

**POPULATION DELINEATION AND
WINTERING GROUND INFLUENCE
ON VITAL RATES
OF WHITE-WINGED SCOTERS**

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By

Cindy Jean Swoboda

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ABSTRACT

North American populations of white-winged scoters (*Melanitta fusca deglandi*) have declined markedly over the past several decades. The causes for decline are uncertain, but likely involve a complexity of events occurring on wintering and breeding areas. To gain insight into potential cross-seasonal effects, I delineated Atlantic and Pacific wintering scoter populations and linked them to a shared breeding area using stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) ratios in feathers. By applying this methodology to a marked breeding population at Redberry Lake, Saskatchewan, I assigned females to putative wintering areas and determined: (1) population structure; (2) the extent of winter site philopatry; and, (3) differences in vital rates and other variates in relation to winter origin. Discriminant function analysis of isotopic ratios in feather samples from known wintering locations resulted in classification probabilities of 96% ($n = 149$) for Pacific and 78% ($n = 32$) for Atlantic wintering scoters. Using this methodology, I determined that the Redberry Lake breeding population is comprised of approximately 75% Pacific and 25% Atlantic wintering birds, and its members exhibit high degrees of winter region philopatry based on the classification of successive recaptures over three field seasons. Annual variations in population structure, as well as differences in nest initiation dates and blood contaminant loads in relation to winter area suggest seasonal interactions may influence survival and reproductive success of this population. To gain insight into potential seasonal interactions, I examined nest success and female survival in relation to winter area. No significant differences in nest success in relation to winter area were found, but nests that failed before mid-incubation were not sampled. Adult female survival rate for 2000-2004 was estimated as 0.85, with no significant difference detected between wintering areas. This study demonstrated that it is important to link breeding and wintering areas to better understand the factors influencing population dynamics and to effectively address conservation issues.

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1. GENERAL INTRODUCTION

1.1 CROSS-SEASONAL EFFECTS AND INFLUENCE ON VITAL RATES

Population size fluctuates dynamically from one year to the next as a result of changes in reproductive success, survival, and movement of individuals into and out of a population. Understanding population dynamics requires identification of the ecological factors that affect these various components. However, this becomes increasingly complex to do for migratory bird species as they are exposed to a wider array of biotic and abiotic factors over a larger geographical extent than non-migrants (Marra and Holmes 2001). Gaining insight into population dynamics for migratory species requires linking different areas that individuals occupy throughout the annual cycle and, therefore, studying populations at a larger spatial scale than what has been conventionally done in the past (Clark et al. 2004).

The breeding season has an important influence on population size as population growth is driven by reproductive success. However, as migratory bird species spend most of their lives on non-breeding areas, events outside the breeding season may have significant impacts on reproductive success, and therefore, population dynamics (Marra et al. 1998, Alisauskas 2002, Webster et al. 2002). The effect of ecological events within one season exerting influence on events in a subsequent season defines the terms “cross-seasonal effects” and “seasonal interactions” (Runge and Marra 2005). There is increasing evidence supporting the importance of seasonal interactions at the individual level through carry-over effects from one season to the next (reviewed in Webster and Marra 2005).

Events during winter, such as weather, exposure to contaminants, or hunting pressure, may influence physical condition (Fournier and Hines 1994, Takekawa et al. 2002, Bearhop et al. 2004, Bechet et al. 2004), which, in turn, could reduce immediate probability of survival (Grand et al. 1998, Fournier and Hines 1994) or limit subsequent reproductive success (Stott and Olson 1972a, 1972b, Stapp et al. 1999,

Davidson 1981, Bearhop et al. 2004). For example, ecological conditions such as weather or quality of habitat during migration can affect adult body condition (Marra and Holmes 2001, Alisauskas 2002, Ardia 2002) and timing of arrival on the breeding grounds (Traylor et al. 2004, Mara et al. 1998), which in turn can influence nest initiation date and reproductive success, resulting in either larger post-breeding populations after favorable winters or reduced populations after non-favorable winters (Saino et al. 2004, Bearhop et al. 2004, Norris et al. 2004, Sillett et al. 2000). Reduced population size may also occur when increased mortality on non-breeding areas results in loss of potential breeding individuals for the following season (Sillett and Holmes 2002, Marra and Holmes 2001, Owen & Black 1991, Ward et al. 1997). Seasonal interactions have the potential to influence events not just from one season to the next, but for periods of a year or more (Brommer et al. 2004).

The ability to link populations to breeding and wintering areas is essential for conservation and management of a species and can improve efficiency of management strategies by identifying areas that may limit population growth. This can be especially important for populations that winter in geographically disjunct or ecologically different areas as they are exposed to a wider variety of factors with different effects on resident populations (Clark et al. 2004). If a breeding population is comprised of individuals from more than one wintering area, knowledge of winter origin permits stratification of the local breeding population. Such stratification by winter provenance provides estimates of population structure as the proportion of individuals from each wintering area can be determined; it also permits inference about the influence of these winter areas on respective vital rates of local breeding populations. Otherwise, unstratified rates within a local population would typically only be expressed as an average of the groups and potential carry-over effects from the winter areas would go unnoticed (Møller and Hobson 2004, Mehl et al. 2004).

In practice, it is often extremely difficult to draw boundaries between populations as the geographic areas they occupy, as well as the distances they migrate, are large. The linkage between breeding and non-breeding areas, termed migratory connectivity (Webster et al. 2002), can have weak associations, where there is a high degree of mixing between different breeding and wintering populations, or strong associations,

where individuals of the same breeding area all migrate to the same non-breeding area exclusively. Migratory individuals may exhibit high site fidelity, returning to the same areas consistently year after year, or they may emigrate to other areas. Recent advances in development and application of techniques using intrinsic markers to track migratory species are providing better understanding of winter and breeding area linkages (Haig et al. 1997, Chamberlain et al. 1997, Wennerberg 2001, Rubenstein et al. 2002), site philopatry (Mehl et al. 2004) and seasonal interactions on population dynamics (Norris et al. 2004, Gunnarsson et al. 2005).

Research for this thesis was motivated by the desire to address factors that affect population dynamics of white-winged scoters (*Melanitta fusca deglandi*) across more than one season, as a combination of factors on both breeding and non-breeding areas is likely responsible for the noted population declines of this species across North America (Alisauskas et al 2004, Sea Duck Joint Venture Management Board 2001). Stable isotopes were used to link wintering and breeding areas to investigate the influence of winter origin on body size, body condition, clutch volume, egg hatchability, blood contaminant loads, nest success and adult female survival. Although this study was not able to determine specific winter factors that influence breeding season events, linkage of individuals nesting at Redberry Lake to putative wintering areas may uncover differences in vital rates in relation to winter origin, and potentially identify areas responsible for limits to reproductive success and to recruitment. Results from this study may have relevance to much of the continental population as this population mixes with other breeding populations on the wintering areas, as determined by satellite telemetry studies (Nysewander, pers. comm.) and band recoveries (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data). In addition to an improved understanding of cross-seasonal effects on breeding, this work provides important information relevant to current conservation concerns of population declines of white-winged scoters (Alisauskas et al. 2004) and may assist the focus of future management strategies to particular regions of concern.

1.2 STUDY SPECIES

White-winged scoters (*Melanitta fusca deglandi*) winter along the Atlantic and Pacific coasts of North America and breed in the interior from Alaska through the boreal forest and parkland regions of western Canada (Brown and Frederickson 1997), with small numbers wintering on the Great Lakes (Figure 1.1). On winter areas, scoters dive for prey in water up to 20 metres deep to feed mainly on mollusks and crustaceans at or near the bottom substrate (Stott and Olson 1973), whereas amphipods appear to be the preferred food on breeding areas (Brown and Fredrickson 1986). White-winged scoters are among the last waterfowl species to arrive on the breeding areas in Saskatchewan in mid-May (Brown and Fredrickson 1989), with peak nest initiation typically occurring during the third week of June (Traylor et al. 2004). All species of scoters belong to the sea duck tribe, *Mergini*, and are long-lived species with delayed maturity (breeding first attempted at 2-3 years of age; Kehoe et al. 1989, Palmer 1976, Brown and Houston 1982).

The continental population has declined by greater than 50% during the past 4 decades and has disappeared from much of the prairie biome (PNR Sea Duck Team 2000, Alisauskas et al. 2004). The decrease in scoter numbers on the wintering areas appears to be equal to or greater than those recorded for the breeding areas (Kehoe 1994, Trost 1998a, 1998b), with Atlantic winter populations presumably having declined at a greater rate (National Audubon Society 2006). White-winged scoters are one of the least studied species of waterfowl (Brown and Frederickson 1997), so causes for continental population declines are unknown and estimates of vital rates are limited. Most data have come from the breeding population at Redberry Lake, Saskatchewan, which show that white-winged scoters have high adult survival rates (0.84, Alisauskas et al. 2004) and highly variable rates of nesting success (68.4%, Brown 1981; 29.5%, Traylor 2003, this study). Research at Redberry Lake and at other areas across their breeding range suggest white-winged scoters have a low renesting propensity (Brown 1981, Traylor et al. 2004), relatively low breeding propensity (Safine 2005), and high variation in duckling survival (Traylor et al. 2004, Safine 2005). This variability in reproduction suggests recruitment may have the greatest influence on population fluctuations, but population size and stability depends more on adult survival because

adult survival ultimately determines how often individuals will breed over a lifetime (Crone 2001).

Specific priorities that need to be addressed include estimation of survival and production rates across their range, population delineation, and linkage of wintering areas to breeding areas in order to address conservation and management concerns (SDJV Management Board 2001).



Figure 1.1. Current winter and breeding distribution of white-winged scoters in North America.

1.3 THESIS FORMAT AND OBJECTIVES

The goals of this study were to: 1) determine if stable isotopes could be useful to complement a mark-recapture study in linking breeding individuals to wintering areas, and 2) determine if events on a breeding area may be influenced by previous winter area occupation. This thesis contains 5 main chapters. General descriptions of study area and field methods pertinent to all data chapters are presented in Chapter 2 to reduce redundancy. Chapter 3 assesses the ability to delineate wintering populations of white-winged scoters using stable isotope techniques and applies this methodology for stratification of a nesting population by winter origin. Chapter 4 examines differences in estimates of vital rates of scoters that breed sympatrically but are from different winter strata. Chapter 5 is a synthesis discussing main conclusions from this study and suggestions for future research. Specific objectives of this study were:

- 1) Delineate wintering populations of white-winged scoters using stable isotope analysis of feathers collected from known wintering locations.
- 2) Examine population structure by determining the proportion from both wintering grounds that nest at Redberry Lake.
- 3) Determine the degree of winter site philopatry using stable isotope analysis of feathers from recaptures in successive years.
- 4) Determine cross-seasonal effects on adult female survival, body size, body condition, clutch volume, egg hatchability, nest success and blood contaminant loads (cadmium, mercury, lead and selenium) of females nesting at Redberry Lake in relation to winter origin.

2. STUDY AREA AND GENERAL METHODS

2.1 STUDY AREA

During 2002-2004, work was conducted at Redberry Lake (52° 0' N, 107° 10' W), approximately 100 km NW of Saskatoon, Saskatchewan. Redberry Lake is in the Aspen Parkland ecozone, and the shoreline and most of the surrounding habitat within 500 meters remain in a semi-natural state as only relatively small portions have been developed (Schmutz 1999). Land use in the surrounding area is primarily for crop production and grazing cattle, and there is light recreational use of the lake with a regional park and a small number of private cabins located on the Northwest shore. Redberry Lake was designated as a federal migratory bird sanctuary in 1925 and a global biosphere reserve in 2000, and it supports more than 180 bird species including the highest known nesting density of white-winged scoters in North America (Brown and Fredrickson 1997). Detailed descriptions of the area are provided by Brown (1981), Kehoe (1989) and Traylor (2003).

White-winged scoters marked at Redberry Lake with leg bands have been recovered on both the Atlantic and Pacific coasts (Houston and Brown 1983, Canadian Wildlife Service Bird Banding Laboratory, unpubl. data). Most scoters nest on three islands, Gull Island, Pelican Island, and New Tern Island, located in the western portion of the lake (Figure 2.1), with small numbers of nests found on Old Tern Peninsula (Swoboda, pers. obs.). Pelican Island and New Tern Island are presently connected by a land bridge because of receding water levels over the last 100 years; this has also raised salinity content and increased accessibility to the islands by mammalian predators such as coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) (Schmutz 1999). Additional predators that inhabit and nest on the islands include California gulls (*Larus californicus*), ring-billed gulls (*Larus delawarensis*) black-billed magpies (*Pica pica*), American crows (*Corvus brachyrhynchos*), great horned owls (*Bubo virginianus*), and red-tailed hawks (*Buteo jamaicensis*).

