickson et al. 2012). We computed confidence intervals for PSR estimates by raising the 95% confidence interval for DSR to the  $n$  power (Johnson 1979).

Ninth (9<sup>th</sup>) primary feather lengths at captures and daily feather growth rates from Dickson et al. (2012) were used to estimate the average number of exposure days per individual in each age and sex class of molting scoters (exposure days = day the bird regained flight or last day the bird was heard ( $j$ ) – deployment day + 7-day censor period; Iverson and Esler 2007). One of the objectives of this study was to determine factors within the molting period that were related to survival, which we intended to accomplish by comparing *a priori* defined models in Program MARK using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Models to be included in the analysis accounted for species, the four age-sex classes for each species (ASY and SY male and female), study site locations, molt stage, and mass. Mass was treated as an individual covariate, addressing the hypothesis that heavier birds could better accommodate energetic demands of remigial molt. After preliminary analysis, however, no mortalities were detected within the sample of birds that were confirmed to live beyond the censor period; therefore, there was no variation in survival that could be related to the attributes described above.

Because no birds died after the 7-day censor period, DSR and PSR were 1.00 and invariant (see Results). To determine if these high survival rates during remigial molt were potentially a function of small sample size, short exposure period, or other

factors, we modeled potential molting survival rates by adding simulated mortalities into the data set and generating subsequent survival estimates and variance. This simulation provided a sensitivity analysis by describing the magnitude of change in estimated survival rates in response to potentially realistic levels of mortality (Iverson and Esler 2007, Hogan et al. 2013).

To perform the simulation, we randomly inserted 1, 2 and 3 mortalities into the encounter history. To maximize potential mortality rates, all inserted mortalities were given to random individuals that had 9<sup>th</sup> primary lengths of 0 mm at capture ( $i=7$ ), lived one week from the end of the censor period ( $j=14$ ), and were simulated to be dead by the next day ( $k=15$ ). All species, locations and age and sex class were analyzed together to generate survival estimates ( $n=143$ ). Because the maximum duration for the flightless period for scoters was determined to be 49 days (Dickson et al. 2012), this time period became the number of occasions (days) included in our analysis and the number of days used to determine PSR for the molt period. Our simulation assumed constant survival throughout the monitoring period and we calculated 95% confidence intervals for each estimate.

While this sensitivity analysis allowed us to compute potential survival rates and confidence intervals when simulated mortalities were added to the dataset, this was not what was actually observed. In reality, after accounting for the 7-day censor period, we observed zero mortalities. We recognize that actual scoter survival during remigial molt of 1.00 is biologically improbable. We performed another sensitivity analysis to estimate the probability of observing zero mortalities given potentially realistic mortality levels for the population. We used the binomial probability distribution and the survival rates from our analysis of simulated mortality to calculate the probability of observing zero mortalities given potentially true daily survival rates for scoters during remigial molt. A random number between zero and one was generated for every day of the study period and every monitored scoter. This generated random number was compared to DSRs of 0.9996, 0.9993 and 0.9990 from the analysis of simulated additional mortalities (Table 2.2). A mortality was recorded if the random number was greater than the DSR, and we computed the percentage of times no mortalities were observed at the 3 levels of DSR. To get stable results we ran 100,000 simulations at each level of DSR. Scoter species and age and sex class were lumped to include all 143 transmitters monitored following

the censor period and we used the average number of exposure days (post-censor period) that scoters were monitored of 21.3 days for this analysis (see Results). All simulations were written in SAS (v. 9.2, SAS Institute, Inc., Cary, NC; Environmental Systems Research Institute, Inc., Redlands, CA).

## 2.4. Results

During the periods of remigial molt in 2008 and 2009, we tracked the fates of 66 surf scoters and 39 white-winged scoters in Southeast Alaska and 44 surf scoters and 18 white-winged scoters in the Salish Sea (Table 2.1). A total of 24 transmitters were censored from the analysis, including 6 transmitters that were never heard after deployment, 8 transmitters heard during the censor period but not thereafter, 8 transmitters on individuals that died during the censor period (see below), and 2 transmitters on individuals that completed remigial molt before the 7-day censor period was over (Table 2.1). Eighty-eight surf scoters and 55 white-winged scoters were included in our survival analyses.

Of the 167 scoters outfitted with VHF transmitters, 8 were confirmed to have died (Table 2.1). All 8 of these mortalities occurred within the 7-day censor period or were never heard alive after the censor period and all were surf scoters. If these 8 mortalities were included in the dataset (151 individuals,  $i=7$ ,  $j=14$ ,  $k=15$ ), it would result in a DSR for surf scoters during the remigial molt period of 0.997 (95% CI: 0.995-0.999), and a PSR of 0.88 (95% CI: 0.78-0.94) for a 49 day flightless period. However, we suggest that these mortalities are very unlikely to represent natural mortalities, given the body of research that describes short-term effects of capture, handling, and radio attachment on wild waterfowl (Esler et al. 2000, Hupp et al. 2006, Iverson et al. 2006). Also, lack of subsequent mortalities further indicates low rates of natural mortality in our study system. Analyses excluding birds that died during the censor period resulted in a DSR during remigial molt for both species of scoters of 1.00, without a measure of variation (95% CI: 1.00-1.00) and subsequently, the PSR for the molting period was also 1.00.

Our survival estimates should be representative and reliable, as our monitoring occurred throughout most of the molt period. Specifically, we deployed transmitters on

birds that had recently initiated remigial molt (scoters that received transmitters had mean 9<sup>th</sup> primary lengths of 31.18mm ( $\pm$  3.06 SE) for surf scoters and 38.91mm ( $\pm$  4.61 SE) for white-winged scoters). Moreover, the mean number of exposure days was 21.1 days ( $\pm$  0.89 SE) for surf scoters and 21.7 days ( $\pm$  1.17 SE) for white-winged scoters. These results indicate that birds were monitored early in the feather growth process and for a sufficient duration of time during the flightless period to confidently estimate survival probabilities during the molt period.

Adding up to 3 simulated mortalities did not appreciably reduce DSR or PSR (Table 2.2), with the 3 added mortalities resulting in a DSR of 0.9990 (95% CI: 0.9997-0.9999; Table 2.2) and a PSR of 0.9513 (95% CI: 0.8566-0.9840). Assuming an observed DSR of 0.9996, based on 1 simulated mortality, we had only a 30.3% chance of observing zero mortalities (Table 2.2), suggesting that this high DSR is underestimating the true DSR for scoters during remigial molt. If scoters have a DSR of 0.9999 during remigial molt, which equates to a PSR of 0.9950 for the 49 day period, 74% of the time we would obtain a data set with zero mortalities (Fig. 2.2). These simulations indicate that only at very high levels of survival would we expect to observe the result of zero mortalities.

## **2.5. Discussion**

We found that survival of surf and white-winged scoters during remigial molt was very high (DSR and PSR of 1.00) across a broad latitudinal sampling area, suggesting that the remigial molt stage of the annual cycle does not constitute a demographic constraint on scoter populations. Further, survival of molting scoters did not vary by species, age, sex, mass, season, or location. Although a survival rate of 1.00 for any species during any period of the annual cycle is unlikely, our simulations suggest that only very high levels of DSR are likely to result in our observation of zero mortalities. Even in simulations with added mortality, our conclusion that scoters have very high survival during the remigial molt period remained the same.

A concurrent study found that scoter body mass increased during molt (Dickson 2011), and foraging effort was similar to that during winter (VanStratt 2011), suggesting

that scoters were not experiencing energetic or nutritional constraints during remigial molt. Furthermore, the long duration and wide range in timing of molt indicated that molting scoters were not under strong temporal constraints (Dickson et al. 2012). These results indicated that scoters have a successful strategy for remigial molt and are using high quality habitats that are relatively safe and productive.

The high survival that we documented was consistent with high survival described for other species of sea ducks during remigial molt, including Barrow's goldeneye (DSR=0.994 and PSR=0.95; Hogan et al. 2013) and harlequin ducks (DSR=0.999 and PSR=0.99; Iverson and Esler 2007). Scoter survival during molt was higher than those found for other species of waterfowl, including dabbling ducks such as male American black ducks (*Anas rubripes*) (PSR=0.89; Bowman and Longcore 1989), adult female northern pintails (*Anas acuta*) (DSR=0.993 and PSR=0.79; Miller et al. 1992) and adult female mallards (*Anas platyrhynchos*) (PSR = 0.77; Fleskes et al. 2010). It has been suggested that waterfowl may select molting sites based on trade-offs between predation risk, food resources, and energetic profitability. However our findings suggest that scoters choose molting areas that are both safe and provide high foraging opportunity (Fox and Kahlert 2005, Dickson 2011). Sea ducks may be less vulnerable to predation than dabbling ducks as they tend to forage in open water habitats where they are less susceptible to land-based predators and are able to escape predators by diving (Hogan 2012).

