

**SITE USE AND MIGRATION OF SCOTERS (*Melanitta* spp.)
IN RELATION TO THE SPAWNING OF PACIFIC
HERRING (*Clupea pallasii*)**

by

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Dipl. T., British Columbia Institute of Technology, 2003
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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

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SIMON FRASER UNIVERSITY

Spring 2008

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Site use and migration of scoters (*Melanitta* spp.) in relation to the spawning of Pacific herring (*Clupea pallasii*)

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ABSTRACT

I investigated movements and site use by two scoter species during late winter and spring. In the Strait of Georgia, British Columbia, I found that radio-transmitter-tagged pre-migratory surf scoters (*Melanitta perspicillata*) and white-winged scoters (*Melanitta fusca*) left the areas where they had spent the winter and moved to Pacific herring (*Clupea pallasii*) spawn sites coincident with spawn availability in March. In southeast Alaska, I identified stopover and staging sites of satellite-transmitter-tagged migrating surf scoters and identified one site, Lynn Canal, as particularly important. I found that herring spawn availability and proximity to the mainland coast were strong predictors of site use, suggesting that the resource availability and geography of southeast Alaska provide important stopover habitat for migrants. Overall, there was strong phenological correspondence between the northward progression of scoter migration and herring spawn availability, suggesting that herring spawn is a valuable resource for scoters in late winter and spring.

Keywords: habitat use; herring spawn; migration; radio telemetry; satellite telemetry; surf scoter; white-winged scoter

Subject Terms: Ducks -- British Columbia -- Georgia Strait Region; Sea birds -- British Columbia -- Georgia Strait Region; Ducks British Columbia; Ducks Habitat; Ducks Alaska; Migration Birds North America

ACKNOWLEDGEMENTS

I have been very lucky to work with an amazing group of researchers and students, and this thesis would not exist without their contributions. I would first like to thank my primary supervisor, Dr. Dan Esler, because his guidance and scientific mentorship are the reasons this thesis was completed. I feel very privileged to have worked with such a dedicated and insightful scientist, and am grateful for his support, enthusiasm, and unending sense of humour. I would also like thank Dr. Kristina Rothley and Dr. Ron Ydenberg for serving on my supervisory committee and helping shape this project, and Dr. Mary Willson for serving as my external examiner and contributing so much to this thesis in just a few short hours. I would also like to thank Dr. Sean Boyd and Dr. John Takekawa for their mentorship, suggestions, and vast array of knowledge. Primary funding for my research came from the Sea Duck Joint Venture, with additional thanks to the Environment Canada Science Horizons Program, Simon Fraser University, and the Centre for Wildlife Ecology.

This project would not have been possible without data provided by my research partners and other agencies. Thanks to John Takekawa and Susan-Wainwright-De La Cruz from the U.S.G.S. San Francisco Bay Estuary Field Station, David Ward from the U.S.G.S. Alaska Science Centre, and Dave Nysewander and Joe Evenson from the Washington Department of Fish and Wildlife for all their data and support. Thanks to the Alaska Department of Fish and Game and the Department of Fisheries and Oceans Canada for herring spawn data. And thanks to David Albert from the Nature Conservancy for providing the shoreline habitat database for southeast Alaska.

I would like to thank all the people who helped in the field and with logistics. Eric Anderson, Sam Iverson, Matthew Wilson, and Cooper provided many hours of hard work and hilarity. Thanks also to the Alaska Department of Fish and Game in Ketchikan for all their help, particularly Steve Heinl, Bo Meredith, Andy Leitz, Phil Doherty, and Boyd Porter. Thanks to Gwen Baluss for her birding expertise, and to Dave Douglas for his generosity in providing a place to stay in Juneau. I would also like to thank pilots Lynn Bennett and Dave Doyon for many safe hours in the air. Many thanks also to all the scoter people who came before me: Molly Kirk, Tyler Lewis, and Deb Lacroix, and the entire Sustainable Shellfish Aquaculture Initiative crew who collected the data used in Chapter 2.