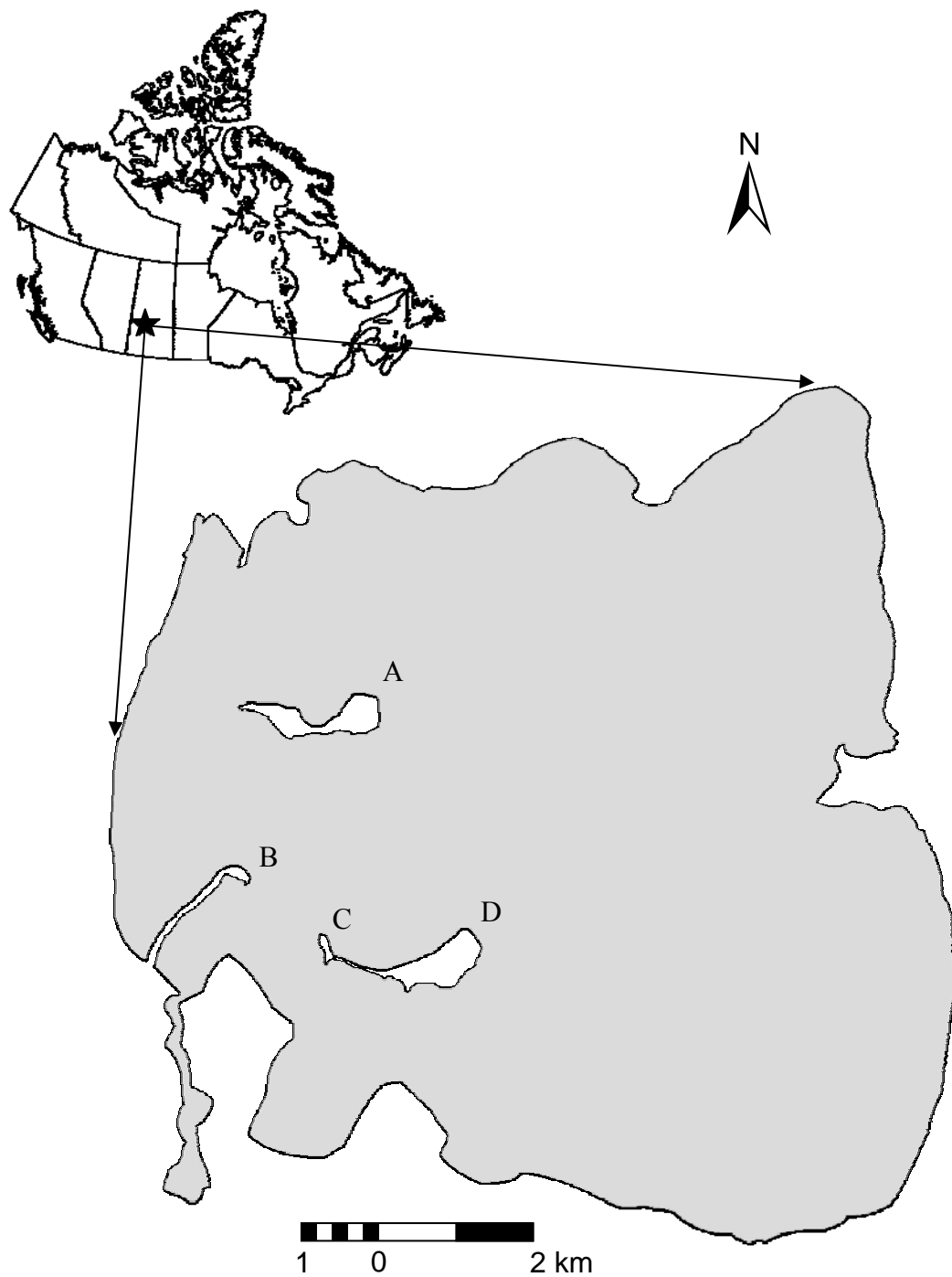


Figure 2.1 Map showing relative size and location of islands in Redberry Lake, SK. A= Gull Island (51 ha), B= Old Tern Peninsula (6 ha), C= New Tern Island (3 ha), D= Pelican Island (50 ha).

2.2 GENERAL FIELD METHODS

2.2.1 Nest Searches

Nest searches were conducted by 2 or more observers walking line transects on the islands from mid June until late July. Nest searching was not done on the shoreline due to low densities of nests (1 nest/60 hours of searching; Brown and Frederickson 1989, Traylor pers. comm.). Nest locations were recorded using a hand-held GPS unit. No visible markers were used so that visual cues for predators were minimized (Hein and Hein 1996, Armstrong 1996). Eggs were numbered with indelible ink, length and width measured using dial calipers (± 0.1 mm), and volume calculated using Hoyt's (1979) equation. Nests were revisited every 6-10 days to determine clutch size, egg attrition rate, and nest fate. Incubation stage was determined by candling eggs (Weller 1956), and initiation dates were estimated by back-dating, assuming a laying interval of 1.5 eggs per day (Brown and Brown 1981). Hatch dates were also estimated from the incubation stage assuming an average incubation period of 28 days (Brown 1977). Nests were considered *successful* if at least one egg hatched. For *failed* nests, nest fates were recorded as *abandoned*, *abandoned due to observer disturbance* (if eggs were cold and at same incubation stage as the previous visit), or *depredated* (Klett et al. 1986).

2.2.2 Capture and Marking

Nesting female white-winged scoters were trapped during mid-incubation (~14 days incubation) or later using hand-held nets, marked with a standard USFWS leg band, and weighed using a Pesola spring scale (± 10 g). Culmen length, bill width, head length, tarsus, and wing cord were measured using dial calipers (± 0.1 mm) (Dzubin and Cooch 1993). Morphometric measurements were used for deriving an index of structural size.

Captured females were fitted with permanent nasal markers consisting of unique colour and shape combinations of nylon nasal discs attached through the nares using wire (Sugden and Poston 1968, Lokemoen and Sharp 1985). All females captured during the 2002-2004 field seasons were marked with permanent nasal tags, including females banded in previous years that had been marked with temporary nasal tags. This allowed us to detect the presence of additional females by resighting nasal tags for birds not associated with a nest as not all females that attempted to nest were available for

capture due to nest failure before the mid-incubation stage was reached (Swoboda, pers. obs.).

All captured females ($n = 240$) had 3-4 feathers removed from each of three feather tracts (head, back and flank) for later use in isotope analysis (Mehl et al. 2005). A small amount of blood (4-6 cc) was also sampled from some of the captured females ($n = 122$) for heavy metal analysis. Hatching ducklings were marked with plasticine-filled leg bands (Blums et al. 1994, 1999). All research methods were approved by the Animal Care Committee, University of Saskatchewan, on behalf of the Canadian Council on Animal Care.

2.3 GENERAL LABORATORY METHODS

2.3.1 Winter Feather Collection

During 2002-2004, I obtained contour feathers (head, back, and flank) of 223 adult black scoters (*Melanitta nigra*), surf scoters (*Melanitta perspicillata*) and white-winged scoters from known wintering locations on both the Atlantic and Pacific coasts of North America (Figure 2.2). The samples were labeled by species using the corresponding four letter AOU code (surf = SUSC, black = BLSC, and white-winged = WWSC).

Scoters were captured along the east coast of Vancouver Island during banding operations in December - March 2002-2004 ($n = 129$; 53 female and 58 male WWSC, 3 female SUSC, 15 male SUSC) and in Alaska during banding operations in late January 2004 ($n = 3$; 1 male and 2 female WWSC). Feathers from hunter-killed scoters were collected during the regular hunting season (October - January) for Maine ($n = 17$; 10 male and 2 female WWSC, 5 female SUSC), New York ($n = 5$; 4 male and 1 female WWSC), Maryland ($n = 10$; 4 male and 2 female WWSC, 3 male and 1 female BLSC), Massachusetts ($n = 4$; 1 male and 3 female WWSC), New Brunswick ($n = 8$; all male WWSC), Nova Scotia ($n = 4$; 2 male WWSC, 1 male SUSC, 1 male BLSC), California ($n = 1$ female SUSC) and Washington ($n = 35$; 21 male and 10 female WWSC, 3 male and 1 female SUSC). Samples were salvaged from carcasses that washed up on beaches in Oregon from November – mid March ($n = 7$; 3 male and 2 female WWSC, 2 female SUSC). Three tracts were sampled from all individuals to determine which tract provided the best isotopic segregation of wintering populations. To increase sample

sizes and coverage from wintering areas, samples were collected from all three scoter species and were used to determine if a combination of scoter species could be used in the analysis or whether it was best to use only white-winged scoter feathers.



Figure 2.2 General locations of scoter feather sampling sites at known wintering locations (○) in relation to locations of band recoveries (●) from white-winged scoters banded at Redberry Lake (★). Feathers were collected from either captured or hunter-killed scoters. Sites from north to south on the Pacific coast are: AK, BC, WA, OR and CA and sites on the Atlantic coast are NB, NS, ME, NY, MA, MD.

2.3.2 Stable Isotope Analysis

Feathers were cleansed of surface oils by rinsing with a solution of 2:1 chloroform to methanol and allowed to air dry for 24 hours. A 0.95-1.05 mg portion of each sample was enclosed in a tin cup, then combusted in a Robo Prep elemental analyzer interfaced with a Europa 20:20 continuous-flow isotope ratio mass spectrometer (Hobson and Schell 1998) at the Department of Soil Science, University of Saskatchewan. By convention, the isotope ratios are reported in delta notation as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ according to:

$$\delta X = \left| \frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right| \times 10^3 \text{‰}$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, $R = {}^{13}\text{C}:{}^{12}\text{C}$ or ${}^{15}\text{N}:{}^{14}\text{N}$, and std = PeeDee Belemnite (PDB) for ${}^{13}\text{C}$ and atmospheric N_2 (AIR) for ${}^{15}\text{N}$. The measurement errors are estimated to be $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ values based on replicate analyses of internal laboratory standards (albumen).

2.3.3 Blood Contaminant Analysis

Blood samples were transferred to nitric acid-washed vials, kept cool in the field and then frozen upon returning to the field house at the end of the day. Samples were prepared and analyzed according to methods described by Wayland et al. (2007) and sent to laboratories for residue analysis. Samples analyzed for mercury, selenium and lead were analyzed at Environment Canada's National Wildlife Research Centre according to methods described by Neugebauer et al. (2003). Cadmium was analyzed at the Institut National de Santé Publique du Québec according to Stoeppler and Grant (1980). Cadmium concentrations were expressed on a volumetric basis and mercury, selenium and lead concentrations were expressed on a wet weight basis.

3. DELINEATION OF WINTERING POPULATIONS AND WINTER AFFINITIES OF BREEDING WHITE-WINGED SCOTERS

3.1 INTRODUCTION

The conventional approach to understanding migratory connectivity for avian species relies on band recoveries. This can be effective for intensely hunted waterfowl species which results in high probabilities of band recovery. However, recovery rates are lower for sea duck species such as white-winged scoters (Brown and Fredrickson 1997, Sea Duck Joint Venture Management Board 2001). Geographic variation in hunting effort may also influence recovery rates so that inferences about winter distributions are affected not only by the proportional use by birds, but also by hunting pressure (Ewins and Houston 1992, Robertson and Cooke 1999). The influence of hunting pressure on recovery rates may lead to biased conclusions about the relative importance and use of non-breeding areas. Recent advances in technology provide alternate methods that include indirect methods based on biogeochemical information (Hobson 1999).

The use of naturally occurring stable isotopes is a relatively non-invasive method to study migratory connectivity on a broad scale. This method results in much larger sample sizes as every bird sampled can be considered a recovery (Hobson 1999). Different time frames in an animal's life can be examined depending on the type of tissue chosen (Hobson and Clark 1992a). Feathers contain stable isotopic signatures representing local food webs of the area where feathers are grown and are an ideal tissue to use because they are metabolically inactive after synthesis (Mizutani et al. 1990, Hobson and Clark 1992b); the stable isotope signature is fixed into the feather keratin and is retained on the bird until the feather is molted. White-winged scoters molt their body feathers twice annually. Alternate plumage is acquired shortly after the breeding season and basic plumage is acquired on the wintering grounds and retained throughout

the summer (Brown and Frederickson 1997), thus, body feathers collected during the breeding season should contain the isotope signature of the wintering region.

Naturally occurring stable isotope ratios have been used successfully to delineate geographically distinct populations (Alisauskas and Hobson 1993, Caccamise et al. 2000) and to link wintering and breeding areas for other avian species (Hobson and Wassenaar 1997 and 2001, Hobson et al. 2001, Webster et al. 2002, Chamberlain et al. 2000, Hobson 1999, Mehl et al. 2005). In North America, most studies that used stable isotopes to address migrational connectivity in birds have examined terrestrial species (Chamberlain et al. 2000, Hobson and Wassenaar 1997, 2001). Although this technique has been applied to determine breeding and molting origin of freshwater waterfowl species (Hebert and Wassenaar 2005a, 2005b), and winter origin of some marine-wintering sea duck species (Mehl et al. 2004, Braune et al. 2005, Lawson 2006), none to my knowledge have attempted to use this technique for white-winged scoters.

Carbon (C) and nitrogen (N) isotopes are commonly used in studying marine food webs (Michener and Schell 1994). Geographic patterns for these isotopes are not as well understood or developed relative to that of deuterium in terrestrial habitats, although patterns have been established for some arctic waters. East to west gradients of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values have been documented in arctic marine food webs (Dunton et al. 1989, Saupe et al. 1989, Schell et al. 1998), with western seas more enriched relative to eastern. This isotopic gradient was used to trace seasonal migration of the western North American population of Bowhead Whales (Schell et al. 1989), and formed the basis to investigate winter origins of King Eiders breeding in the central arctic (Mehl et al. 2004, 2005). Although white-winged scoters occupy more southern wintering ranges than eiders, similar isotopic differences may be present in temperate oceans. Common prey items of white-winged scoters (mollusks, crustaceans) show that there is great variation and overlap in carbon and nitrogen isotope values within the Pacific and Atlantic coastal wintering range (Table 3.1). However, samples between studies may not be directly comparable as some studies removed lipids while others did not. As lipids are generally more depleted in ^{13}C compared to other tissues and concentrations of these lipids can vary among individuals and tissue type (Hobson and Welch 1992), lipid

Table 3.1 Isotopic values from marine (Atlantic and Pacific coasts) and freshwater prey items commonly consumed by white-winged scoters. Asterick (*) denotes lipids were not removed from sample.