We found that scoter survival during the molt period was much higher than during other periods of the annual cycle. We generated PSR for the overwintering period (129 days, Chapter 3) to put molt survival in the context of other annual cycle stages and to help determine which periods in the annual cycle may be constraining scoter populations. Using the simulated DSR with 2 mortalities during the molting period, when extrapolated over approximately 4.5 months remaining in the non-breeding period post-molt, the winter PSR would be 0.9176 (95% CI: 0.7093 -0.9787). This estimate is appreciably higher than average overwintering survival rates found for surf scoters of 0.7399 (95% CI: 0.6014-0.8367) in Southeast Alaska and 0.8631 (95% CI: 0.7833-0.9151) in BC (Chapter 3).

Despite potential for increased predation risk during the flightless remigial molt period, we observed low rates of predation during this period of the annual cycle, consistent with other studies of molting sea ducks (Iverson and Esler 2007, Hogan et al. 2013). A portion of the remigial molt period for scoters coincides with salmon spawning along the Pacific coast, which may provide potential scoter predators, particularly bald eagles (*Haliaeetus leucocephalus*), with an alternative food source. Further, birds may select remigial molt sites at least in part based on safety from predators (Salomonsen 1968).

We did not observe a single mortality of a white-winged scoter during our study, suggesting that white-winged scoters were successful at minimizing the potential costs associated with molt, were better suited at coping with stresses associated with capture and handling, and have very high molt survival. In a study where both surf and white-winged scoters were marked during winter at a single site, mortality of surf scoters was nearly 50% higher than that of white-winged scoters (Anderson et al. 2012). Other studies have found that larger birds are better able to deal with stresses (Conroy 1989, Jamieson et al. 2006). When compared to surf scoters, white-winged scoters are >50% larger, and may be a less manageable prey item for small predators such as mustelids (Anderson et al. 2012).

We suggest that the molting period does not constitute a period of population constraint in the life cycle of scoters and that scoters employ successful strategies to mitigate risks and costs associated with the molting period. However, despite the high survival rates for scoters during molt under normal conditions, all three scoter species experienced large die-offs during molt in 1990, 1991, and 1992 in Southeast Alaska (Henny 1995). The reason for these die-offs remains unknown although many of these scoters showed high levels of cadmium. Harmful biotoxins associated with algal blooms also can kill seabirds including scoters, and these blooms usually occur during mid-late summer when scoters are undergoing remigial molt (Jessup et al. 2009, Du et al. 2011, Phillips et al. 2011). Sea ducks also are particularly vulnerable to marine oil pollution during the molting period (Piatt et al. 1990, Dickson and Gilchrist 2002). Because molting scoters form large aggregations and are unable to leave, they are vulnerable to rare, local perturbations that can cause catastrophic mortality. We suggest that factors causing observed, persistent, continental-scale declines in scoter numbers are not

occurring during the remigial molt period and that managers should focus their efforts to determine and mitigate underlying causes of declines on other stages of the annual cycle.

## 2.6. Tables and Figures

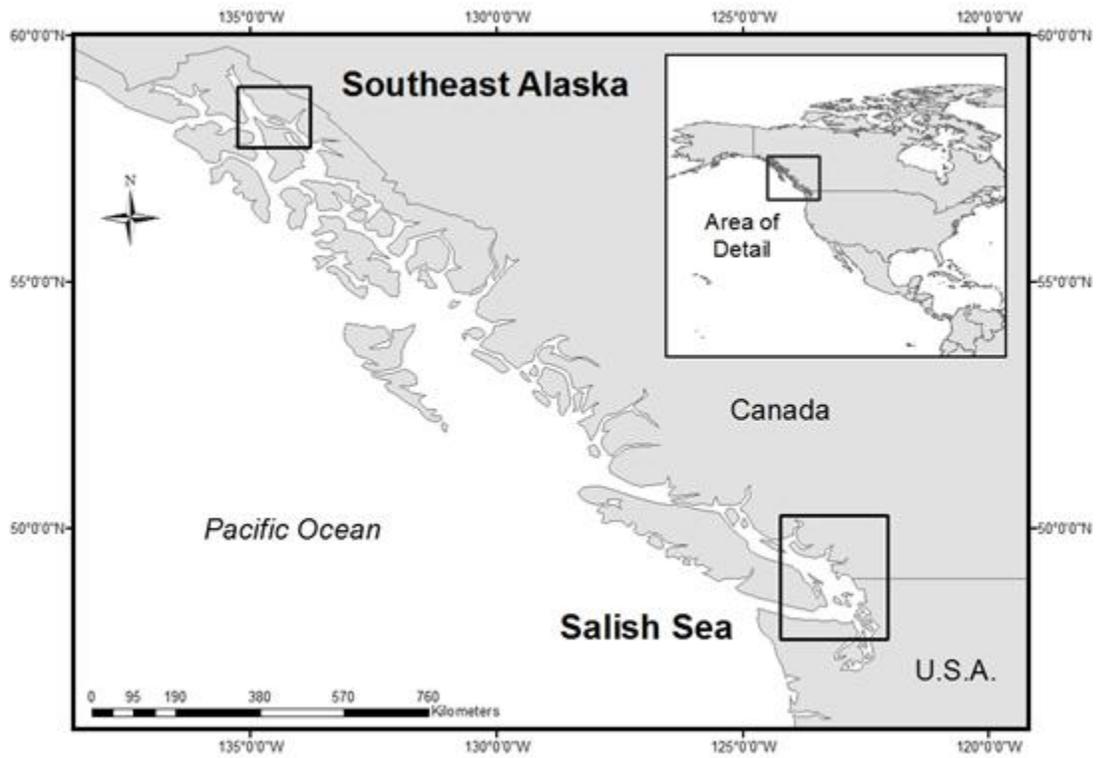
**Table 2.1.** *Numbers of very high frequency (VHF) transmitters deployed on scoters by category. Numbers are reported separately for study sites (AK = Southeast Alaska, WA = Salish Sea), species (SUSC = surf scoter, WWSC = white-winged scoter) and age (ASY = after second year [adult], SY = second year [juvenile]) and sex class (F = female, M = Male).*

Species and Age and Sex Class	Transmitters Deployed		Transmitters Never Heard		Never Heard Post Censor Period <sup>a</sup>		Censored Mortalities		Included in Survival Estimates	
	AK	WA	AK	WA	AK	WA	AK	WA	AK	WA
<b>SUSC MASY</b>	27	18	1	1	3	0	2	2	21	15
<b>SUSC FASY</b>	21	19	2	1	3	0	0	1	16	17
<b>SUSC MSY</b>	3	2	0	0	0	0	0	0	3	2
<b>SUSC FSY</b>	15	5	1	0	2	0	3	0	9	5
<b>SUSC Total</b>	66	44	4	2	8	0	5	3	49	39
<b>WWSC MASY</b>	18	10	0	0	2	0	0	0	16	10
<b>WWSC FASY</b>	2	7	0	0	0	0	0	0	2	7
<b>WWSC MSY</b>	8	0	0	0	0	0	0	0	8	0
<b>WWSC FSY</b>	11	1	0	0	0	0	0	0	11	1
<b>WWSC Total</b>	39	18	0	0	2	0	0	0	37	18

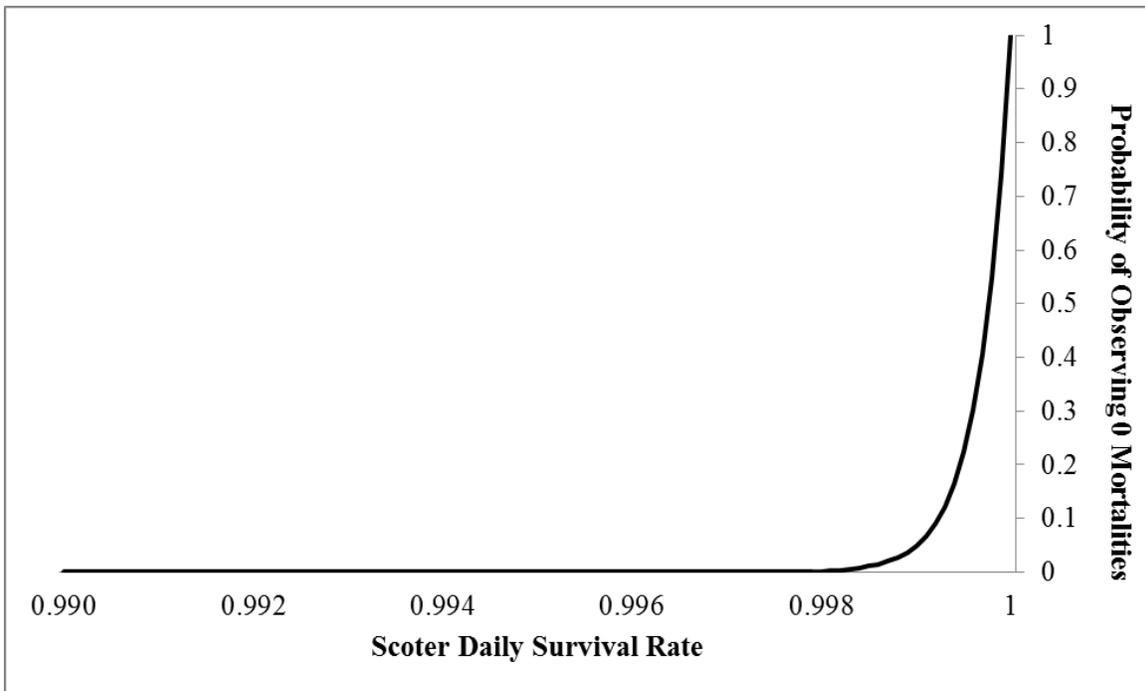
<sup>a</sup>Includes 2 SUSC that regained the ability to fly before the 7-day censor period was completed in AK