In the CWE, Connie Smith, Judy Higham, and Monica Court have been infinitely helpful with the logistics of everything imaginable. Lab meetings with the Ydenberg, Green, and AWEL labs provided much support and feedback for projects and presentations, thanks to: Jenn Barrett, Jeanine Bond, Kathy Brodhead, Lindsay Farrell, Samantha Franks, Kristen Gorman, Dan Guertin, Megan Harrison, Joel Heath, Rebecca Harrold, Sofi Hindmarch, David Hope, Sarah Jamieson, Iain Jones, Christina Kereki, Molly Kirk, Tyler Lewis, Heather Major, Josh Malt, Shelley Marshall, Lindsay McBlane, Holly Middleton, Kyle Morrison, Andrea Pomeroy, Sam Quinlan, Dora Repard, Pat Robinson, Christine Rock, Tina Semeniuk, Mike Silvergieter, and Caz Taylor. A particularly huge thanks to Molly for all her scoter/data/fashion/life advice.

And finally, wholehearted thanks to my wonderful family and friends for their moral, financial, emotional, and nutritional support during this whole process. I definitely owe you one. Or six.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Thesis Background

The ability to acquire and store energy and nutrients directly influences the survival and reproductive success of an individual. Consequently, optimization of energy and nutrient acquisition plays a key role in selection of habitat and food resources (Schoener 1987). Migrating animals face habitat and food resources that vary considerably, both spatially and temporally, across local, regional, and continental scales. Habitat and food choices of pre-migratory and migrating animals can have important effects on nutrient and energy acquisition, which in turn influence habitat use, behaviour, and demography in subsequent annual cycle stages (Webster et al. 2002). As a result, the energy management strategies that migratory animals employ when confronted with varying conditions have important conservation implications.

Many waterfowl acquire energy and nutrient reserves for migration and reproduction at spring migration stopover sites (Ankney and MacInnes 1978, Krapu 1981, Alisauskas and Ankney 1992, Gauthier et al. 2003, Reed et al. 2004, Schmutz et al. 2006) and spring migration conditions have important implications for waterfowl productivity. Energy intake and body mass often increase during the pre-breeding season, including spring staging and migration, presumably to meet the high costs of reproduction (Alisauskas and Ankney 1992). It is widely recognized that nutritional status of individuals upon arrival at breeding areas has important effects on reproductive performance, including timing of nesting, clutch size, re-nesting propensity, and growth and survival of young (Lack 1968, Reynolds 1972, Ankney and MacInnes 1978, Cooke et al. 1984, Toft et al. 1984, Rohwer 1992, Perrins 1996, Bêty et al. 2003, Drent et al.

2003). Habitat conditions and nutrient reserve levels during spring migration have been implicated as important factors affecting broad-scale and long-term population declines in lesser scaup (*Aythya affinis*) (Anteau and Afton 2004), indicating the potential demographic importance of spring migration habitats.

In addition to the reproductive implications of spring habitat conditions, body mass and energy intake tend to increase prior to migration, as many species accumulate fat reserves to be used as fuel during journeys over less suitable habitat (Biebach et al. 1986). Many migrating birds require stopover sites with sufficient resources for building or restoring reserves that will be used to fuel continued migration and/or reproduction. As a result, the route and timing of migration are not influenced solely by foraging conditions in start and end habitats (i.e., wintering and breeding) but also by habitat conditions along the route. Consequently, migration strategies are influenced by both the spatial and seasonal variability of food resources (Ottich and Dierschke 2003).

A variety of biotic and abiotic factors influence the distribution of a species, including the distribution and abundance of food resources (Womble et al. 2005). Animals modify their behaviour to utilize seasonally available energy pulses (Odum et al. 1995), and many animals depend on seasonally superabundant food for survival, reproduction, or fueling migration (Botton et al. 1994, Restani et al. 2000). Migrating herbivorous birds are speculated to strategically time migration phenology to take advantage of emergent spring growth of forage plants at stopover and staging sites (van der Graaf et al. 2006). This green wave hypothesis posits that birds travel along a climatic gradient while migrating from wintering areas to arctic breeding areas to follow the wave of emergent spring vegetation at higher latitudes (Owen 1980). In coastal ecosystems,

many avian species exhibit aggregative responses to ephemeral seasonal resource pulses such as Pacific herring (*Clupea pallasii*) and eulachon (*Thaleichthys pacificus*) spawning events, which provide important food resources (Haegele 1993, Marston et al. 2002, Sullivan et al. 2002, Rodway et al. 2003). The use of these ephemeral and energy-rich resources has been documented for both mammals and birds on local and regional scales (Marston et al. 2002, Rodway et al. 2003, Womble et al. 2005, Žydelis and Esler 2005), but have not been considered on a continental or migratory scale.