Location	Latin name	Common name	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Reference
Atlantic					
Delaware estuary	<i>Mytilus edulis</i>	Blue muscle	-20.2	9.10	Fantle et al. 1999*
	<i>Geukensia demissa</i>	Ribbed mussel	-18.5	8.0	
Chesapeake Bay	<i>Macoma balthica</i> ,	Baltic clam	-19.5	13.2	Haramis et al. 2001*
	<i>Macoma mitchelli</i> ,	Narrowed clam	-17.0	12.6	
	<i>Mya arenaria</i> ,	Soft shell clam	-20.6	13.4	
	<i>Rangia cuneata</i>	Atlantic rangia	-21.0	13.7	
Georges Bank		mussels	-17.9	6.9	Fry 1988*
		scallops	-17.5	6.0	
Placentia Bay/ Trinity Bay NFLD		amphipods	-20.9	9.7	Sherwood and Rose 2005*
		shrimp	-19.2	13.8	
Cape Cod	<i>Mytilus edulis</i>	Blue mussel	-18.3	7.7	Carmichael et al. 2004*
	<i>Gemma gemma</i>	Amethyst gem clam	-17.5	7.3	
	<i>Mya arenaria</i>	Soft shell clam	-18.8	7.7	
	<i>Geukensia demissa</i>	Ribbed mussel	-18.1	7.2	
	<i>Mercenaria mercenaria</i>	quahog	-18.2	9.3	
Pacific					
San Francisco Bay	<i>Potamocorbula amurensis</i>	Asian clam	-22.7	12.2	Fry 1999
San Francisco Bay	<i>Potamocorbula amurensis</i>	Asian clam	-23.9	11.5	Stewart et al. 2004*
Tijuanna Estuary	<i>Mytilus edulis</i> , <i>Prothaca staminea</i> , <i>Tagelus californiansis</i>	Blue mussel, Common littleneck clam, California jackknife clam	-18.0 -18.0 -17.7	10.0 12.2 10.8	Kwak and Zedler 1997
Barkley Sound, Vancouver Island	<i>Mytilus californianus</i> <i>Mya arenaria</i>	California mussel Soft shell clam	-18.3 -17.2	9.7 9.9	Hobson et al. 1994
Gulf of Farallones	<i>Euphausia pacifica</i> , <i>Thysanoessa spinifera</i>	Krill -crustaceans	-20.2	11.2	Sydean et al. 1997
Prince William Sound, AK	<i>Euphausia pacifica</i> , <i>Thysanoessa spinifera</i>	Krill -crustaceans	-19.3	10.2	Kline 1998*
Cow Bay, BC (West coast Vancouver Island)	<i>Mysis relicta</i>	Mysids	-16.9	---	Mulkins et al. 2001*
West Coast Vancouver Island		Euphausiids	-19.0	10.8	Wu et al. 1999*
Fresh water					
Lake Oneida, NY	<i>Dreissena polymorpha</i>	Zebra mussel	-32.0	7.9	Mitchell et al. 1996*
Western Lake Erie	<i>Dreissena polymorpha</i>	Zebra mussel	-17.5	9.3	Garton et al. 2005*
Lake Wawasee, IN	<i>Dreissena polymorpha</i>	Zebra mussel	-27.5	10.2	Nichols and Garling 1999*
Huron River and 4 Mile Lake		Unionid mussels	-32.4	9.6	
Lake Superior	<i>Mysis relicta</i>	shrimp	-27.3	5.5	Harvey and Kitchell 2000*
	<i>Diporeia hoyi</i>	amphipod	-28.2	4.4	
Lake Ontario	<i>Mysis relicta</i>	shrimp	-27.2	10.3	Johannsson et al. 2001
Lake Ontario	<i>Diporeia hoyi</i>	amphipod	-27.3	---	Leggett et al. 1999
Lake Erie	<i>Dreissena polymorpha</i>	Zebra mussel	-21.9	7.2	Mazak et al. 1997

removal can change ^{13}C values by up to 2‰ (Johannsson et al. 2001, Kline 1999). From these literature values alone, it is unclear if isotopic differences between Pacific and Atlantic wintering scoters would be sufficient to discriminate between the two populations.

I tested if white-winged scoters from Atlantic and Pacific winter populations could be discriminated based on stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in feathers. If successful, results would allow assignment of breeding females from the Redberry Lake population to winter areas. Breeding white-winged scoters from Redberry Lake have been recovered on both the Atlantic and Pacific wintering areas (Houston and Brown 1983), but precise proportions are not known because of low recovery rates (Alisauskas et al. 2004), and potential differences in harvest and reporting rates between east and west coasts (Krementz et al. 1997).

3.2 STATISTICAL ANALYSES

3.2.1 Species and Tract Preference

Bivariate plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each feather tract were used to assist with interpretation of amount of overlap between Atlantic and Pacific populations.

Discriminant Function Analysis (DFA, PROC DISCRIM; SAS 1999) was used on a subsample to assess which feather tract and grouping of scoter species would provide the best ability to discriminate between Atlantic and Pacific populations based on carbon and nitrogen isotopic ratios. I tested for homogeneity of within-covariance matrices using a chi-square test of homogeneity (POOL=TEST option in SAS). Since the variances were not different at the $\alpha=0.05$ level, they were pooled and linear DFA was performed. Prior probabilities were set equal to sample sizes for each group and separate DFAs were performed using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from all possible combinations of the three feather tracts, including each tract independently. To determine the most useful feather tract(s) for discriminating between wintering populations, the performance of each DFA was evaluated based on the error rate from cross-validation. All statistical analyses were performed using SAS (SAS Institute 1999).

3.2.2 Delineation of Atlantic and Pacific Populations

The ability to discriminate between Atlantic and Pacific wintering populations based on isotopic ratios from the most informative feather tract(s) was assessed using Discriminant Function Analysis (DFA, PROC DISCRIM; SAS 1999). The performance of each DFA was evaluated based on the error rate from cross-validation. As most variation between populations was due to $\delta^{13}\text{C}$ values, as revealed by graphical representation of the data, the ability to delineate populations using only $\delta^{13}\text{C}$ values was tested. Both male and female wintering samples were included for both areas, as sample sizes for females from the Atlantic coast were very small ($n = 8$). I tested for effects of collection date and sex on ^{13}C and ^{15}N head feather values within wintering groups using separate MANOVAs.

3.2.3 Assignment of a Breeding Population to Winter Area

I classified unknown samples obtained on the breeding area as wintering in Atlantic or Pacific areas using linear DFA based on the discriminant function obtained from the analysis of carbon and nitrogen isotope ratios of scoter feathers of known winter origin (Appendix 1). To assess potential differences in hunting pressure and reporting rates between Pacific and Atlantic wintering areas, I compared the proportions of female scoters that wintered in either Atlantic or Pacific areas, as inferred from isotope analysis, to those indicated by band recoveries (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data) using chi-square analysis.

3.2.4 Winter Philopatry

Estimates of winter site philopatry were obtained for females that were captured in more than one year during the study period and were based on the proportion of females that returned to the same area to winter in subsequent years as determined by DFA classification probabilities obtained from isotope analyses.

3.3 RESULTS

3.3.1 Species and Tract Preference

In comparison to use of all scoter species, use of only white-winged scoter isotopic values showed the least amount of variation and provided the best discrimination between Atlantic and Pacific populations (Figure 3.1, Figure 3.2, and Table 3.2). Of the three feather tracts analyzed (head, back, flank), head feathers displayed the greatest difference in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between Atlantic and Pacific coast winter populations (Table 3.3) and provided the best discrimination (Table 3.2). Thus, only white-winged scoter head feathers were used in further analyses, and hereafter all references made to scoters are restricted to white-winged scoters.

3.3.2 Delineation of Atlantic and Pacific Populations

Examination of bivariate plots of carbon and nitrogen values showed six signatures (5 from Atlantic females and 1 from a Pacific female) with extremely depleted carbon values relative to all others, indicative of freshwater signatures. As these feathers were not molted on coastal wintering areas, they were excluded from the discriminant function analysis. White-winged scoters from Pacific coastal areas had slightly enriched $\delta^{13}\text{C}$ values, and to a lesser extent, enriched $\delta^{15}\text{N}$ values, relative to the Atlantic wintering population (Fig 3.3). The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values was sufficient to segregate the two wintering populations (Table 3.3). Carbon values appear to be most important for correct classification as only 3% of the classification bias was corrected by the addition of $\delta^{15}\text{N}$ values. After removal of the six samples with depleted carbon values, date and sex within wintering groups were unrelated to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Atlantic (date: MANOVA_{22,34}, $F=1.09$, $p=0.40$; sex: MANOVA_{2,17}, $F=1.42$, $p=0.27$) or Pacific (date: MANOVA_{94,164}, $F=0.90$, $p=0.71$; sex: MANOVA_{2,82}, $F=1.09$, $p=0.34$) wintering scoters.

3.3.3 Assignment of a Breeding Population to Winter Area

Isotopic values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feather samples of white-winged scoters from wintering populations provided reference data for stratification of breeding scoters captured at Redberry Lake according to winter origin. The Redberry Lake nesting

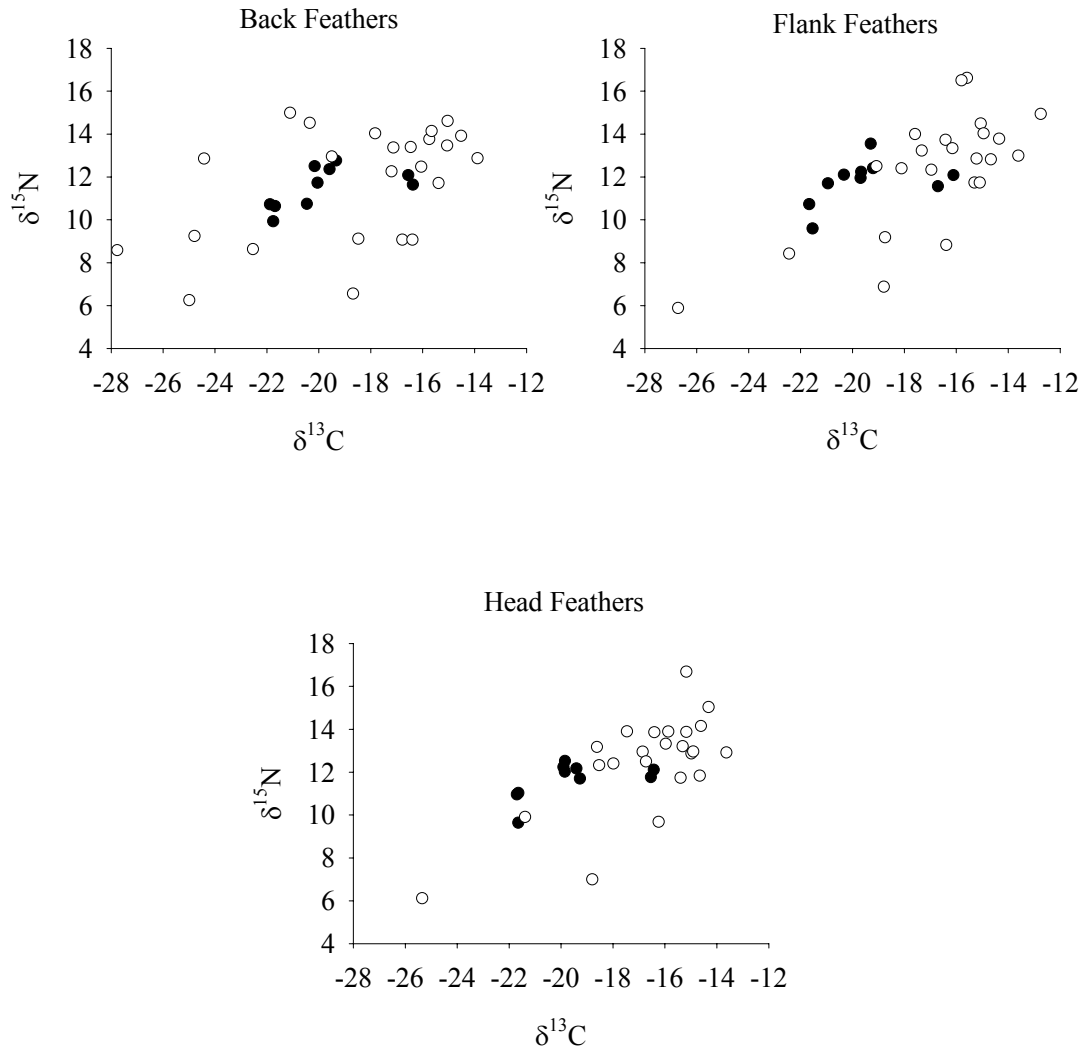


Figure 3.1 Isotopic values from head, back, and flank feathers of white-winged and surf scoters captured or collected on the Pacific ($n = 24$, open circles), and Atlantic ($n = 10$, closed circles) coast. Scoter species and sexes were pooled.