**Table 2.2. Simulated daily (DSR) and period (PSR) survival rates, and probability of observing zero mortalities during remigial molt when 1, 2, and 3 mortalities were added to the study.**

<b>Mortalities</b>	<b>DSR (95% CI)</b>	<b>PSR (95% CI)</b>	<b>% Zero Mortalities</b>
<b>1</b>	0.9996 (0.9976-1.0000)	0.9835 (0.8887-0.9977)	30.3
<b>2</b>	0.9993 (0.9973-0.9998)	0.9672 (0.8754-0.9917)	12.2
<b>3</b>	0.9990 (0.9969-0.9997)	0.9513 (0.8566-0.9840)	5.0



**Figure 2.1.** *Locations of study sites of molting surf scoters and white-winged scoters.*



**Figure 2.2.** *Probability of attaining a dataset with zero scoter mortalities during remigial molt as a function of daily survival rate when 143 individuals are monitored for 21.3 days.*

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### **3. Variation in winter survival of surf scoters: interacting effects of latitude, mass, age and sex**

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#### **3.1. Abstract**

To understand population dynamics and identify when and where demographic or distributional constraints may exist within the annual cycle, it is important to quantify sex, age, and condition-related variation in survival across a species' range. We evaluated variation in winter survival probability of a migrant sea duck, the surf scoter (*Melanitta perspicillata*), which ranges over nearly 35 degrees of latitude on the Pacific coast of North America during the non-breeding season. During 2001-2010, 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, (2) the range core in British Columbia, (3) and the southern periphery in Baja California. We estimated model averaged daily survival to be 0.9985 (95% CI: 0.9979-0.9989) for all age and sex classes at all locations from the end of November to the beginning of April, which corresponded to 129-day cumulative survival of 0.82 (95% CI: 0.76-0.87). Cumulative survival averaged lower at the range peripheries, Southeast Alaska 0.75 (95% CI: 0.62-0.85) and Baja California 0.80 (95% CI: 0.58-0.93), than in the range core, British Columbia 0.86 (95% CI: 0.79-0.91), and was lower during mid-winter than during late winter at all sites. Also, mass was positively correlated with survival. Although age and sex classes did not have direct effects, mass effects led to differential survival patterns among age and sex classes. Adult males of average 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 after controlling for mass. Our observations help to explain patterns of differential migration reported for this species, wherein wintering flocks at high latitudes are composed of a greater proportion of adult males and wintering flocks at lower latitudes are composed of greater proportions of females and juveniles. Our results also highlight periods (mid-winter) and locations (range peripheries) of elevated levels of mortality for important age and sex classes (adult females).

### **3.2. Introduction**

Quantifying sources and timing of variation in demographic attributes, such as survival, is important for understanding wildlife population dynamics and identifying when and where demographic or distributional constraints exist within the annual cycle (Lebreton et al. 1992, Alisauskas et al. 2004). For species whose life histories are characterized by long life-spans, delayed reproductive maturity and low annual productivity (Kehoe et al. 1989, Goudie et al. 1994), proportional variation in adult survival has a stronger effect on population dynamics than does variation in other factors, such as reproductive performance (Schmutz et al. 1997, Heppel et al. 2000, Saether and Bakke 2000, Calvert et al. 2009, Flint 2012). Therefore, documentation of variation in season-specific survival, and factors related to that variation, can provide important insight into wildlife population dynamics (Hupp et al. 2008).

While studies of the ecology of northern hemisphere birds have focused disproportionately on the breeding period (Calvert et al. 2009, Bridge 2011), it is important to document variation in demographic rates throughout the annual cycle to identify potential periods of demographic constraint. There is increasing recognition that factors within the non-breeding period can have important effects on population dynamics (Kery et al. 2006, Calvert et al. 2009). The non-breeding period represents the majority of the annual cycle for waterfowl and includes the critical periods of remigial molt, fall migration, winter, and spring migration. Waterfowl may be more vulnerable to mortality risks during the non-breeding period, and mortality during winter may be particularly high (Conroy et al. 1989, Gauthier et al. 2001, Calvert et al. 2009). Potential stresses associated with the overwintering period include increased thermoregulatory

costs (Lehikonen 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. 2002, Elliot et al. 2007). These factors may have differential effects among individuals, based on age, sex, mass, condition, or other attributes (Lebreton et al. 1992).

Surf scoters 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 (Savard et al. 1998). On the Pacific Coast the surf scoter wintering range extends more than 5000 km over nearly 35 degrees of latitude stretching from the Aleutian Islands in Alaska to the Baja Peninsula in Mexico (Savard et al. 1998). Many previous studies on surf scoters have evaluated the role of food availability on distribution, abundance, movements, foraging behavior, and physiological condition (Žydelis et al. 2006, Lewis et al. 2008a,b, Anderson and Lovvorn 2008, Kirk et al. 2008, Anderson et al. 2008, VanStratt 2011). Lacking are estimates that quantify fitness consequences of responses to habitat variation, and that identify when and where demographic or distributional constraints occur within the annual cycle. Understanding the influences on geographic variation in demographic traits can indicate factors that affect distribution of animals at a given annual cycle stage (Ozugal et al. 2006, Ciannelli et al. 2007, Saracco et al. 2010). Challenges facing scoters during the non-breeding period vary across a latitudinal gradient. For example, 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 a less energetically costly migration compared to scoters wintering in the southernmost portion of the range (Baja California). Variation in survival due to individual characteristics such as age, sex, or mass, along with environmental factors, may lead to differential migration and latitudinal distributions skewed by age and sex classes (Cristol et al. 1999, Nebel et al. 2002, O'Hara 2006). Scoters exhibit differential migration along the Pacific coast, as higher proportions of males and adults winter at more northern latitudes, while higher proportions of females and juveniles winter at more southern latitudes (Iverson et al. 2004). Therefore it is informative to study individual and geographic variability of populations and their effects on demographic attributes (Lebreton et al. 1992). Few

studies have examined variation in winter survival rates at a continental scale or considered the trade-offs associated with wintering site selection, despite the implications for population dynamics, distribution, and conservation. We measured scoter survival over the latitudinal span of their wintering areas, allowing for consideration of geographical variation in survival and influences on surf scoter demography and distribution. Our objective was to determine if winter survival of surf scoters influenced continental population dynamics or distributions, and to determine if attributes of individuals was related to survival variation.

### **3.3. Methods**

#### **3.3.1. Study Areas**

During 2001–2010, we attached very high frequency (VHF) radio transmitters to surf scoters during winter in three areas (Figure 3.1): Southeast Alaska (hereafter SE AK), the Strait of Georgia, British Columbia (hereafter BC), and Baja California, Mexico (hereafter Baja). The SE AK site was near the northern extent of the wintering range of surf scoters (Savard et al. 1998) near Juneau, Alaska, U.S.A. (58.4°N, 134.5°W). Hodges et al. (2008) estimated that ca. 77,000 scoters (*Melanitta spp.*) winter in SE AK, with surf scoters being the most numerous species. Deep channels and fjords are characteristic of the area. Blue mussels (*Mytilus edulis*) were common and widespread in rocky intertidal areas, and constituted the primary prey of surf scoters (J. Hupp, United States Geological Survey (U.S.G.S.), unpublished data). Predators of surf scoters were widespread throughout the region; bald eagles (*Haliaeetus leucocephalus*) and American mink (*Mustela vison*) were documented as common predators and/or scavengers of surf scoters (Anderson et al. 2012).