Scoters are sea ducks (Tribe Mergini) that winter along the Pacific coast from the Aleutian Islands southward into Mexico and breed throughout the northern boreal and southern taiga regions of Alaska and western Canada (Savard et al. 1998). In wintering areas, surf scoters (*Melanitta perspicillata*) feed primarily on bivalves, consuming mussels in rocky substrates and clams in soft-bottomed areas (Vermeer 1981, Iverson 2002, Lewis et al. 2005). White-winged scoters (*Melanitta fusca*) feed primarily on clams and are more closely associated with soft-bottomed areas (Lewis et al. 2005). Spring migration ecology is poorly documented for scoters, and little is known about the specific habitats and attributes that determine use of staging and stopover areas (Savard et al. 1998). Along the Pacific coast, scoters are known to congregate at herring spawn sites during late winter and early spring (Vermeer 1981, Vermeer et al. 1997, Sullivan et al. 2002), and it has been speculated that they proceed northward during migration in association with the northward progress of herring spawn (Vermeer 1981, Savard et al. 1998), but these observations are anecdotal and have not been quantified.

The general objective of this thesis was to gain a better understanding about habitat use by scoters during late winter and spring migration, with particular emphasis

on the use of herring spawn as an ephemeral resource. More specifically, the purpose of this thesis was to (1) evaluate how scoters move in response to the presence of herring spawn prior to spring migration, (2) identify important stopover sites for spring migrating surf scoters, and the habitat attributes of these sites, and (3) examine the site use by spring migrating surf scoters in relation to herring spawn activity at regional and migratory scales.

Surveys throughout the annual cycle have indicated continental declines in numbers of scoters (USFWS 1999, Nysewander et al. 2004) and the causes of these declines are uncertain. Considering the population implications of survival and reproduction, studies that document patterns of habitat use and energy acquisition by waterfowl may be used to identify critical stages and habitats in the annual cycle (LaGrange and Dinsmore 1988). The objectives addressed in this thesis will have direct implications for the identification of important coastal habitats, and the management of these areas.

1.2 Study Areas

On a local scale, we considered movements of pre-migratory scoters wintering in Baynes Sound, British Columbia. Baynes Sound is on the east coast of Vancouver Island, on the western side of the Strait of Georgia. It is a shallow coastal channel characterized by many protected bays, intertidal mud and sand flats, and low-gradient deltas. Baynes Sound is recognized as an Important Bird Area by Bird Studies Canada and Nature Canada, and is considered globally important due to the large number of over-wintering water birds. Surveys in the winters of 2002-2003 and 2003-2004 indicated a mean (\pm SE) of 6500 ± 250 surf scoters and white-winged scoters (Lewis et al. 2005) and a maximum

of 9000 scoters (Canadian Wildlife Service, unpublished data). Behavioural observations and scoter fecal samples indicate that the scoters here forage almost exclusively on clams in the soft-bottom beaches (Lewis et al. 2007).

On a regional and continental scale, we concentrated our studies of site use by migrating scoters in southeast Alaska. The coastal area of Southeast Alaska is extremely variable, from highly exposed west aspect shores of the Pacific Ocean to very sheltered fjords and tidewater glaciers along the protected inside passages. The southern part of southeast Alaska is characterized by extensive networks of islands and protected bays and channels, while the northern part of southeast Alaska is comprised of numerous long fjords and several large soft-bottomed river deltas.

1.3 Thesis Outline

The purpose of this thesis was to document site use by scoters in both late winter and during spring migration, with particular emphasis on the use of herring spawn. It is intended to be broad in geographic scope, addressing habitat use from local to continental scales.

Chapter 2 documents the movements and habitat use of pre-migratory surf scoters and white-winged scoters in relation to herring spawn events in the Strait of Georgia. Responses were evaluated on a local scale, emphasizing the movements and numerical responses of surf scoters and white-winged scoters to the presence of an ephemeral abundant food resource.