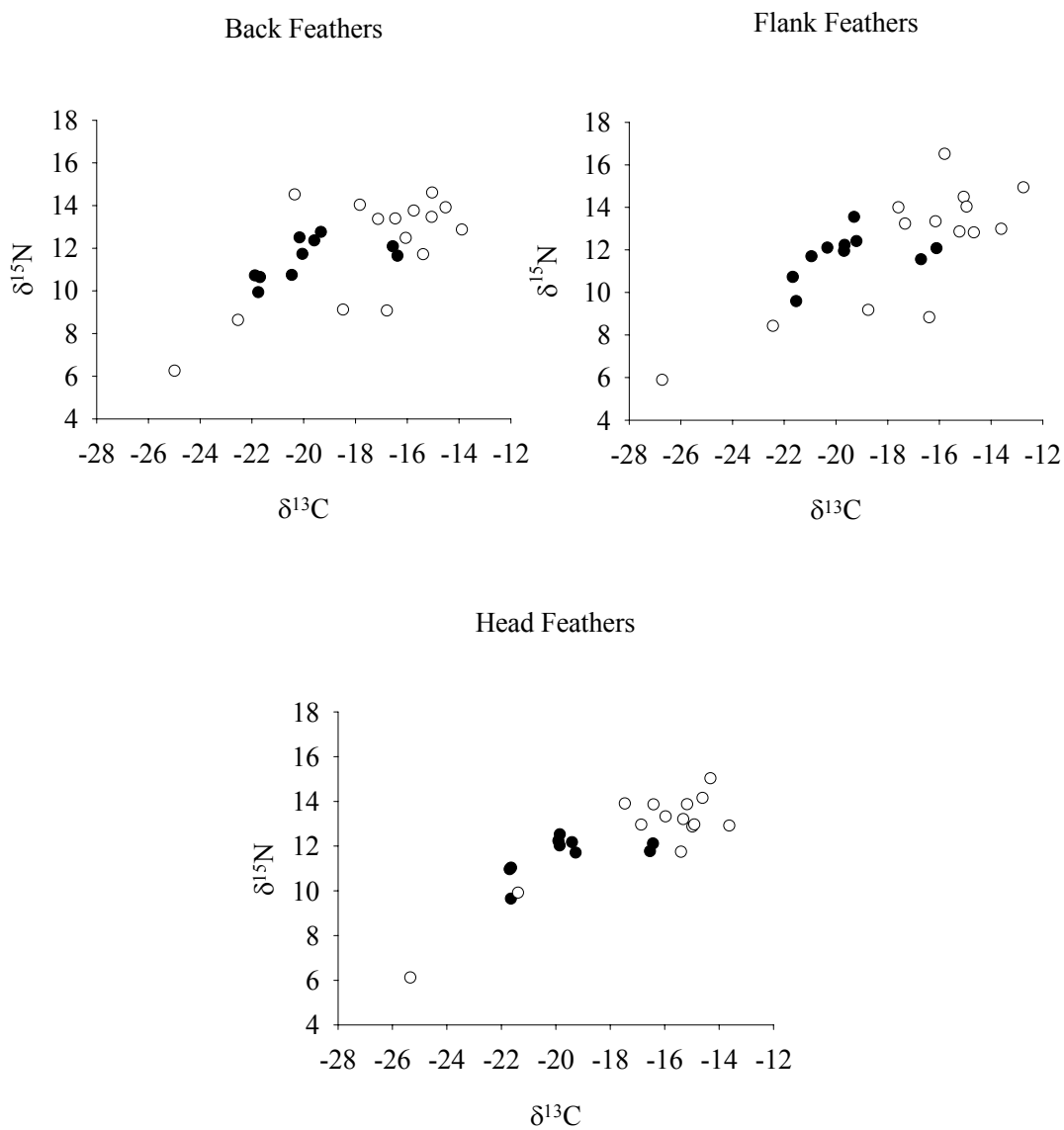


Figure 3.2 Isotopic values from head, back, and flank feathers of white-winged scoters captured and collected on the Pacific ($n = 15$, open circles) and Atlantic ($n = 10$, closed circles) coast. Sexes were pooled.

Table 3.2 Classification probabilities (%) of linear discriminate function analysis based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from feathers of Pacific and Atlantic coastal wintering populations for all three scoter species, and for white-winged scoters. Feather tract(s) are listed in order of classification success for Atlantic populations. Sexes were pooled.

Feather Tract(s)	All scoter species					White-winged scoters only				
	Atlantic		Pacific			Atlantic		Pacific		
	<i>n</i>	%	<i>n</i>	%	Bias ^a	<i>n</i>	%	<i>n</i>	%	Bias ^a
Head	49	70	174	92	22	32	78	149	96	18
Flank	10	60	25	92	32	10	60	17	100	40
Back, Flank	10	60	25	80	20	10	60	17	82	22
Back, Head	10	60	25	76	16	10	60	17	88	28
Back	10	50	25	96	46	10	70	17	100	30
Back, Flank, Head	10	50	25	80	30	10	40	17	82	42
Flank, Head	10	40	25	84	44	10	40	17	88	48

^aBias represents $\% \text{Success}_{\text{Pacific}} - \text{Success}_{\text{Atlantic}}$ where bias represents favour toward the Pacific population.

Table 3.3 Mean isotopic values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of feathers collected from all three scoter species on known Pacific and Atlantic coastal wintering areas. Values for sexes were pooled.

Feather tract	Population	n	Feather $\delta^{15}\text{N}$		Feather $\delta^{13}\text{C}$	
			Mean	± 1 SD	Mean	± 1 SD
Back	Atlantic	10	11.51	0.95	-19.79	1.97
	Pacific	24	11.73	2.84	-17.43	3.02
Flank	Atlantic	10	11.79	1.05	-19.52	1.86
	Pacific	23	11.89	3.20	-17.08	3.58
Head	Atlantic	10	11.62	0.91	-19.33	1.98
	Pacific	23	12.25	2.59	-16.71	3.09

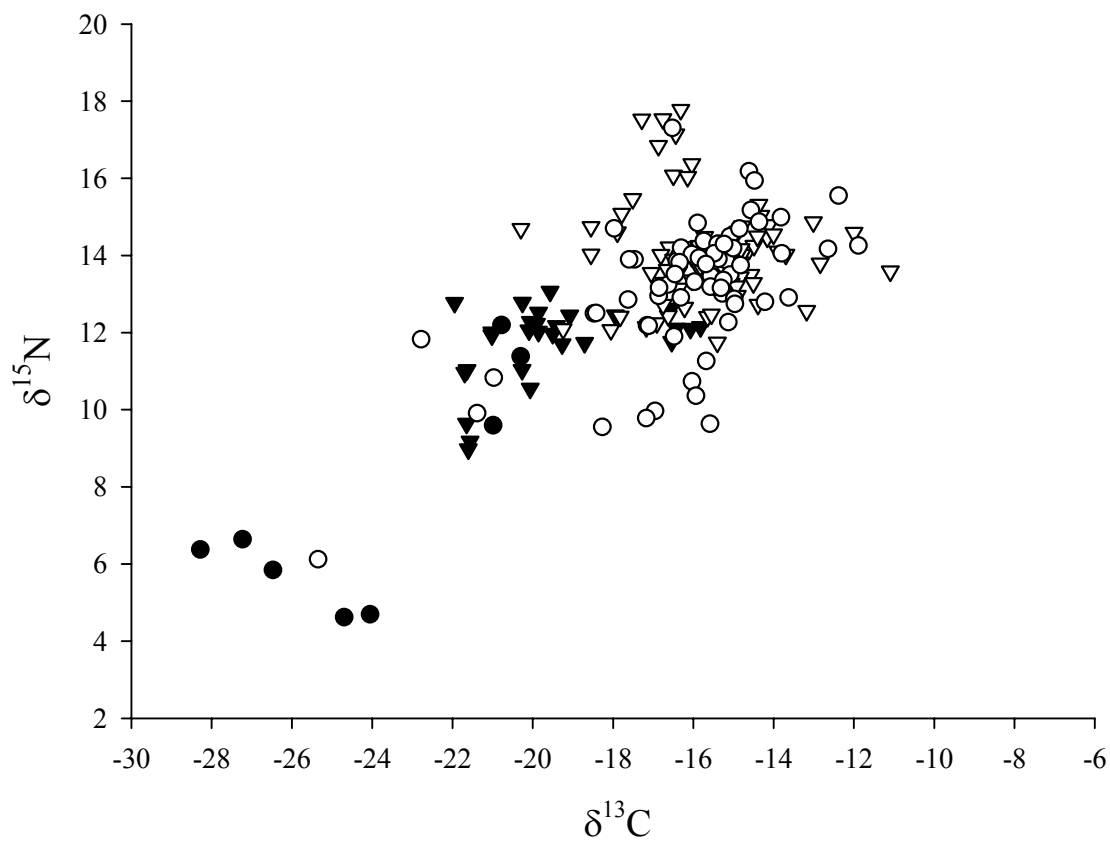


Figure 3.3 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of white-winged scoter head feathers from known wintering locations. The symbols represent values from: Atlantic females (closed circles, $n = 8$), Atlantic males (closed triangles, $n = 29$), Pacific females (open circles, $n = 67$), and Pacific males (open triangles, $n = 83$).

population had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values similar to that of the wintering populations (Figure 3.4). Linear DFA determined that the Redberry Lake breeding population was composed of a greater proportion of Pacific wintering birds. The estimated proportions that wintered in either the Atlantic or Pacific remained consistent in 2002 and 2003 (~25% E, 75% W); however, in 2004, there was a larger proportion of scoters wintering in the Pacific relative to the two previous years (Table 3.4). Precision around the classification estimates was greater during 2002, with 90% (65 of 72) of all individuals having >90% probability of wintering in the respective Atlantic or Pacific areas, compared with 82% (80 of 97) of individuals with >90% probabilities during 2003, and 78% (57 of 73) during 2004 (Figure 3.5). These proportions differ from those expected based on band recoveries ($\chi^2_2 = 88.2$, $p < 0.001$), as nearly equal proportions (11 east, 11 west) have been recovered in both wintering regions (Canadian Wildlife Service Bird Banding Laboratory, unpubl. data).

3.3.4 Winter Philopatry

A total of 62 female white-winged scoters were captured more than once from 2002 to 2004. Most individuals (90%, $n = 56$) appeared to return to the same coast to winter in the subsequent year. However, six females possibly switched between Atlantic and Pacific wintering areas among years, although the evidence for this was not strong (Table 3.5). One banded bird, based on isotopic data, wintered on the Pacific coast one year and was recovered on the same coast the following winter. Because this bird was captured only once at Redberry Lake, it was not included with the above data but was consistent with winter site philopatry.

3.4 DISCUSSION

3.4.1 Species and Tract Preference

Head feathers provided the best discrimination likely due to their relatively small size in relation to feathers of the other tracts. Small size requires less material to replace feathers, and in turn, requires a shorter period of growth (Thompson and Drobney 1996). Thus the average isotopic input can be incorporated into the tissue over a shorter time,

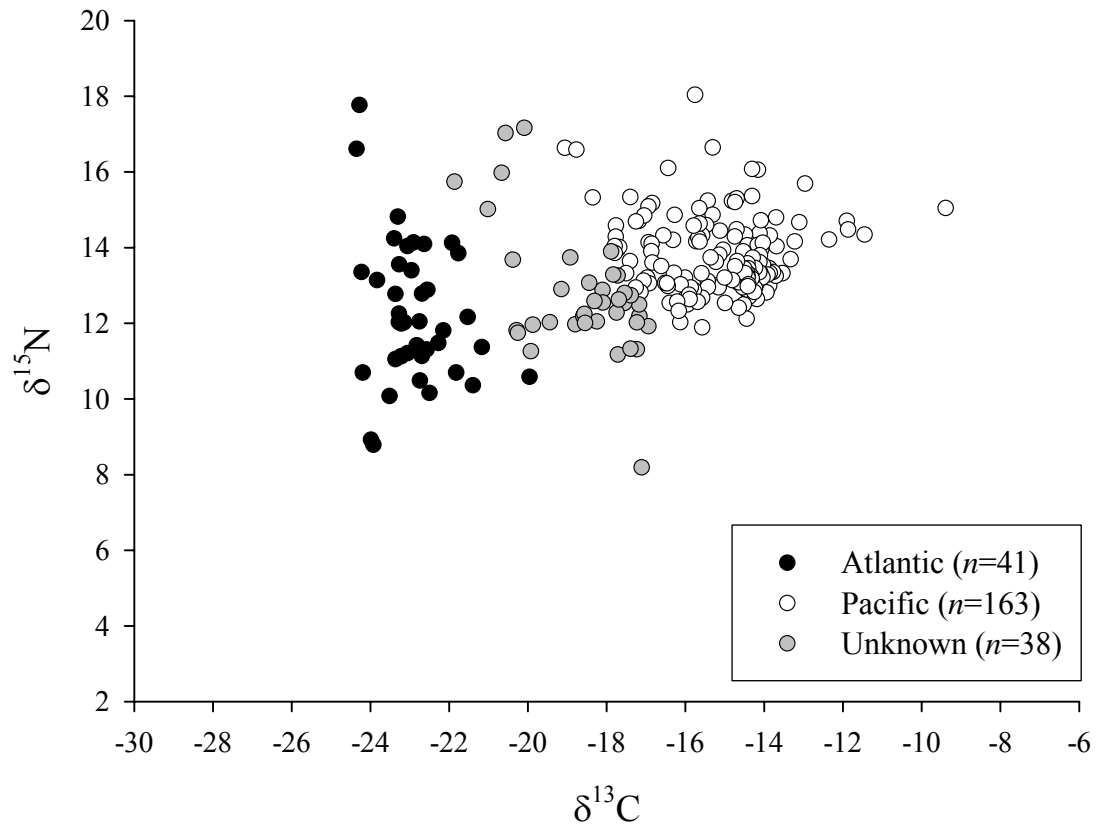


Figure 3.4 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of white-winged scoter head feathers from Redberry Lake females ($n=242$), showing individuals with $>90\%$ classification probabilities grouped into respective Atlantic or Pacific wintering region and those with $< 90\%$ classification probabilities grouped as unknown wintering region.

Table 3.4 Estimated proportions of white-winged scoters nesting at Redberry Lake that wintered on either the Atlantic or Pacific coast as inferred from stable isotope analysis.