We collected survival data at the core of the surf scoter wintering range in BC at 2 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. Similar to the SE AK site, this area is 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 (Dawe et al. 1998). Avian predators, particularly bald eagles, were abundant at these sites (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), which 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 (*Callinassa spp.*; D. Ward, U.S.G.S., 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. Ward, personal communication).

### **3.3.2. Captures and Monitoring**

Surf scoters were captured during early winter (November and December) using floating mist nets (Kaiser et al. 1995) at all study sites. We recorded body mass of all captured scoters ( $\pm 1$  g) and each was marked with a uniquely numbered metal tarsal band. We determined sex on the basis of plumage characteristics, and age class (hatch year [HY]) or after hatch year [AHY]) on the basis of plumage characteristics and bursal depth (Mather and Esler 1999, Iverson et al. 2003). VHF radio transmitters were fitted to 297 individuals, distributed among sex and age classes, as well as year and region (Table 3.1). Transmitters deployed in SE AK and Baja were attached using subcutaneous prongs and super glue (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 hr. 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).

Captures of scoters and deployment of VHF radios occurred during four winters in the Strait of Georgia, BC, three of them in Baynes Sound (2001-2002, 2002-2003 and 2003-2004) and one 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 birds were captured during the 2003-2004 field season (2 December 2003) and these individuals were not subject to a post-capture censor period (see below).

### **3.3.3. Analysis**

We used a modified Mayfield method of nest survival analysis procedures in Program MARK (v. 6.2) to generate daily (DSR) and cumulative survival rates (CSR) during the overwintering period for surf scoters (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 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 day of capture (i), the last day the transmitter was heard 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 d post capture for externally-mounted transmitters and 14 d for implanted transmitters (Esler et al. 2000a, Iverson et al. 2006). Mortalities of 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. 2000a). Birds that died during the censor period or were never heard alive after the censor period were excluded from analyses. The date 17

November 2009 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 2009 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 we monitored for survival was 1 April, giving us a 129 day study period (24Nov-1April).

To investigate variation in DSR through winter, we evaluated a candidate set of 48 multiple linear logistic regression models. Five variables were included as potential explanatory variables and evaluated as main effects and in interactive combinations. These included: (1) study area location (LOCATION), (2) period of winter (PERIOD), (3) age (AGE), (4) sex (SEX), (5), and location-adjusted residual mass (MASSLOC). Individual main effects, and all additive combinations of main effects were considered.

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 between years at each location by adding individual covariates for year effect into the dataset. We found that between-year differences in survival were quite small within sites. 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.

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-late January) and late-winter (early February-early April) representing 64 and 65 days, respectively (i.e. Esler et al. 2000b).

We also considered effects of mass on variation in survival, comparing two measures of deviation from average mass, and hypothesized that there could be survival costs associated with mass (Haramis et al. 1986, Lima 1986, Rotella et al. 2004, Conroy et al. 1989). We calculated residual mass (deviation from average mass) in two ways: by location irrespective of age and sex class (MASSLOC) and by age and sex class and location (MASSCOH). MASSLOC was calculated by subtracting average 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 and sex class, i.e., whether overall lighter or heavier birds were at higher or lower mortality risk. MASSCOH was calculated by subtracting average mass of individuals within a specific age and sex class at a certain location from mass of each radio-marked individual within that age and 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 MASSCOH on survival, and incorporated them into Program MARK as individual covariates. We found that MASSLOC ( $\omega_i=0.01$ ,  $\sum\omega_i=0.77$ ) was better supported than MASSCOH ( $\omega_i=0.00$ ,  $\sum\omega_i=0.11$ ) suggesting that mass relative to the overall average within a location, irrespective of age and sex class, had a stronger influence on survival than mass relative to the average within a age and 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 and late winter periods.

Because our research questions were focused on spatial differences in survival, we focused on location and interacting effects of location and other main effects. To determine if the effect of location differed between the periods of winter, age and sex classes, and with body mass, we included 4 models with LOCATION, one of the main effects, and a 2-way interaction term with LOCATION (e.g., LOCATION + PERIOD + LOCATION\*PERIOD), and 5 models that included all main effects and a LOCATION 2-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 4 individual age and 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 2-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 on probability of survival (Burnham and Anderson 2002). Using Akaike's Information Criterion adjusted for small sample size (AICc), multiple a priori hypotheses, expressed as candidate models, were ranked by comparing models using  $\Delta\text{AICc}$  scores and Akaike weights ( $w_i$ ) (Burnham and Anderson 2002). The  $\Delta\text{AICc}$  scores were calculated as the difference between each model and the most parsimonious model. To determine the relative support for each model, AICc weights were used. A model averaged estimate of DSR (with unconditional 95% Confidence Intervals) was generated and from this a CSR was calculated for the overwintering period (129 days) as  $\text{DSR}^n$  where  $n$ = days in the period (Johnson 1979). Confidence intervals for CSR were calculated using the delta method (Seber 1982, Powell 2007). Survival estimates are reported with 95% Confidence Intervals.

### 3.4. Results

Thirty-four mortalities were detected among 297 surf scoters monitored post-censor (Table 3.1). Of the 48 models compared in Program MARK to examine factors explaining variation in surf scoter winter survival rates, the PERIOD + SEX + MASSLOC model was most parsimonious ( $w_i=0.24$ ; Table 3.2). Two other models had high degrees of support relative to the best supported model (i.e.,  $\Delta\text{AICc} < 2.0$ ; Table 3.2), including the LOCATION + PERIOD + SEX + MASSLOC ( $w_i =0.16$ ,  $\Delta\text{AICc}=0.86$ ), and PERIOD + AGE + SEX + MASSLOC ( $w_i =0.12$ ,  $\Delta\text{AICc}=1.35$ ) models. In contrast, our null model, which assumed constant survival irrespective of period, sex, age, mass or location received little support ( $w_i =0.00$ ,  $\Delta\text{AICc}=8.75$ ), indicating that 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 and sex classes at all locations, and 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 ( $\sum w_i=0.38$ ), and was included in the second best supported model (LOCATION + PERIOD + SEX + MASSLOC) and two other models within the top ten (Table 3.2). 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 average wintering CSR among locations, 0.75 (0.62-0.85; Fig. 3.2). Scoters in BC, the core of the wintering range for surf scoters, had the highest CSR, 0.86 (0.79-0.91). Scoters in Baja at the southern periphery of their wintering range had an average CSR 0.80 (0.58-0.93), which fell between rates for BC and SE AK.

The explanatory variable PERIOD was included in the 4 highest ranked models and had the third highest parameter likelihood ( $\sum\omega=0.81$ ) indicating that scoter survival varied over the course of the winter. In all cases, late winter survival was higher than mid-winter survival (Fig. 3.2). The average period survival rate (PSR) for the 64 day mid-winter period (late November-late January), 0.87 (0.81-0.91), was markedly lower than the PSR for late winter (65 days; early February-early April), 0.95 (0.91-0.98).

The MASSLOC variable had the highest parameter likelihood ( $\sum\omega=0.86$ ) and was included in 9 of the 10 best supported models (Table 3.2). Birds with higher location-adjusted residual masses (MASSLOC) had higher winter survival rates, particularly at the peripheries of the range and during mid-winter (Fig. 3.3).

We observed differences in model-averaged CSR across age and sex classes, with adult birds having higher survival rates than young birds and females having higher survival than males (Fig. 3.2). Juvenile males (MHY) had the lowest overall average 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 ( $\sum\omega=0.82$ ) and received more support than AGE ( $\sum\omega=0.40$ ) suggesting that differences between sexes had a greater influence on surf scoter survival than age. Models that addressed age and sex class influences on survival through an AGE x SEX interaction were not well supported in the data (i.e., AGE + SEX + AGE\*SEX;  $\omega_i = 0.00$ ,  $\Delta AICc=11.47$ )

We recognize that, although there was a high degree of variation in body mass within age and sex classes, effects of body mass and effects of age and sex class on survival are best calculated and interpreted simultaneously, given covariation between class and mass. Average mass of males was higher than that of females, and AHY age

classes of both sexes had higher average mass than the corresponding HY age class (Fig. 3.4); these patterns are consistent with those of most waterfowl. We also found that scoters captured at the more northerly latitudes generally had higher body masses, both within and across age and sex class, with birds in SE AK generally being heaviest, followed by birds from BC, while scoters in Baja were lightest (Fig. 3.4). When we combined categorical effects of period, location, age, and sex (Fig. 3.2) with the continuous effect of body mass variation (Fig. 3.3), we found that important patterns emerged in the survival estimates (Fig. 3.5). By virtue of their higher mass, AHY males of average mass in SE AK had slightly higher survival than AHY males of average mass at other locations (Fig. 3.5). In contrast, AHY female survival for individuals of average mass within locations was highest in the range core of BC (Fig. 3.5). For HY scoters of both sexes, survival rates of individuals of average, location-specific mass were highest in the range core and/or the southern periphery relative to the northern periphery of SE AK (Fig. 3.5).

### **3.5. Discussion**

We found that surf scoter winter survival was influenced by a combination of location, period of winter, age and sex class, and mass. Surf scoter winter survival estimates averaged higher at the range core than at peripheries (Fig. 3.2). Population dynamics may vary across species ranges, with range cores tending to be more stable, while individuals at periphery locations may have increased extinction or turnover rates (Brown et al. 1995, Doherty et al. 2003). Other studies have found winter survival of waterfowl may vary by location (Krementz et al. 1987, Johnson et al. 1992, Krementz et al. 1997b), as factors such as weather conditions (Saether et al. 2000), competition, food availability (Cramer et al. 2012), and predators (Anderson et al. 2012) differ among locations and can affect survival rates. In an associated study, VanStratt (2011) showed that foraging effort (amount of time spent feeding) was lowest in SE AK, and highest in Baja, with intermediate levels in BC, suggesting differences in foraging conditions. Based on our finding of lower average winter survival in SE AK relative to our other sites, we conclude that foraging conditions were not influencing winter scoter survival. Winter

severity and extreme weather events can influence survival probability and population size (Bergan and Smith 1993, Blums et al. 2002, Ronka et al. 2005, Kery et al. 2006) as waterfowl wintering at northern latitudes are subject to increased energy costs associated with increased wind and wave action, and lowered air and water temperatures (Owen and Reinecke 1979, Prince 1979). Climate differences between locations also may affect survival particularly given our results on the influence of mass, age, and sex on survival (see below).

Over the candidate model set, MASSLOC was well supported and indicated that mass was positively related to survival. This is consistent with previous findings for surf scoters (De La Cruz et al. 2012) and other waterfowl species, as individuals with higher mass tend to have higher winter survival, and may be better suited to meet energetic costs associated with winter thermoregulation (Haramis et al. 1986, Hepp et al. 1986, Conroy et al. 1989, Bergan and Smith 1993). Further, the influence of mass on survival is highest for sea ducks, compared to other waterfowl tribes (Krementz et al. 1997b). Carrying larger nutrient reserves may have associated costs, such as higher risk of predation (Lima 1986), but this does not appear to be affecting survival in our study.

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 (Fig. 3.2). Model averaged estimates of survival for each winter period differed between sex and age classes and were more pronounced for young birds (Fig. 3.2). 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. 2000b). Mid-winter generally has 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 (Gullemette et al. 1996), including scoters in our study areas (Lewis 2005, Kirk 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 may shift their diet in late winter from mussels to the abundant herring spawn and epifaunal invertebrates (Anderson and Lovvorn 2011).

Age, sex, and mass all influenced survival, and the combination of these effects resulted in different patterns of survival across latitudes by age and sex class. Sex and age class have been related to waterfowl survival in other studies, with young birds having lower survival than adults (Johnson et al. 1992, Blums et al. 1996, Jamieson et al. 2006, Mittelhauser 2008, Thomas and Robertson 2008, Opiel and Powell 2010). Waterfowl cohorts differ in mass (males>females, AHY>HY), and there is typically a positive relationship between sea duck survival probability and body mass (Krementz et al. 1997b). Our data indicate that differences in survival across locations and age and sex classes were largely related to mass differences among these classes. AHY males of average mass for their class and location had highest survival at the northern range periphery in Alaska, whereas AHY females and HY individuals of both sexes, after accounting for mass effects, had higher survival at the range core or the southern periphery. We conclude that these patterns may contribute to the observed differential migration of surf scoter age and sex classes.

Surf scoters may choose wintering sites by trading off foraging opportunity and mortality risk, and these trade-offs may differ among age and sex classes at different latitudes. Iverson et al. (2004) found that scoters exhibit differential migration along the Pacific coast, as higher proportions of males and adults winter at more northern latitudes, while higher proportions of females and juveniles winter at more southern latitudes. We suggest that the smaller body mass of juvenile surf scoters imposes greater constraints on meeting the energy demands of extreme climates. At higher latitudes (SE AK), heavier (males) individuals may choose to winter due to good foraging conditions, while lighter (females) and less experienced (juveniles) individuals may choose to winter at lower latitudes (Baja) where, although thermoregulatory requirements are lower, foraging conditions are not as good (VanStratt 2011). Most species of waterfowl, including surf scoters, exhibit male-biased sex ratios, and population dynamics are sensitive to changes in breeding age female survival (Johnson et al. 1992). Management actions aimed at improving foraging conditions at mid and southern latitudes, where greater numbers of females and juveniles winter, might improve population trends.

Harvest pressure for scoters along the Pacific Coast of North America is much less than it is along the Atlantic Flyway, where 80-90% of the harvest occurs (Krementz

et al. 1997a, Savard et al. 1998). We speculate that increased mortality for surf scoters in SE AK may be a result of lower temperatures and shorter day length than elsewhere in the wintering range. Individuals wintering in Baja would not incur the same thermoregulatory costs associated with more northerly latitudes, and we speculate that low overwintering survival observed in Baja relative to the range core might be related to poorer foraging conditions (VanStratt 2011).

De La Cruz et al. (2012) found winter survival (16 December – 7 April) for surf scoters wintering near San Francisco, California to be 0.796. This rate was similar to our CSR for scoters at Baja (0.8039), our nearest study area to San Francisco. Our overall winter survival estimates were also similar for other species of waterfowl (e.g., Dugger et al. 1994, Miller et al. 1992), including other sea duck species (Cooke et al. 2000, Esler et al. 2000b, Mittelhauser et al. 2008, Esler and Iverson 2010). These winter survival estimates for sea ducks are much lower than survival rates estimated during other stages of the non-breeding period. An associated study (Chapter 2), 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 constraints on scoter populations (Dickson et al. 2012, Chapter 2). The male-biased sex ratios observed in waterfowl populations may result from decreased adult female survival during incubation (Devries et al. 2003). To fully understand surf scoter population declines, stage specific estimates, such as adult female survival during the breeding period, need to be addressed further.

However, given our results of low survival rates during winter, and the sensitivity of sea duck population dynamics to variation in adult survival, we suggest that winter survival may be an important driver of population trends, as well as a demographic attribute that could be targeted for improvement through management actions.

Our findings suggest that a multitude of factors influence scoter wintering survival and stress the importance of the non-breeding period in the annual cycle for sea ducks. This study highlights the importance of comparing demographic rates among locations to understand where and when population constraints may be occurring. Sea duck survival has rarely been quantified during other stages of the annual cycle (i.e., breeding,

staging, migration) limiting a full understanding of the population demographics of sea ducks. Surf scoters that winter along the Atlantic and Pacific Coasts appear to comingle on the breeding grounds, and individuals in some sea duck populations switched between Atlantic and Pacific wintering locations (Mehl et al. 2004). Links between Atlantic and Pacific populations of surf scoters should be addressed further to get a continental scale perspective of population dynamics. Nevertheless, based on our results managers may be able to most effectively influence survival of sea ducks by targeting the winter period and locations and age and sex classes with high mortality, perhaps through the conservation of critical foraging areas that have positive influences on body mass.