Year	Estimated Proportion					
	Atlantic	95% CI	<i>n</i>	Pacific	95% CI	<i>n</i>
2002	0.25	0.15-0.37	18	0.75	0.63-0.85	54
2003	0.26	0.17-0.36	25	0.74	0.64-0.83	72
2004	0.12	0.06-0.22	9	0.88	0.78-0.94	64
All years	0.21	0.13-0.31	52	0.79	0.69-0.87	190

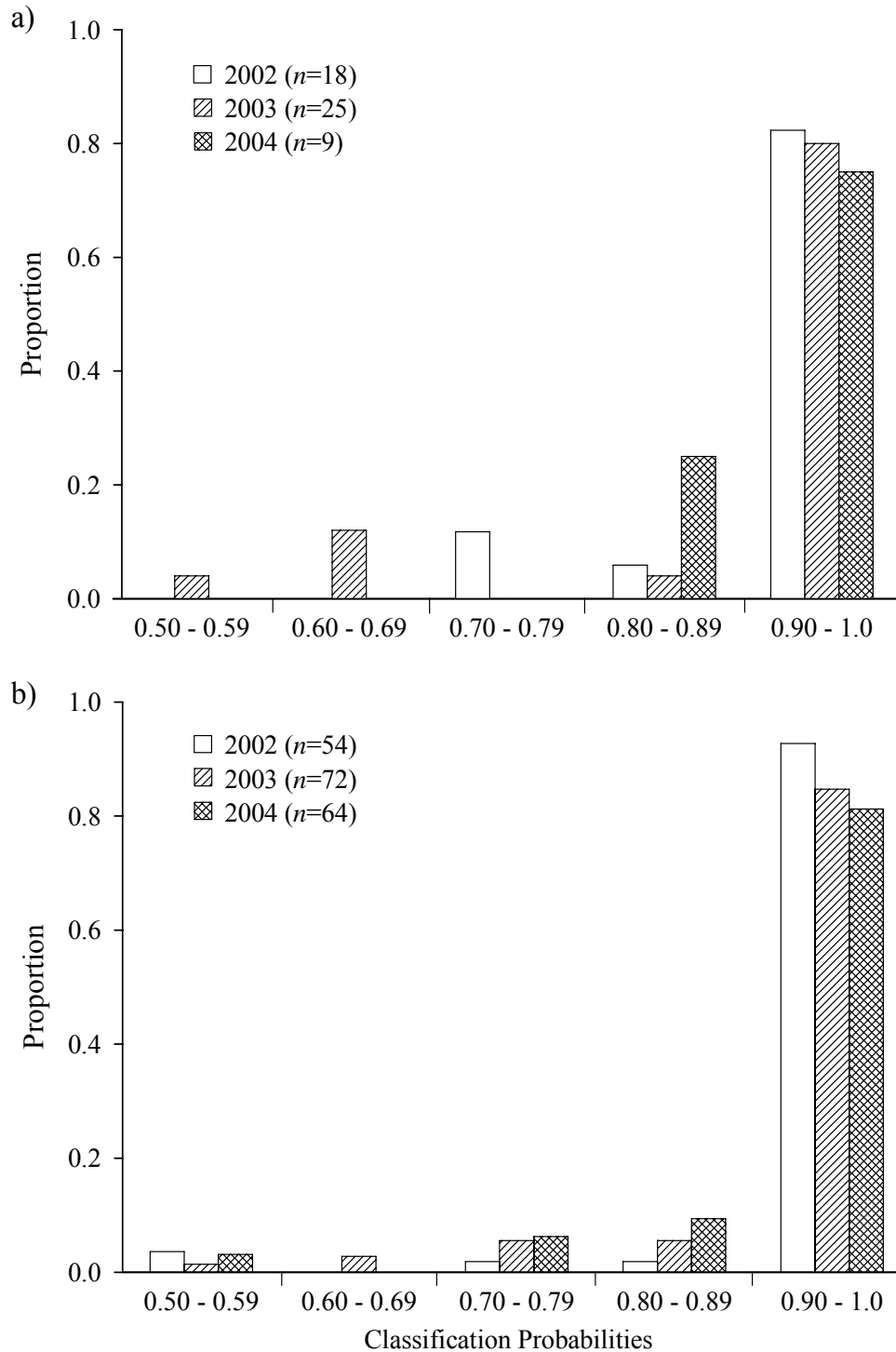


Figure 3.5 Proportional occurrence of classification probabilities for adult female white-winged scoters nesting at Redberry Lake, Saskatchewan and wintering on the (a) Atlantic and (b) Pacific coasts during 2002, 2003, and 2004. Classification probabilities were based on linear discriminant function performed in SAS (SAS Institute Inc. 1999) and reflect the probability that an individual white-winged scoter wintered in that region.

Table 3.5 Classification probabilities for six individuals that were classified as switching wintering areas between years, out of a total of 62 female white-winged scoters captured more than once between 2002-2004. Only one scoter (individual 2) suggests a strong probability of switching from the Pacific (P) in 2002 to the Atlantic (A) in 2003.

Individual	2002		2003		2004	
	Classification Probability	Winter Area	Classification Probability	Winter Area	Classification Probability	Winter Area
1	0.99	A	0.99	A	0.73	P
2	0.92	P	0.93	A	0.53	P
3	0.76	P	0.99	A	--	--
4	0.97	P	0.73	A	--	--
5	0.52	A	0.96	P	--	--
6	--	--	0.99	A	0.76	P

thereby constraining the size of foraging area and reducing any geographic variation in signatures of composite diets (Mehl et al. 2005). Improved discrimination obtained by the use of head feathers from white-winged scoters alone rather than combined scoter species may reflect interspecific differences in selection of prey items and feeding sites within the same area, as white-winged scoters generally select larger prey in deeper water than the other two scoter species (Vermeer and Bourne 1984, Savard et al. 1998, Bordage and Savard 1995, Brown and Frederickson 1997). Probabilities of correct classification were much higher for Pacific than for Atlantic wintering birds, possibly due to differences in sample sizes between the two regions ($n = 149$ Pacific, $n = 32$ Atlantic). A larger sample size from the Atlantic, covering a wider geographical area, may have improved classification probabilities. I was unable to obtain additional samples from Atlantic wintering areas in 2004, despite many attempts to do so.

3.4.2 Delineation of Atlantic and Pacific Populations

Although isotopes were effective in discriminating between wintering populations in this study, there were overlapping values between wintering areas. This may have been due to lack of differences in carbon and nitrogen isotopes signatures between Pacific and Atlantic regions, as reflected in the literature values for food items; however, the sampling period may have also contributed to this overlap. Head and body feathers are molted twice annually, with new plumage acquired during the prealternate molt, typically in July-September, and then again during the prebasic molt in March-April, before migrating to breeding areas (Brown and Frederickson 1997). My samples were collected throughout the fall, but were largely restricted to the regular hunting season (October - January) for Atlantic samples. Thus, my samples may have included feathers grown on the breeding area and therefore, may not have captured isotopic signatures specific to the winter area. Breeding samples would reflect appropriate winter areas, as the prebasic molt is completed before arrival on breeding areas and retained through the summer (Brown and Frederickson 1997).

Presence of highly depleted carbon values in six female samples suggest that molt occurred on freshwater, and were likely the result of samples collected before prebasic molt was completed (i.e. feather growth occurred on breeding areas). These depleted

values were most likely due to differences in timing of molt and arrival on wintering areas between male and female scoters. Male ducks are known to undergo molt earlier than females (Palmer 1976, Austin and Fredrickson 1986) and arrive on wintering areas sooner than females; whereas increased energy demands and time associated with incubation and brood rearing delay arrival of females onto wintering grounds (Leafloor and Ankney 1991, Johnson and Richardson 1982). Thus some females, particularly successful breeders, likely complete their prealternate molt on freshwater breeding areas before arrival on the wintering grounds. If the prealternate molt is delayed, the prebasic molt would also occur later than in males. Male white-winged scoter feathers collected during the hunting season may provide isotope signatures that are more reliable for determining winter area, compared to females, as earlier arrival by males to winter areas increases the likelihood that molt occurs strictly on marine winter habitats. Consistent sampling throughout the winter period would help tease apart sex specific molt chronology.

Mehl et al. (2005) found that enrichment in ^{15}N explained most of the variation in stable isotope signatures of eastern and western wintering king eiders. This difference was attributed to upwellings in the Chukchi Sea providing nitrogen enrichment to regional food webs. In this study, enrichment in ^{13}C was responsible for most of the variation in isotopic values for white-winged scoters and inclusion of $\delta^{15}\text{N}$ values reduced classification bias by only 3%. Terrestrial freshwater sources are depleted in ^{13}C relative to marine carbon sources (Tieszen and Boutton 1988), with average ^{13}C values for freshwater equal to -26‰, and values depleted below -20‰ indicative of freshwater sources (Fry and Sherr 1988). Depleted ^{13}C values observed in head feathers from the Atlantic wintering areas may have been a result of scoters feeding in more estuarine habitats during winter than Pacific wintering scoters. Another explanation is the use of freshwater habitats by Atlantic wintering scoters for prolonged periods during fall staging, before continuing migration to coastal wintering areas.

Increased usage of the Great Lakes by both diving and sea ducks has been noted following the zebra mussel invasion in the late 1980s (Wormington and Leach 1992, Mitchell and Carlson 1993, Petrie & Knapton 1999, Mitchell et al. 2000) and lengthier staging on these areas has occurred in recent years as a result of longer ice-free periods

during the winter. For example, white-winged scoters have been observed in recent years on Lake Ontario in the fall through to January (M. Schummer pers. comm.), and useage by scoters has increased by more than 400% (Petrie and Schummer 2002). Unfortunately, we were unable to collect samples from the Great Lakes for isotopic comparison; however, the importance of the Great Lakes as staging areas for breeding populations that winter on the Atlantic coast requires further investigation. Zebra mussels in the Great Lakes bioaccumulate contaminants at higher concentrations than native clam species (Brieger and Hunter 1993) and waterfowl that exploit zebra mussels have significantly higher contaminant loads than those that do not (Mazak et al. 1997). Thus, zebra mussels may directly impact survival and reproduction of white-winged scoters consuming this food source (de Kock and Bowmer 1993).

3.4.3 Assignment of a Breeding Population to Winter Area

Carbon and nitrogen isotope values for scoters breeding at Redberry Lake typically fit the pattern of the known wintering area samples. However, scoters classified as wintering in the Atlantic indicated more depleted carbon isotope values relative to those from known wintering areas. This suggests an even stronger freshwater influence for scoters that nested at Redberry Lake. Females migrating from Redberry Lake to winter on the Atlantic coast may be potentially staging for extended periods on the Great Lakes or other inland freshwater lakes during both spring and fall and consequently molting there. Redberry Lake banded females have been recovered on the Great Lakes in the fall (Houston and Brown 1983), providing support that the Great Lakes are used as a staging area by this population. One band recovery from the Great Lakes in January (Bird Banding Lab, unpublished data) suggests an extended stay.

Fewer Atlantic wintering scoters nested at Redberry Lake during 2004 than the two previous years. This can be likely attributed to differential factors on the non-breeding areas that either reduced: 1) breeding propensity, or 2) the return of female scoters to Redberry Lake from the Atlantic regions. Prior to the 2004 breeding season, portions of the Atlantic coast encompassing the wintering range of white-winged scoters experienced one of the coldest winters on record since 1895 (NOAA 2006). Severe weather events may have negatively affected body condition such that scoters were

unable to surpass the nutrient reserve threshold critical to attempt breeding (Esler et al. 2001, Anteau 2006), or resulted in higher mortality rates such that fewer scoters survived to return to breed (Blums et al. 2002, Suter and van Eerden 1992).

Band recovery data suggested that the Redberry Lake breeding population is composed of nearly equal ratios of Atlantic and Pacific wintering scoters; however, isotope data from this study suggested the breeding population is comprised of primarily Pacific wintering females. Differences between isotope data and recovery data could reflect the strong tradition of sea duck hunting along the Atlantic coast, as 80% of North American scoter harvest occurs on the eastern seaboard (Savard et al. 1998, Krementz et al. 1997). Band recovery data are useful in understanding migration routes but caution must be taken when interpreting these results because differential hunting pressure or band reporting rates between areas may bias conclusions about the relative importance and use of non-breeding areas (Ewins and Houston 1992, Robertson and Cooke 1999).

3.4.4 Winter Philopatry

Strong philopatry to non-breeding areas has been documented for several sea duck species (Savard 1985, Robertson and Cooke 1999, Robertson et al. 2000, Flint et al. 2000, Alison 1974, Iverson et al. 2004). Similarly, mark recapture studies and satellite telemetry studies (this study, Nysewander et al. 2005, Kirk et al. 2005) support strong philopatry to winter areas for white-winged scoters. High rates of philopatry to both breeding and non-breeding areas may result in finer scale population structuring than that detectable through genetic analyses (Iverson et al. 2004). This can have important conservation implications for local populations because, at the local level, populations are more vulnerable to long-term habitat changes (Rimmer and McFarland 2001, Webster and Marra 2005). In summary, philopatry to breeding, molting, and wintering sites can have significant consequences for individual fitness and population dynamics (Robertson and Cooke 1999), as migratory birds must rely on a variety of habitats throughout their annual cycle.

3.5 CONCLUSION

Naturally occurring stable isotopes may be an effective tool to link wintering and breeding areas for many avian species (Rubenstein and Hobson 2004, Hobson 2005). Stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in white-winged scoter head feathers were useful for discriminating Atlantic and Pacific wintering populations with fair precision, and have provided the discrimination necessary to stratify breeding scoters at Redberry Lake by winter area. Sixteen percent (38/242) of all captured individuals had <90% probability of wintering in either the Atlantic or Pacific and were thus classified as belonging to unknown wintering areas. The Great Lakes and other freshwater staging areas are most likely responsible for the isotopic segregation between the two populations, as scoters classified as wintering in the Atlantic showed highly depleted $\delta^{13}\text{C}$ values relative to Pacific wintering scoters, indicating a freshwater input. However, the exact mechanism driving the differences, as well as long-term temporal variation, between Atlantic and Pacific isotopic values is unknown.