### 3.6. Tables and Figures

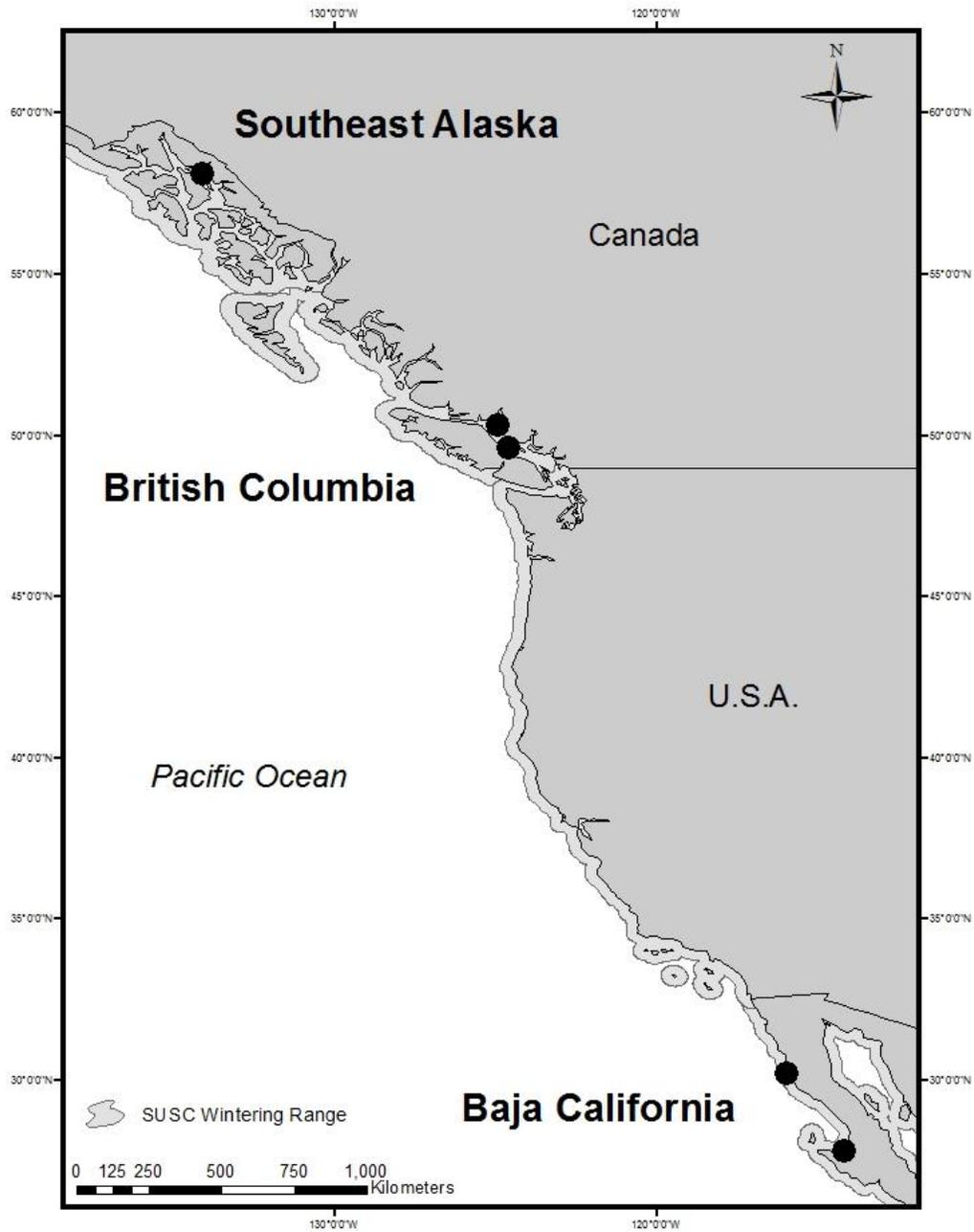
**Table 3.1.** Numbers of very high frequency (VHF) radio transmitters deployed on wintering surf scoters and monitored beyond a post-capture post censor period, by location, year and, age and sex class. Numbers in parentheses are confirmed surf scoter mortalities included in the analysis.

Location and Year	Age & Sex Class <sup>a</sup>				Total
	M AHY	F AHY	M HY	F HY	
Southeast Alaska 2008-2009	12 (1)	7 (0)	11 (4)	8 (3)	38 (8)
Southeast Alaska 2009-2010	12 (1)	15 (2)	9 (1)	9 (2)	45 (6)
Strait of Georgia, BC 2001-2002	17 (1)	8 (1)	5 (2)	3 (1)	33 (5)
Strait of Georgia, BC 2002-2003	24 (4)	10 (0)	1 (0)	2 (0)	37 (4)
Strait of Georgia, BC 2003-2004	16 (3)	7 (1)	1 (0)	2 (0)	26 (4)
Strait of Georgia, BC 2004-2005	26 (1)	14 (1)	14 (1)	19 (0)	73 (3)
Baja 2006-2007	8 (0)	8 (0)	7 (3)	7 (0)	30 (3)
Baja 2007-2008	4 (0)	5 (1)	0 (0)	6 (0)	15 (1)
<b>Total</b>	119 (11)	74 (6)	48 (11)	56 (6)	297 (34)

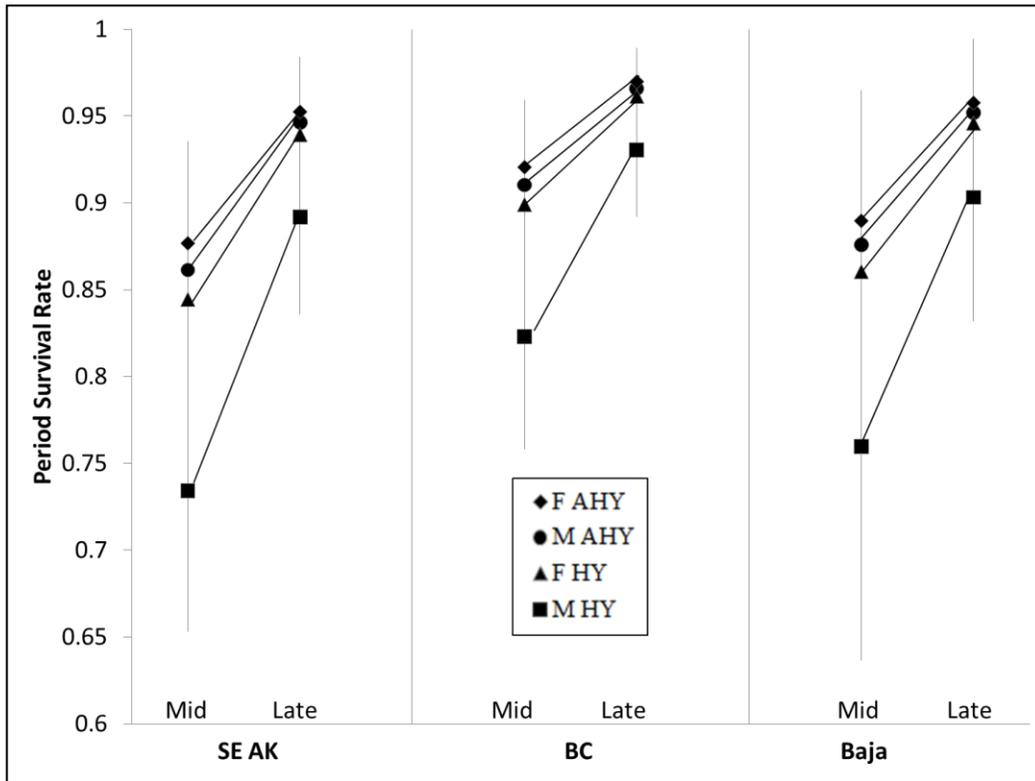
<sup>a</sup>. Age and sex class abbreviations include: M=Male, F=Female, AHY=after hatch year, and HY=hatch year.

**Table 3.2. Model selection results for the 10 best supported models from analyses of variation in winter survival of surf scoters at 3 locations along the Pacific coast of North America (Southeast Alaska, British Columbia, Baja California). Winter was delineated into two periods, mid (late November - late January) and late (Early February – early April). MASSLOC is residual mass of individuals calculated as the difference between mass at capture and average mass of all individuals captured at each study area. Four sex and age classes were included (males and females, after hatch year and hatch year).**

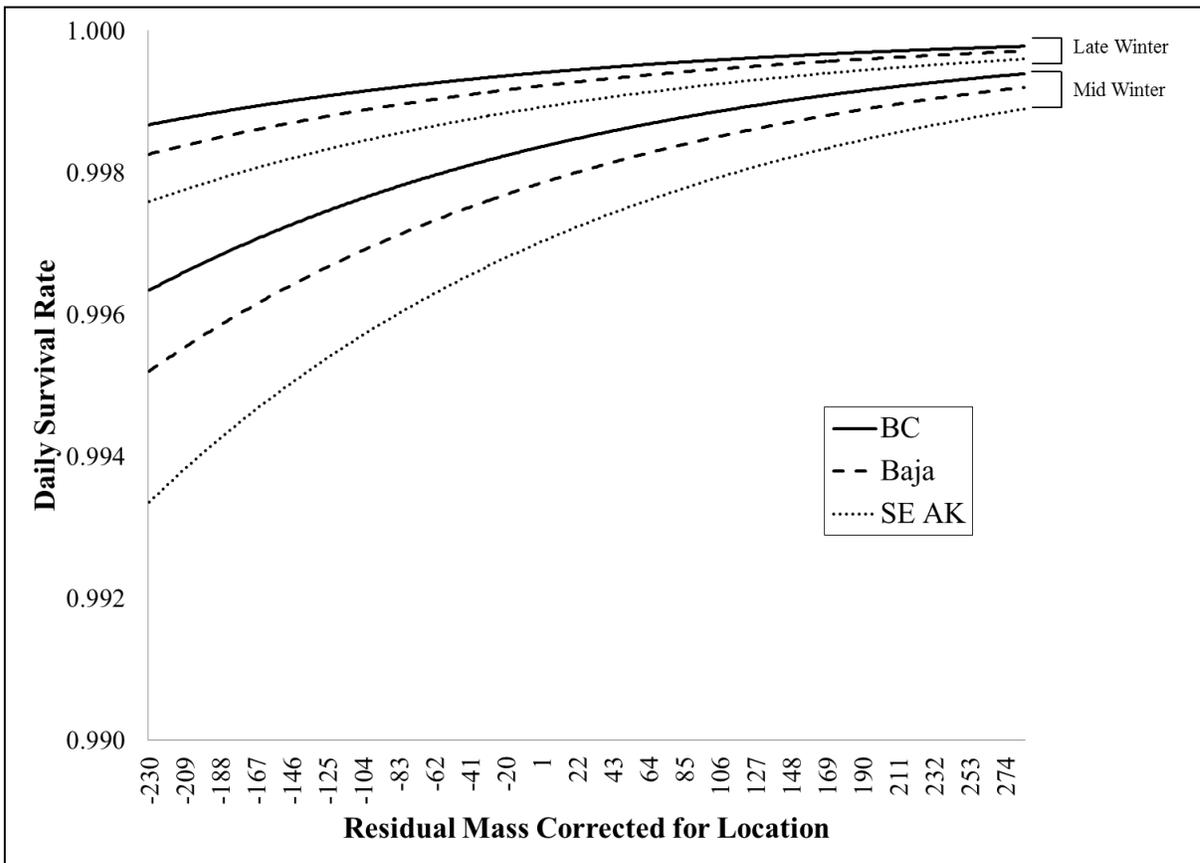
Model	AICc	delAICc	AICc Weights	k	Deviance
Period + Sex + MASSLOC	391.83	0.00	0.24	5	381.82
Location + Period + Sex + MASSLOC	392.68	0.86	0.16	7	378.68
Period + Age + Sex + MASSLOC	393.17	1.35	0.12	6	381.17
Location + Period + Age + Sex + MASSLOC	394.61	2.78	0.06	8	378.60
Sex + MASSLOC	395.06	3.23	0.05	3	389.05
Location + Sex + MASSLOC	395.10	3.27	0.05	5	385.09
Period + MASSLOC	395.76	3.94	0.03	4	387.76
Age + Sex + MASSLOC	395.97	4.14	0.03	4	387.97
Period + Age	396.20	4.37	0.03	4	388.20
Period + Age + MASSLOC	396.46	4.64	0.02	5	386.46



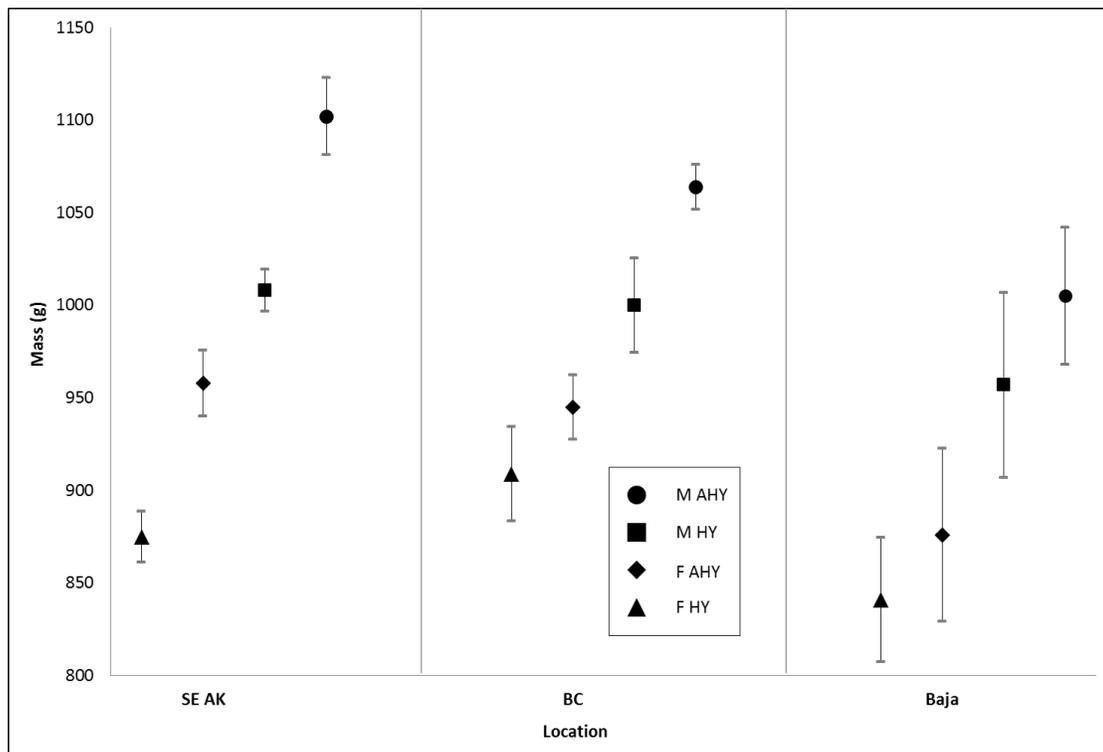
**Figure 3.1.** Surf scoter wintering range on the Pacific coast of North America and locations where surf scoters were marked with radio transmitters.



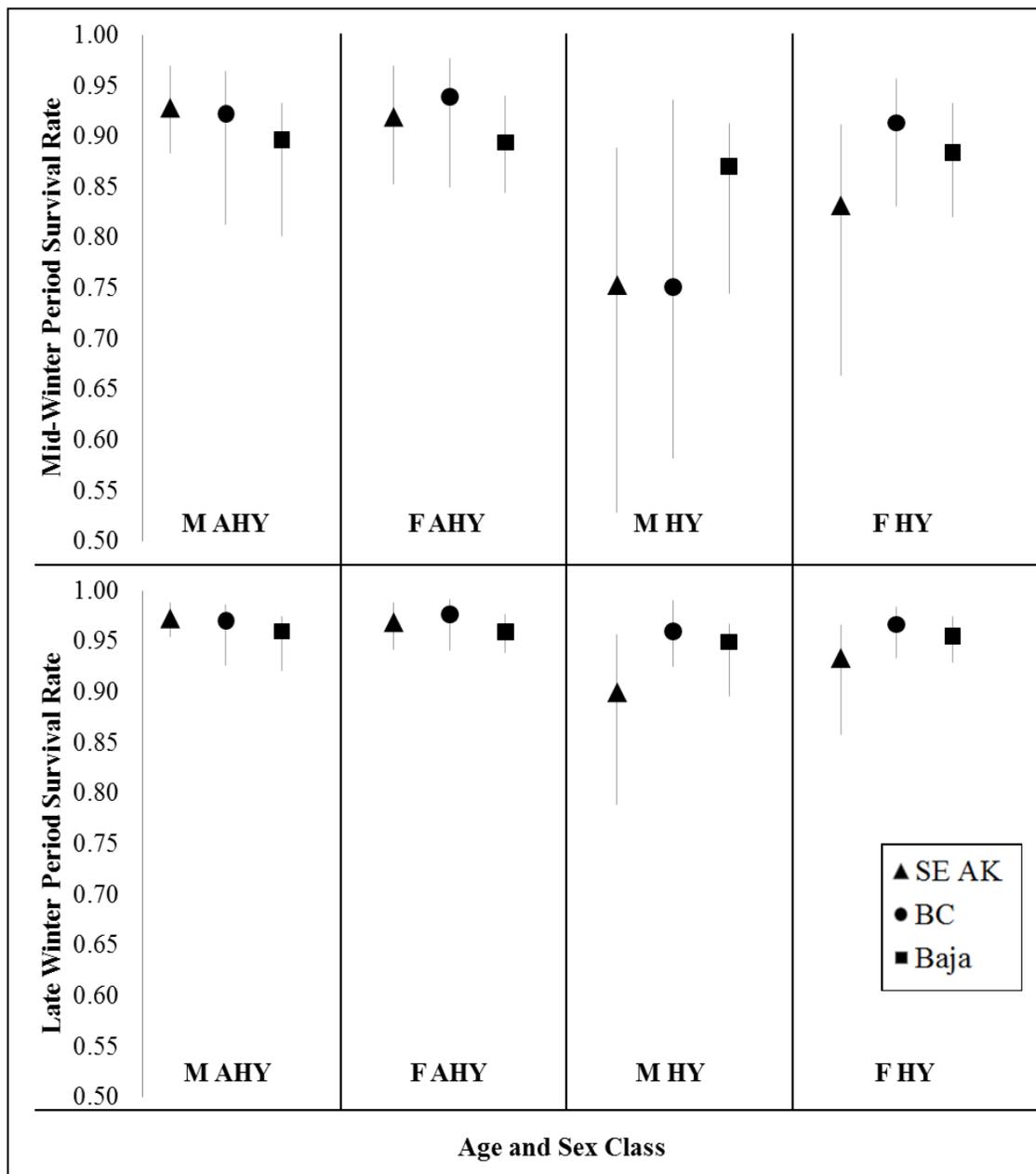
**Figure 3.2.** *Model-averaged period survival rate ( $\pm$ SE) of wintering surf scoters assuming average mass (irrespective of age-sex class) at 3 locations along the Pacific Coast of North America contrasted between mid (64 days, end November – end January) and late winter (65 days, end January-early April) and among sex and age classes (F=Female, M=Male, AHY=after hatch year, HY=hatch year).*



**Figure 3.3.** *Daily survival rates of surf scoters during mid-winter (64 days, late November – late January) and late winter (65 days, early February – early April) in Southeast Alaska, British Columbia and Baja California, 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 average mass of all individuals, irrespective of age-sex class, captured at each study area.*



**Figure 3.4.** Surf scoter mass (mean  $\pm$  95% CI) at 3 locations along the Pacific Coast of North America (Southeast Alaska = SE AK, British Columbia = BC, and Baja California=Baja) and among age-sex classes (F=Female, M=Male, AHY=after hatch year, HY=hatch year).