Similarities in the proportion of scoters that nested at Redberry Lake during 2002-2003, coupled with a relative decline in the proportion of scoters that wintered in the Atlantic during 2004, suggests that factors on non-breeding areas may act differentially on each winter population. These data provide the necessary ground work to further investigate delineation of Atlantic and Pacific winter populations of white-winged scoters using stable isotope analysis. Future studies should consider: 1) inclusion of feather samples from the Great Lakes, and 2) incorporation of additional isotopes that allow for freshwater segregation which may reveal greater precision in assigning winter area based on analysis of stable isotopes from the breeding area. Linking wintering areas to breeding areas may provide insight into the continental declines of this species and may enable us to determine if specific wintering grounds limit reproductive success, survival, and recruitment on the breeding areas.

4. VITAL RATES OF WHITE-WINGED SCOTERS FROM ATLANTIC AND PACIFIC WINTER AREAS ON A SHARED BREEDING AREA

4.1 INTRODUCTION

Individuals from a single breeding area may also share the same winter areas (Esler 2000). These individuals are exposed to a similar range of ecological factors throughout their entire life cycle. Alternatively, individuals that share a common breeding area but winter in separate areas can be exposed to differences in contaminants, harvest pressures, and other factors that may affect survival, breeding propensity and reproductive success (Marra et al. 1998, Sillett et al. 2000, Webster et al. 2002). Technological advances in the use of intrinsic markers to investigate migrational connectivity allow stratification of sympatric breeding populations by winter area (Mehl et al. 2004, Moller and Hobson 2004, Marra et al. 1998). Stratification by winter provenance permits examination of potential differences in vital rates of local breeding populations in relation to winter origin. Otherwise, unstratified rates within a local population would typically only be expressed as an average of the groups and potential carry-over effects from the winter areas could go unnoticed (Møller and Hobson 2004, Mehl et al. 2004).

To date, attempts have been made to link winter and breeding areas of scoter populations through satellite telemetry studies (Nysewander et al. 2005, Perry et al. 2005, and Ward et al. 2005). These studies provide valuable information regarding migration linkages, but logistics involved limit sample sizes and difficulty in accessing areas make it impossible to be able to draw strong conclusions regarding influences on breeding area activities. To my knowledge, none have explored the potential for carry-over effects from one season influencing the events on the breeding grounds for white-winged scoters. This study used intrinsic markers, which allowed for larger sample sizes and a means of linking breeding populations to their winter areas providing the potential to examine seasonal interactions on population dynamics.

To investigate cross-seasonal effects of wintering area on breeding, I examined body size, body condition, clutch volume, egg hatchability, nest initiation dates, blood contaminant loads, nest success, and adult female survival in relation to putative winter origin based on classification probabilities obtained from isotope analysis (Chapter 3). Taking a conservative approach to ensure correct classification, only individuals with classification probabilities >0.90 were considered in the comparative analyses between wintering areas. Although this study was not able to determine specific winter factors that influenced breeding season events, linkage of individuals nesting at Redberry Lake to putative wintering areas allowed me to: 1) examine vital rates relative to winter origin, and 2) identify potential winter areas that may limit reproductive success and recruitment.

4.2 ANALYSIS

4.2.1 Winter Area Effect on Breeding Parameters and Blood Contaminant Loads

I used Principle Components Analysis (PCA, PROC PRINCOMP, SAS Institute Inc.) on the correlation matrix of three morphometric measurements of tarsus, culmen, and head lengths obtained using dial calipers (Alisauskas and Ankney 1990) to obtain an index of body size for each individual. Scores (PC1 scores) along the first principal component (PC) axis were interpreted as metrics of body size. Loadings were positive and of similar magnitude, indicating covariation (Pimentel 1979:57-58). General linear models were used to regress body weight on PC1. Residuals of mass corrected for structural size, incubation stage, and initiation date, were used as index of individual body condition (Weatherhead and Brown 1996) and used to classify females as either in poor condition (negative residual) or good condition (positive residual) relative to the measured breeding population.

Nest initiation dates were calculated by back-dating from known laying dates, or from estimated incubation stages by candling eggs (Weller 1956), assuming an incubation length of 28 days (Brown 1977) and a laying interval of 1.5 eggs per day (Brown 1977, Brown and Brown 1981). Clutch volume was calculated from egg length and width measurements (dial calipers, ± 0.1 mm) using Hoyt's (1979) equation. Egg

hatchability was calculated for each nest as number of eggs hatched/number of eggs in nest during last visit.

I used MANOVA (PROC GLM, SAS 1999) to evaluate the effect of year and winter area (Atlantic or Pacific) on the following five parameters related to breeding activity: body size, body condition, nest initiation date, clutch volume and egg hatchability. The significance of the overall model was tested with Wilks' Lambda. Significant independent variables from MANOVA were subsequently analyzed for each response variable using univariate ANOVAs to determine which response variables were significantly influenced by predictor variables. Best approximating models for significant breeding parameters were selected using Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson 2002).

To evaluate the effect of year and wintering area (Atlantic or Pacific) on blood contaminant loads of lead (Pb), mercury (Hg), cadmium (Cd), and selenium (Se), I used MANOVA (PROC GLM, SAS 1999). The significance of the overall model was tested with Wilk's Lambda. As before, significant independent variables from MANOVA were subsequently analyzed for each response variable using univariate ANOVAs. Best approximating models for significant breeding parameters were selected using Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002). All analyses were performed using SAS statistical software (SAS Institute Inc., version 8.0).

4.2.2 Winter Area Effect on Nest Success

I used the nest survival model in program MARK to estimate survival of nests in relation to winter origin (White and Burnham 1999). Nest success relative to winter origin was biased high because, although most nest failures occurred early in the nesting period, wintering area could not be determined until after feathers were sampled during capture at mid-incubation (Chapter 3). Nonetheless, this method provided a conservative estimate if nest success differed between wintering areas. To address the amount of bias, a time invariant null model (S.), using data for all found nests, was considered to calculate Mayfield (1975) estimates of nest success for comparison with previously published results. I used only data for nests of females with classification probabilities >0.90 . I first estimated a null model (S.), calculated using a logit-link

function as the simplest model with no covariates. I considered 6 candidate models for nest success and selected the best approximating model(s) using Akaike's Information Criteria (Akaike 1973) adjusted for sample size (AICc; Burnham and Anderson 1998). I used the best model to estimate daily survival rate (hereafter, DSR). As all nests had equal survival probability to mid-incubation, my assessment of temporal variation in nest age was limited to models with DSR that were either: (1) constant over the 49-day nesting cycle, $\{S.\}$, or (2) constant over the 49-day nesting cycle in each year (i.e., testing annual differences, $\{S_{\text{year}}\}$). I developed a set of a priori models for each analysis to explain variation in DSR. In addition to a constant survival model, I assessed year, winter location (Atlantic or Pacific), nest initiation date and island used for nesting (Gull, Pelican, Old Tern). Island location of each nest was included because nest success may differ by island due to different predation pressures.

I back-transformed logit-scale regression equations to get real DSR estimates, and raised DSR estimates to the power of the nesting duration (49 days, Traylor 2003) to obtain period-specific survival. I ranked each set of candidate models based on Akaike's Information Criterion corrected for sample size (AICc; Akaike 1973, Burnham and Anderson 2002). I calculated variable weights to assess the relative importance of each by summing the Akaike weights of models that included the variable of interest (Burnham and Anderson 2002). In addition to evaluating the effects of different sources of variation on survival, I used the best model to estimate survival estimates.

4.2.3 Winter Area Effect on Apparent Survival of Adult Females

To estimate adult female survival for Atlantic and Pacific wintering females, I used multistate models in Program Mark (White and Burnham 1999) to estimate: (1) apparent survival, ϕ , (2) recapture probability, p , and (3) movement or transition probability, Ψ , (probability of switching between wintering areas) of both nasal-marked hens that were re-sighted and any captured hens. The data set included 5 encounter occasions (2000-2004) with 3 attribute groups (Atlantic, Pacific, and Unknown wintering individuals). Knowledge of wintering area was only available for females captured in 2002-2004. Encounter histories were reorganized to reflect females that wintered in the Atlantic with >0.90 certainty (A), Pacific with >0.90 certainty (P), or unknown (U) wintering

areas, if probability of correct classification was <0.90 or isotope data were not obtained.

I tested the global model for goodness-of-fit using the median \hat{c} option from within program MARK and calculated Quasi-Akaike's Information Criterion (QAIC_c) from AIC_c using a variance inflation factor (\hat{c}) to correct for small sample size and overdispersion (Akaike 1985, Burnham and Anderson 2002). I considered 14 candidate models to investigate apparent survival in relation to winter area. The most parsimonious model was chosen using QAIC_c values ($\hat{c} = 1.36$).

4.3 RESULTS

4.3.1 Winter Area Effect on Breeding Parameters and Blood Contaminant Loads

PC1 accounted for 57% of variation in structural size, with loadings of 0.57, 0.64, and 0.51 for culmen, head, and tarsus lengths, respectively.

In 2002-2004, I captured 242 females, of which 203 (84%) had probabilities >0.90 of correct classification to winter area and 198 of those had measures for all parameters of interest. Overall, there was a multivariate difference in breeding parameters of body size, body condition, nest initiation date (NID), clutch volume and hatchability (MANOVA $F_{5,182} = 2.95$, $p > 0.0137$). No significant differences were found for body size or body condition in relation to winter area or year. Best approximating models for significant breeding parameters (NID and egg hatchability) were selected using Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2002).

Nest initiation date varied by both winter location and year (Table 4.1). During 2002, nest initiation date was 5.2 days earlier for females that wintered on the Pacific (95% CI [days after 1 January]: Pacific area: 165.5–169.0; Atlantic area: 169.0–176.0), with overlapping confidence intervals during 2003 (Pacific area: 164.1–167.7; Atlantic area: 165.7–172.0) and 2004 (Pacific area: 167.1–170.8; Atlantic area: 166.6–176.5).

AIC_c model weight (0.75) suggested that egg hatchability varied more between years than between wintering areas (Table 4.2). Egg hatchability was significantly higher

Table 4.1 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in nest initiation dates for 192 white-winged scoters at Redberry Lake, Saskatchewan during 2002-2004. Models are based on ANOVA with nest initiation date as dependent variable and winter location and year as explanatory variables. AIC_c weight represents relative support of each model in the model set and sums to one.

MODEL	RSS ^a	K^b	AIC_c	ΔAIC_c	AIC_c weight
<i>location, year</i>	8146	5	729.90	0.0000	0.6957
<i>location</i>	8456	3	732.87	2.9761	0.1571
<i>location, year, location*year</i>	8106	7	733.24	3.3410	0.1309
<i>Year</i>	8564	4	737.40	7.4991	0.0164

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

Table 4.2 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in hatch success for 192 white-winged scoters at Redberry Lake, Saskatchewan during 2002-2004. Models are based on ANOVA in hatch success with winter location and year as explanatory variables. AIC_c weight represents relative support of each model in the candidate set and sums to one.

MODEL	RSS ^a	K ^b	AIC _c	ΔAIC _c	AIC _c weight
<i>year</i>	16.80	5	-459.52	0.0000	0.7541
<i>year, location</i>	16.83	3	-457.07	2.4512	0.2214
<i>year, location, location*year</i>	16.84	7	-452.67	6.8514	0.0245
<i>location</i>	19.87	4	-429.38	30.1375	0.0000

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

during 2003, (86.3%, 95% CI: 79.4%-93.3%) than 2002 (57.0%, 95% CI: 49.7%-64.3%) or 2004 (66.2%, 95% CI: 58.4%-74.1%).

During 2002 and 2003, 153 females were sampled for blood, of which 102 had all four heavy metals analyzed as well as probabilities of correct classification to winter area equal to 0.90 or greater. Overall, there was a multivariate difference in blood contaminant loads (MANOVA $F_{4,95} = 22.07$, $p > 0.0001$). Best approximating models for blood contaminant loads (Pb, Se, Cd, Hg) were selected using Akaike's Information Criterion adjusted for sample size (AIC_c) (Burnham and Anderson 2002).

Lead and selenium varied between winter areas but not between years (Table 4.3, Table 4.4, and Figure 4.1). Cadmium varied between winter area and year (Table 4.5, Figure 4.1). Mercury levels did not vary between wintering areas, but did vary between years (Table 4.6, Figure 4.1). Mean Cd levels during 2002 were similar for both wintering groups (Atlantic: 3.32 ng/ml, 95% CI: 1.42-5.23 ng/ml; Pacific: 2.13 ng/ml, 95% CI: 1.03-3.23 ng/ml), but significantly increased for Atlantic scoters during 2003 (11.07 ng/ml, 95% CI: 9.41 – 12.74 ng/ml), while levels for Pacific scoters remained relatively unchanged (2.87 ng/ml, 95% CI: 1.68-4.07 ng/ml). Mean Se and Pb levels were higher for Atlantic wintering scoters (Se: 7.0 µg/g, 95% CI: 6.1 – 7.9 µg/g; Pb: 0.064 µg/g, 95% CI: 0.057 – 0.072 µg/g) than for Pacific wintering scoters (Se: 2.6 µg/g, 95% CI: 2.0 – 3.2 µg/g; Pb: 0.036 µg/g, 95% CI: 0.031 – 0.042 µg/g). Levels of mercury were higher during 2002 (0.27 µg/g, 95% CI: 0.25-0.28 µg/g) than in 2003 (0.17 µg/g, 95% CI: 0.16-0.19 µg/g).