**Figure 3.5.** *Period survival rates of surf scoters of average mass for each age-sex class (M= Male, F=Female, AHY=after hatch year, HY=hatch year), during mid-winter (64 days, late November – late January) and late winter (65 days, early February – early April) in Southeast Alaska (SE AK), British Columbia (BC) and Baja California (Baja).*

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## **4. General Conclusions**

### **4.1. Thesis Summary**

The objectives of this thesis were to quantify surf and white-winged scoter survival during the non-breeding period. I addressed scoter survival during the molt and winter periods of the annual cycle to assess if either period constituted a potential demographic or distributional constraint in the scoter annual cycle. To accomplish this I used data from throughout the non-breeding range of scoters on North America's Pacific Coast and identified variations in scoter survival by location, season, mass, and age and sex class

In Chapter 2, I found that remigial molt survival of surf and white-winged scoters across a broad latitudinal sampling area was very high. Further, I found that survival rates of molting scoters did not vary annually, nor by species, age, sex, mass, season, or location. I performed a simulation to estimate the probability of obtaining my result of zero scoter mortalities during remigial molt, and another simulation where additional mortalities were inserted into the data to describe the magnitude of change in estimated survival rates in response to potentially realistic levels of mortality. These simulations confirmed my results of very high scoter remigial molt survival, because only at very high survival rates were we likely to observe zero mortalities. Even with added, simulated mortality, my conclusion that scoters have very high survival during the remigial molt period remained the same. Concurrent studies found that scoter body mass increased during molt (Dickson et al. 2012), and foraging effort was similar to that during winter (VanStratt 2011), suggesting that scoters were not experiencing energetic or nutritional constraints during remigial molt (Dickson 2011). I found that scoter survival rates during the molt period were much higher than in other periods of the annual cycle, and high remigial molting survival for scoters is consistent with high survival found for other species of molting sea ducks during remigial molt (Iverson and Esler 2007, Hogan et al.

2013). These results indicate that the remigial molt stage of the annual cycle does not constitute a demographic constraint on scoter populations.

In Chapter 3, I quantified winter survival of surf scoters across their Pacific winter range to consider how geographical variation in survival may influence surf scoter distributions and population dynamics. I found that surf scoter winter survival was much lower than survival during remigial molt, and was influenced by a combination of location, period of winter, age and sex class, and mass. Surf scoter winter survival estimates averaged higher at the range core (British Columbia) than at peripheries (Southeast Alaska and Baja, California). At all locations and for all age and sex class, survival during late winter was much higher than during mid-winter. Mid-winter generally has the harshest weather conditions and shortest day length (Systad et al. 2000), suggesting that this particular portion of the annual cycle may have high mortality (Esler et al. 2000).

Age, sex, and mass all influenced survival, and the combination of these effects resulted in different patterns of survival across latitudes by age and sex class. Differences in survival across locations and age and sex classes were related to mass differences among these classes. My results indicate that mass was positively related to survival as individuals with higher mass, irrespective of age and sex class, tended to have higher winter survival and may be better suited to meet energetic costs associated with winter thermoregulation (Haramis et al. 1986, Hepp et al. 1986, Conroy et al. 1989, Bergan and Smith 1993, Krementz et al. 1997). Adult male scoters of average mass for their age and sex class and location had highest survival at the northern range periphery in Alaska, whereas adult females and juvenile individuals of both sexes, after accounting for mass effects, had higher survival at the range core or the southern periphery. Climate differences between locations could be influencing survival particularly given our results on the influence of mass, age, and sex on survival.

My results indicate that remigial molt is a period of low mortality in the annual cycle of scoters, and scoters employ successful strategies to mitigate constraints and costs associated with the molting period. Remigial molt constitutes a relatively short portion 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. In contrast, winter may be a period of particularly high mortality for particular age and sex classes at different locations. I speculate that the observed patterns in surf scoter winter survival may contribute to the observed differential migration of surf scoters, with higher proportions of adult males at higher wintering latitudes and higher proportions of females and juveniles at more southerly wintering areas. My results also highlight times (mid-winter) and locations (range peripheries) in which mortality of critical age and sex classes (adult females) is elevated and thus the potential effects on population dynamics are likely strongest and conservation action would be most productive.

## **4.2. Conservation Implications**

I suggest that the molting period likely does not constitute a period of population constraint in the life cycle of scoters and that scoters employ successful strategies to mitigate risks and costs associated with the molting period. Despite the high survival rates for scoters during molt, all three scoter species experienced large die-offs during molt in 1990, 1991, and 1992 in Southeast Alaska (Henny 1995). The reason for these die-offs remains unknown although many of these scoters showed high levels of cadmium. Harmful biotoxins associated with algal blooms also can kill seabirds including scoters, and these blooms usually occur during mid-late summer when scoters are undergoing remigial molt (Jessup et al. 2009, Du et al. 2011, Phillips et al. 2011). Sea ducks also are particularly vulnerable to marine oil pollution during the molting period (Piatt et al. 1990, Dickson and Gilchrist 2002). Because molting scoters form large aggregations that are not capable of high mobility, they are vulnerable to local perturbations that can cause catastrophic mortality. Large numbers of scoters molt in relatively few sites, and thus describing these sites should be a priority. I suggest that factors causing observed, continental-scale declines in scoter numbers are not occurring during the remigial molt period, and that managers should focus their efforts to determine and mitigate underlying causes of declines on other stages of the annual cycle.

The results of this study suggest that a multitude of factors influence scoter wintering survival and stress the importance of the non-breeding period in the annual

cycle for sea ducks. This study highlights the importance of comparing demographic rates among locations to understand where and when population constraints may be occurring. Surf scoters may choose wintering sites by trading off foraging opportunity and mortality risk, as selective pressures may differ among age and sex classes at different latitudes. Iverson et al. (2004) found that scoters exhibit differential migration along the Pacific coast, as higher proportions of males and adults winter at more northern latitudes, while higher proportions of females and juveniles winter at more southern. We suggest that this differential migration exists due to smaller body mass imposing greater constraints on meeting the energy demands of extreme climates. At higher latitudes (SE AK), heavier (males) and more experienced (adults) individuals may choose to winter due to good foraging conditions, while lighter (females) and less experienced (juveniles) individuals may choose to winter at lower latitudes (Baja) where, although thermoregulatory requirements are lower, foraging conditions are not as good (VanStratt 2011). Most species of waterfowl, including surf scoters, exhibit male-biased sex ratios, and population dynamics are sensitive to changes in breeding age female survival (Johnson et al. 1992). Management actions aimed at improving foraging conditions at mid and southern latitudes, where greater numbers of females and juveniles winter, might improve population trends. Improving foraging conditions at the southern periphery of the surf scoter wintering range may also have cross-seasonal benefits, allowing females to be in better condition when arriving on breeding grounds (Sherry and Holmes 1996).

Sea duck survival during other stages of the non-breeding period has rarely been quantified (i.e., staging, migration). Habitat deterioration at important staging sites can lead to decreased body condition and lower winter survival (Schaub et al. 2005). During migration, weather conditions (Butler 2000, Newton 2007), increased harvest, and predation can lead to high mortality rates, and may have differential effects on age and sex classes (i.e., juveniles lack of experience navigating, Wiltschko and Wiltschko 2003). These areas need to be addressed to fully understand the non-breeding population demographics of sea ducks (Calvert et al. 2009). However, based on our results, managers may be able to most effectively influence survival by targeting the winter period of the annual cycle and locations and age and sex classes with low survival, perhaps through influences on mass.

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