4.3.2 Winter Area Effect on Nest Success

For all nests found ($n = 386$), I observed avian depredation rates of 12.7%, 6.3% and 9.4%, mammalian depredation rates of 15.7%, 4.2%, 17.0% and rates of depredation by unknown causes of 7.4%, 9.0%, and 9.4% during 2002, 2003, and 2004, respectively. Abandonment rates were 21.6%, 16.7%, 9.4% in 2002, 2003 and 2004, respectively. High coyote activity, including denning with pups, was observed on Pelican Island in 2003 and on Gull Island in 2004; therefore, observation of abandoned nests may have also included nests where the female was killed but the nest itself was not depredated.

Table 4.3 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in selenium blood concentration for 102 white-winged scoters at Redberry Lake, Saskatchewan during June to July, 2002-2003. Models are based on ANOVA with selenium blood concentration as dependent variable and winter location and year as independent variables. AIC_c weight represents relative support of each model in the model set and sums to one.

MODEL	RSS ^a	K ^b	AIC _c	ΔAIC _c	AIC _c weight
<i>location</i>	662	3	197.01	0.0000	0.6284
<i>Location, year</i>	659	4	198.72	1.7042	0.2680
<i>location, year, location*year</i>	657	5	200.62	3.6068	0.1035
<i>year</i>	1066	3	245.61	48.5931	0.0000

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

Table 4.4 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in lead blood concentration for 102 white-winged scoters at Redberry Lake, Saskatchewan during June to July 2002-2003. Models are based on ANOVA with lead blood concentration as dependent variable and winter location and year as independent variables. AIC_c weight represents relative support of each model in the model set and sums to one.

MODEL	RSS ^a	K^b	AIC_c	ΔAIC_c	AIC_c weight
<i>location</i>	0.048	3	-775.23	0.0000	0.3366
<i>Location, year</i>	0.047	4	-775.21	0.0200	0.3333
<i>location, year, location*year</i>	0.046	5	-775.19	0.0390	0.3301
<i>year</i>	0.063	3	-747.49	27.7372	0.0000

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

Table 4.5 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in cadmium blood concentration for 102 white-winged scoters at Redberry Lake, Saskatchewan during June to July 2002-2003. Models are based on ANOVA with cadmium blood concentration as dependent variable and winter location and year as independent variables. AIC_c weight represents relative support of each model in the model set and sums to one.

MODEL	RSS ^a	K^b	AIC_c	ΔAIC_c	AIC_c weight
<i>location, year, location*year</i>	1171	5	259.57	0.0000	0.9999
<i>location, year</i>	1428	4	277.60	18.0259	0.0001
<i>location</i>	1624	3	288.55	28.9774	0.0000
<i>year</i>	1940	3	306.68	47.1125	0.0000

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

Table 4.6 Akaike's Information Criterion (AIC_c) values for all candidate models explaining variation in mercury blood concentration for 102 white-winged scoters at Redberry Lake, Saskatchewan during June to July 2002-2003. Models are based on ANOVA with mercury blood concentration as dependent variable and winter location and year as independent variables. AIC_c weight represents relative support of each model in the model set and sums to one.

MODEL	RSS ^a	K^b	AIC_c	ΔAIC_c	AIC_c weight
<i>year</i>	0.330	3	-578.59	0.0000	0.6196
<i>location, year</i>	0.328	4	-577.04	1.5474	0.2858
<i>location, year, location*year</i>	0.328	5	-574.83	3.7600	0.0945
<i>location</i>	0.542	3	-527.98	50.6097	0.0000

^aRSS= Residual sums of squares from ANOVA

^bK= No. of parameters

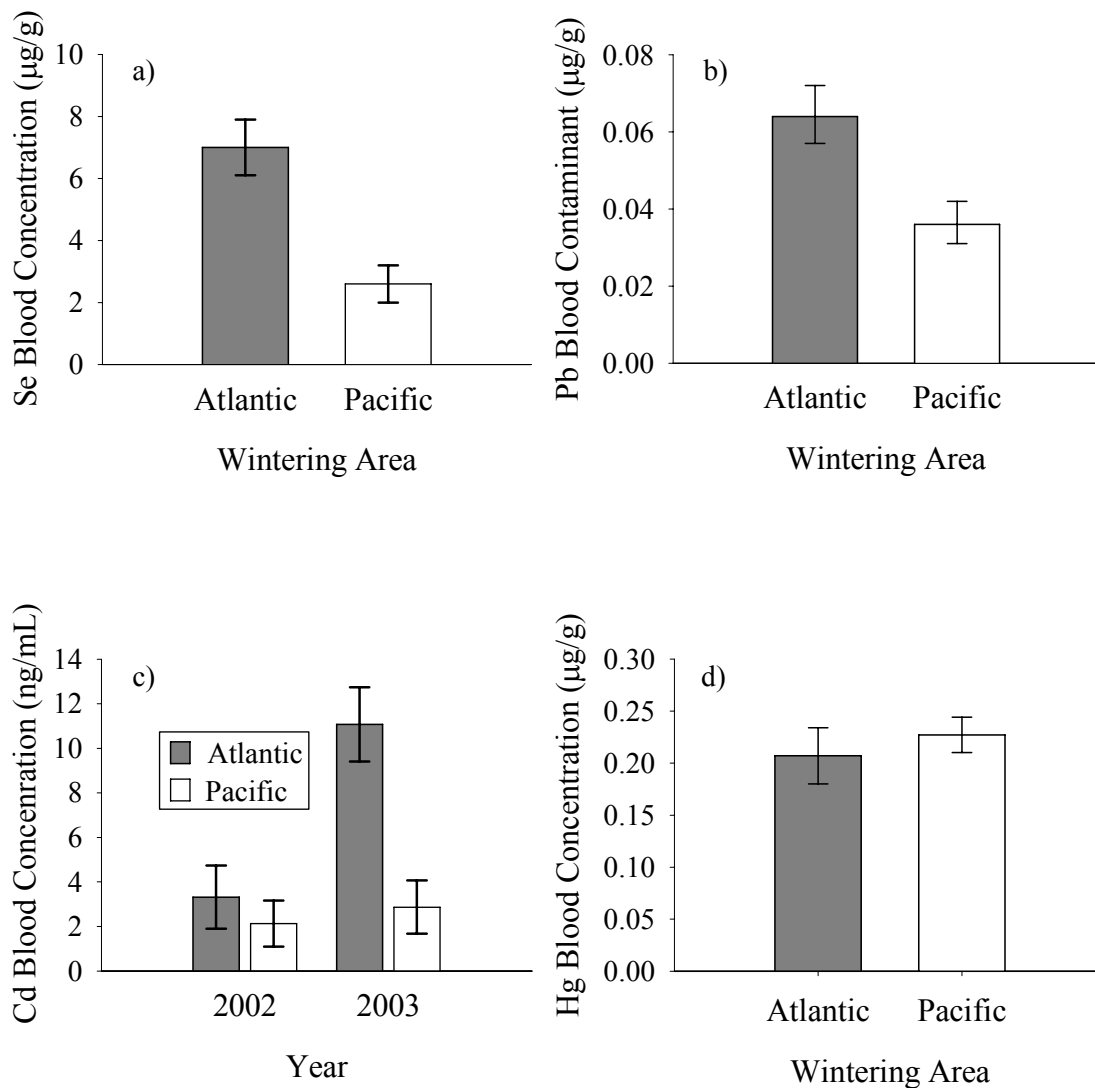


Figure 4.1 Blood concentrations (\pm 95% CI) of four heavy metal contaminants, (a) Se, (b) Pb, (c) Cd, and (d) Hg, sampled from 102 female white-winged scoters at Redberry Lake, Saskatchewan during June to July 2002-2003. Wintering area was determined from stable isotope analysis (2002: $n = 13$ Atlantic, $n = 39$ Pacific; 2003: $n = 17$ Atlantic, $n = 33$ Pacific).

For all nests found, including those with unknown winter classification, Mayfield nest success was 31% (95% CI: 25% - 36%) from model {S.}, containing only an intercept term for DSR. Mayfield nest success estimated for each year from model {S_{year}} was 0.25 (95% CI: 17% - 33%) in 2002, 0.51 (95% CL: 40% - 61%) in 2003, and 0.19 (95% CL: 12% - 27%) in 2004, suggesting strong differences in nest survival among years.

When analysis was restricted to only nests of females for which probability of correct classification of winter area was 0.90 or greater ($n = 193$), Mayfield nest success was 81% (95% CI: 73% - 87%) from model {S.}, which contained only an intercept term for DSR. Clearly, restriction of analysis to females which were captured biased estimates upwards, but this should have applied to both winter areas. Mayfield nest success calculated for each year from model {S_{year}} was 74% (95% CI: 59% - 84%) in 2002, 93% (95% CI: 81% - 98%) in 2003, and 73% (95% CI: 55% - 85%) in 2004, also suggesting differences in nest survival between years. Daily survival probabilities of white-winged scoter nests were primarily a function of year, but the second best model ($\Delta AIC_c > 2.0$) included effects of both wintering location and nesting island (Table 4.7).

4.3.3 Winter Area Effect on Apparent Survival of Adult Females

Encounter histories for multistate analysis of annual apparent survival of adult females consisted of 214 individually marked white-winged scoter females. The best model had 13 parameters with no differences in apparent adult female survival between the two wintering areas (Table 4.8). Parameter estimates from the top model indicated that $\hat{\phi}$ during 2000-2004 was 0.85 (95% CI = 0.80 to 0.90). Recapture probability (\hat{p}) did not vary with wintering group (Atlantic: 0.54 – 0.76; Pacific: 0.56 – 0.78). Transition probabilities (Ψ) for females switching among wintering areas were very low, although the confidence intervals for switching from Atlantic to Pacific were large and overlapped with zero ($\Psi_{A \rightarrow P} = 0.00$; 95% CI = 0.00 to 0.82 and $\Psi_{P \rightarrow A} = 0.01$; 95% CI = 0.001 to 0.12).

Table 4.7 Summary of model selection results used to investigate winter area influence (AP) on nest success for 193 white-winged scoter nests at Redberry Lake, Saskatchewan during 2002-2004.

Model	AIC _c ^a	ΔAIC _c ^b	Wi ^c	K ^d	Deviance ^e
S(year)	218.72	0.00	0.57	3	212.71
S(year + AP + island)	221.10	2.38	0.17	7	207.08
S(year + AP)	221.86	3.13	0.12	6	209.84
S(year + island)	222.92	4.08	0.07	3	216.80
S(.)	222.92	4.20	0.07	1	220.92
S(year + AP + island + NID)	1132.39	913.67	0.00	10	1112.35

^a Akaike's Information Criterion with small sample correction.

^b Difference in AIC_c values between the model with the lowest AIC_c value.

^c Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

^d Number of estimable parameters.

^e Deviance is difference between $-2\log$ -likelihood of the current model and that of the saturated model.

Table 4.8 Summary of model selection results for investigation of winter area influence on apparent adult female survival (ϕ), recapture probability (p), and transition probability (Ψ) for 214 white-winged scoters nesting at Redberry Lake, Saskatchewan during 2002-2004. Models included group effects where parameters varied with wintering area (g) or held constant (.), and time effects, where time varied annually (t), linear trend with time (T), or with no time variation (.). Transition probabilities for switching from Atlantic to Pacific ($\Psi_{A \rightarrow P}$) and Pacific to Atlantic ($\Psi_{P \rightarrow A}$) wintering areas was held constant over time in the top model. Models are ranked in accordance to QAIC_c values and are denoted as additive (+) or interaction (*) models.

Model	ΔQAIC_c	Wi ^a	K ^b	QDeviance
$\{\phi(.) p(g+t) \Psi(g+t) \mid \Psi_{A \rightarrow P} (.) \Psi_{P \rightarrow A} (.)\}$	0.00	0.35037	13	139.074
$\{\phi(.) p(g+t) \Psi(g+t)\}$	0.51	0.27169	13	139.582
$\{\phi(.) p(g+t) \Psi(g^*t)\}$	1.37	0.17624	19	127.217
$\{\phi(.) p(t) \Psi(g^*t)\}$	2.43	0.10373	16	134.953
$\{\phi(.) p(g+T) \Psi(g^*t)\}$	4.62	0.03482	18	132.699
$\{\phi(g) p(g+t) \Psi(g^*t)\}$	5.59	0.02137	21	126.918
$\{\phi(.) p(T) \Psi(g^*t)\}$	5.77	0.01961	17	136.072
$\{\phi(t) p(g+t) \Psi(g^*t)\}$	6.20	0.01577	20	129.792
$\{\phi(g+t) p(g+t) \Psi(g^*t)\}$	9.38	0.00322	23	126.126
$\{\phi(.) p(g) \Psi(g^*t)\}$	10.32	0.00201	15	145.035
$\{\phi(.) p(g+t) \Psi(g)\}$	12.97	0.00050	10	158.479
$\{\phi(g^*t) p(g+t) \Psi(g^*t)\}$	13.51	0.00041	25	125.624
$\{\phi(g^*t) p(t) \Psi(g^*t)\}$	15.22	0.00017	22	134.264
$\{\phi(g^*t) p(g^*t) \Psi(g^*t)\}$	18.08	0.00004	26	127.857

^a Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

^b Number of estimable parameters.

4.4 DISCUSSION

Blood contaminant concentrations are generally related to concentrations in other body tissues (Wayland et al. 2001), thus blood samples are useful to monitor exposure to contaminants such as trace metals. Eastern wintering scoters had higher blood contaminant concentrations of selenium, lead, and cadmium, with no difference in concentrations of mercury. Use of the Great Lakes and consumption of zebra mussels by eastern wintering scoters may be responsible for the elevated levels. Zebra mussels in the Great Lakes bioaccumulate contaminants at higher concentrations than native clam species (Brieger and Hunter 1993) and waterfowl that exploit zebra mussels have significantly higher contaminant loads than those that do not (Mazak et al. 1997). Concentration of lead was consistent with background levels (Pain 1996). Blood contaminant concentrations for cadmium and selenium measured in this study were similar to values reported for other sea duck species (Wayland et al. 2001, Grand et al. 2002, Franson et al. 1999). To date, no evidence has been found to suggest that exposure to elevated Cd or Se levels may be adversely affecting body condition, reproduction, or survival of breeding white-winged scoters (Devink et al. 2007, Wayland et al. 2007). However, long-term exposure to sub-lethal concentrations have the potential to indirectly affect health and survival, as the immune system could be compromised, increasing disease susceptibility (Bennett *et al.*, 2001).

Differences in nest initiation date and contaminant loads may be related to quality of habitat during the non-breeding season, and if individuals are occupying poorer habitats, this may be reflected in reproductive performance (Norris et al. 2004). However, I did not detect differences in nest success among birds from different wintering areas. Nest success estimates were biased high because females were sampled for feathers to obtain winter area identification during mid-incubation, after the period when most nest failures occur (Traylor 2003). Future research should consider sampling techniques that would identify the winter area of nesting females that fail before mid-incubation. Caution must be taken as disturbance during early incubation may increase rates of abandonment (Criscuolo 2001). Nest success in this study varied by year during 2002-2004, but not during 2000-2001 (Traylor 2003). This variation could be due to shifts in predator communities. Intense predation pressure by coyotes was observed during 2003

and 2004. I found evidence of coyotes denning on Pelican Island in 2003, but nest success was still high (0.51). I suggest that higher nesting densities of other avian species on Pelican Island (Pelican and gull colonies) offset predation pressure on the scoters, and resulted in reduced gull predation on nests and ducklings. During 2004, a coyote pair with pups denned on Gull Island and nest success was poor (0.19) with all nests on Gull Island being destroyed as there were no other avian species nesting in large numbers on this island to offset predation. These data suggest that to adequately address factors that may affect populations with highly variable production, long-term studies are needed.

Nest initiation can be influenced by several factors which include body condition and dates of arrival to breeding areas (Drent et al. 2006, Marra et al 1998). Timing of migration to the breeding grounds has been linked to winter habitat quality and body condition during spring migration for other species (Marra et al 1998, Bearhop et al. 2004). Nest initiation dates at Redberry Lake differed between white-winged scoters from Pacific and Atlantic wintering areas in 2002 but not in 2003 or 2004. Mehl (2004) also found western wintering eiders initiated nests in the arctic earlier than eastern wintering eiders during the same year. This suggests a large-scale event (i.e. late spring) on eastern regions may have influenced arrival times of Atlantic wintering females to the breeding grounds resulting in later nest initiation. I was not present at the study site in May when scoters first arrived; thus, I was unable to determine if scoters from both winter areas arrived at Redberry Lake at about the same time. Future observations of marked females during arrival, in conjunction with isotopic data would determine if arrival times differ by winter area. Within a breeding population, timing of nest initiation can have a large influence on reproductive success because broods that hatch earlier in the season are more likely to survive (Blums et al. 1997, 2002, Traylor and Alisauskas 2006).

Body condition can directly influence reproductive output. Individuals in poorer body condition are less likely to attempt breeding and, if they do breed, are less likely to complete incubation, hatch young, or successfully raise ducklings to fledging (Yerkes 2000). I did not detect differences in body condition between wintering areas, but body condition measured during this study may have been equilibrated by early arrival on the

breeding grounds (4 – 5 weeks before they initiate nests; Brown and Fredrickson 1989), with both wintering populations feeding from the same resources before nesting. A threshold amount of mass must be reached before nesting is possible (Bond and Esler 2006, Safine 2005); thus, females in poorer body condition may not attempt to breed, or if they do, they may fail early into incubation. I captured females at mid-incubation to reduce observer-induced nest abandonment, and therefore, only sampled a portion of the breeding population and did not sample non-breeders. This likely biased body condition high for both populations. A large proportion of paired females present on the breeding area may be non-breeders (Safine 2005) which were unavailable for sampling; thus, I was unable to determine if winter area influenced the proportion of non-breeders or body condition of these individuals.

Adult female survival did not differ between winter areas, however, lack of precision associated with small sample size may have left differences undetected. Estimates of female survival for the Redberry Lake population (0.85, this study; 0.84, Alisauskas et al. 2004) are higher than those reported for an Alaska breeding area (Safine 2005, 0.79). Safine (2005) attributed the difference to island nesting at Redberry Lake providing protection from predators and improving summer survival probabilities. Island nesting strategy and nest concealment function well to protect from avian predators but do little to protect nests from mammalian predators that rely on olfaction and can search islands effectively. Historically, the islands may have provided protection from mammalian predators, but as a result of declining water levels, mammalian access to the islands has increased and scoters are now highly vulnerable to a greater number of predation pressures.

4.5 CONCLUSION

This study found differences in nest initiation dates and blood contaminant loads in relation to wintering area, suggesting that seasonal interactions may have the potential to influence reproductive success for this population. In contrast, estimates of nest success varied more between years than between wintering areas. However, nest success was biased high as only nests that survived until mid-incubation could be assigned to winter

strata. Sampling techniques that identify winter area of both non-breeders and females associated with early nest failures would, no doubt, provide a more complete picture of breeding propensity and nest success in relation to winter area. I detected no difference in apparent adult female survival among the two wintering groups, but only three years of identification to winter area was available for estimation of survival probability. Isotope analysis coupled with mark-recapture data collected over a longer term than this study period may increase reliability and refine estimates of adult female survival in relation to winter area.

5. SYNTHESIS

Linking breeding areas to stopover and wintering areas is crucial for effective conservation of white-winged scoters, as this species has undergone apparent drastic population declines within the last fifty years on both the breeding and wintering areas (Alisauskas et al. 2004, Trost 1998a). The ability to link different stages and areas of a migratory species' life cycle is critical to understanding factors that limit population growth on both non-breeding and breeding areas (Marra et al. 1998). Factors such as harvest pressures, food resources, adverse weather, and contaminants on wintering areas have the potential to limit reproductive success and recruitment of individuals on breeding grounds in addition to affecting individual survival (Di Guilo and Scanlon 1984, Stapp et al. 1999, Davidson 1981). This research lead to greater understanding of seasonal interactions affecting population dynamics of white-winged scoters. My main objectives were to: (1) determine if segregation of winter populations was possible using stable isotope techniques, (2) link a breeding population to wintering areas, and (3) examine if winter origin influences breeding parameters, nest success and adult female survival.

Isotope techniques were successful in segregating winter populations during this study, allowing stratification of a local breeding population by winter origin. This isotope technique may be applicable to determine the wintering origins of other breeding populations across their range. However, the extent to which other eastern wintering populations use the Great Lakes as staging areas may determine effectiveness of delineation, as the Great Lakes are likely the driving force for segregation of Atlantic from Pacific scoters. Substantial increases in number of diving ducks and sea ducks on the Great Lakes have likely occurred in response to warmer winter temperatures, reduced ice cover and abundance of a recently introduced species, the zebra mussel (Petrie and Schummer 2002). Importance of this area for the eastern wintering population of white-winged scoters may increase with time, as warming trends are predicted to continue in response to climate change.

Successive recaptures combined with isotope analysis provided insight into winter philopatry on the coarse scale of coastal region, and are consistent with findings of other studies that sea ducks exhibit strong winter philopatry (Savard 1985, Robertson and Cooke 1999, Robertson et al. 2000, Flint et al. 2000, Alison 1974, Iverson et al. 2004; although see Mehl et al. 2004). Strong winter philopatry was further supported by survival analyses in Chapter 4, as very low transition probabilities for females switching between winter areas was estimated. Isotopic analyses provided detailed information on population structure that could not be obtained through limited data provided by conventional methods. Population structure using this method differed significantly from inferences based on recovery data, suggesting bias of recovery data due to differential reporting or harvest rates. Most scoters in the United States (~80%) are harvested in the Atlantic Flyway (Krementz et al. 1997), suggesting the potential for survival rates to be lower for eastern than western wintering scoters. However, I detected no site specific difference. While sea duck harvest occurs at lower levels than for other waterfowl, their populations and reproductive potentials are also lower. Much of the change in population size over time at Redberry Lake appears to be due to changes in recruitment of offspring rather than apparent female survival (Alisauskas et al 2004); however, recruitment is highly dependent on survival of breeding adults. Adult female survival becomes more important for population growth and stability for species that exhibit delayed maturity, such as white-winged scoters, as recruitment is subjected to a lag period (Rockwell et al. 1997, Crone 2001). Efforts to monitor effects of harvest on adult mortality and regulate sustainable harvest are required as part of a management strategy, as white-winged scoter populations are drastically declining, and level of harvest by sport and subsistence hunters is poorly known.

This study also advanced our knowledge of cross-seasonal effects. Differences in nest initiation dates and blood contaminant loads in relation to wintering area, suggests the potential for seasonal and geographical influence on reproductive success. During this study, I did not detect differences in nest success or adult female survival in relation to winter area, but estimates could have been biased due to timing of female capture. Non-breeders and breeders that failed early in the season were not sampled, as females

were captured at mid-incubation to determine winter identity. One wintering area may be comprised of a larger proportion of non-breeders, or breeders that fail early, than the other. Further confounding of winter differences may be explained by the coarse spatial scale at which winter origin was determined. Although I was able to assign nesting scoters to Atlantic and Pacific coasts with high certainty ($>.90$), these individuals may have wintered in different locations along the coast, followed different migration routes, or staged on different areas (Nysewander et al. 2005). Thus, the Atlantic and Pacific wintering groups I delineated are likely composed of many local wintering populations that are exposed to differential factors relative to one another. This could further confound winter factors making them more difficult to distinguish on a regional scale of coastal winter area. Further investigations based on isotopic analysis of feather samples from the Great Lakes, as well as incorporation of other intrinsic markers may help delineate winter areas on the Great Lakes and along each coast to a finer scale.

Caution must be taken when extrapolating these results to other breeding populations, as Redberry Lake may not be representative of the continental population of white-winged scoters. This local population occupies the southern limit of the species' distribution and is exposed to greater human disturbance and different predator regime than most of the breeding population in the boreal forest (Traylor 2003, Alisauskas et al. 2004). Regardless of breeding location, mixing occurs on the wintering areas (Nysewander, pers. comm.), which may allow inferences regarding winter influence on breeding events from the Redberry Lake population to be relevant to the whole. Monitoring and long term data collection at this site should continue, especially as this area is unique in that it is the only area known to have two winter populations breeding sympatrically.

Evidence indicates that population declines of white-winged scoters on the wintering grounds have occurred at similar rates to those on the breeding grounds, with the largest declines occurring along the Atlantic coast (Trost 1998a, 1998b, National Audubon Society 2006). These declines, in addition to winter area differences in contaminant loads, nest initiation dates, and annual variation in population structure found during this study suggest that factors responsible for declines are not limited to the breeding grounds. This study is one of the first to attempt to link winter events to

breeding season outcomes for white-winged scoters, but uncertainties remain about potential seasonal interactions. I suggest that future studies attempt to capture scoters upon arrival to the breeding grounds before nesting. This would allow inclusion of samples from non-breeders and those that may fail nesting early; thus making use of isotopic delineation for a wider range of breeding females (non-breeders and early nest failures) to gain further insight into wintering and breeding area interactions. A potentially important objective for further research is the estimation of breeding propensity. Perhaps using information from blood plasma lipids from birds captured before nesting (Bond 2006, Safine 2005), in conjunction with information about contaminants, body mass, body condition and winter affinity would help elucidate this area.

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APPENDIX A. PREDICTIVE EQUATIONS FOR DELINEATING BETWEEN ATLANTIC AND PACIFIC WINTER POPULATIONS OF WHITE-WINGED SCOTERS.

The basic form of the linear discriminant function of belonging to a particular group can be expressed as $D_{group} = a + b_1 \cdot x_1 + b_2 \cdot x_2 + \dots + b_m \cdot x_m$, where a is a constant and b_1 through b_m are the discriminant coefficients and x_1 through x_m are the discriminating variables. Below is given the linear discriminant function equation based on isotopic values from white-winged scoter head feathers collected on both the Atlantic (n=32) and Pacific (n=149) coasts. The linear classification equation using carbon and nitrogen isotopic ratios was:

$$D_{Atlantic} = -142.65 + [9.07 \quad -8.98] * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix}$$

(A.1)

$$D_{Pacific} = -128.30 + [9.72 \quad -7.79] * \begin{bmatrix} {}^{15}N_i \\ {}^{13}C_i \end{bmatrix}$$

(A.2)

Where ${}^{15}N_i$ and ${}^{13}C_i = \delta^{15}N$ and $\delta^{13}C$ values for observation i , respectively. An individual was classified as wintering in the Atlantic if $D_{Atlantic} > D_{Pacific}$, or in the Pacific if $D_{Pacific} > D_{Atlantic}$.

To calculate the probability of belonging to each population, the following equations (from Mehl et al. 2005) were used:

$$\text{Denominator} = \exp(D_{Atlantic}) + \exp(D_{Pacific})$$

$$\text{Probability}_{Atlantic} = \exp(D_{Atlantic}) / \text{denominator}$$

$$\text{Probability}_{Pacific} = \exp(D_{Pacific}) / \text{denominator}$$