Chapter 3 identifies coastal sites in southeast Alaska with surf scoter aggregations during spring migration based on satellite telemetry. Important staging and stopover sites were identified for satellite tagged surf scoters from sites throughout their wintering

range (Baja California, Mexico; San Francisco Bay; Puget Sound; and the Strait of Georgia), with the intent of drawing inferences about migration habitat use strategies of Pacific surf scoters in general. In addition, the biotic and abiotic habitat attributes of identified sites were related to scoter use during spring migration. Chapter 4 documents the spatial and temporal availability of herring spawn along the Pacific coast and compares the migration strategies of spring migrating surf scoters to herring spawn availability at regional and migratory scales.

Although habitat use during spring has been documented in other sea duck species and recorded anecdotally, these issues have not been quantified specifically for surf scoters. In addition, no other study of sea ducks has monitored migration strategies and habitat use of marked individuals from a broad array of wintering areas. Habitat use by late spring-staging and migrating surf scoters may have important implications for understanding the cross-seasonal effects of habitat conditions and nutrient reserve levels on population dynamics, with subsequent habitat management implications. This study will contribute to general knowledge about spring migration strategies in surf scoters, by contributing to ongoing studies of body mass variation in relation to areas, seasons, and spawn occurrence. This suite of studies will provide an important link for understanding nutritional status and relationships between wintering, migrating, and breeding areas.

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CHAPTER 2 MOVEMENTS OF PRE-MIGRATORY SURF AND WHITE-WINGED SCOTERS IN RESPONSE TO PACIFIC HERRING SPAWN

This chapter has been accepted for publication as follows:

Lok, E. K., M. Kirk, D. Esler, and W. S. Boyd. In press. Movements of pre-migratory Surf and White-winged scoters in response to herring spawn in the Strait of Georgia, British Columbia. *Waterbirds*.

2.1 Abstract

We documented the movement and distribution patterns of wintering surf scoters (*Melanitta perspicillata*) and white-winged scoters (*Melanitta fusca*) in relation to herring spawn events in the Strait of Georgia, British Columbia. Radio-telemetry and surveys were conducted in Baynes Sound, an important wintering area where scoters feed primarily on clams. In early March, herring spawn events in areas adjacent to Baynes Sound provide a short-term pulse of abundant and easily accessible food, which we speculated could affect habitat use by wintering scoters from Baynes Sound. Radio-marked surf scoters and white-winged scoters exhibited limited movements during winter, in contrast to the spring herring spawn season, when both scoter species moved greater distances to access herring eggs. Most individuals were located near spawning locations at least once during the spawning season, and the majority of telemetry locations were close to spawning sites, with surf scoters showing a higher association with spawn for both metrics. A marked decrease (66-98%) in the abundance of both scoter species in Baynes Sound was observed coincident with spawn initiation in adjacent sites. We conclude that scoters altered their movement and habitat use patterns in spring to take advantage of herring roe, an energy-rich food source. This dramatic change in behaviour suggests that herring spawn may be of particular importance to these species.

2.2 Introduction

Many animals modify their habitat use to take advantage of seasonally available foods (Odum et al. 1995) that may enhance survival or reproduction, or fuel migration (Botton et al. 1994, Restani et al. 2000). In coastal ecosystems, mammals and birds are known to aggregate at seasonal resource pulses such as fish spawning events and consume both adult fish and eggs (Bishop and Green 2001, Marston et al. 2002, Sigler et al. 2004, Womble et al. 2005). The annual spawning of Pacific herring (*Clupea pallasii*) is a conspicuous example of a seasonal resource pulse for numerous avian predators. Although herring spawning locations are very localized (DFO 2007), herring eggs are abundant at spawn sites for several weeks during late winter and early spring. Scoters and other sea ducks are known to feed heavily on this resource when it is available (Haegele 1993, Vermeer et al. 1997, Sullivan et al. 2002, Rodway et al. 2003). The importance of herring spawn as a source of nutrients for migration and reproduction in sea ducks has been speculated (Rodway et al. 2003, Žydelis and Esler 2005), but this association has rarely been measured (Bond and Esler 2006).

To evaluate the importance of herring spawn to Pacific scoter populations, the distribution and movement patterns of individual surf scoters (*Melanitta perspicillata*) and white-winged scoters (*Melanitta fusca*) were documented during winter and spring. Although scoters are known to aggregate at spawn sites, the influence of herring spawn on distributions and individual movements of local wintering scoters has never been quantified. We predicted that if herring spawn is an important source of nutrients for scoters in late winter, we would observe: (1) movements to spawn beyond the normal winter foraging range of individuals, (2) a high proportion of individuals using spawn, (3)

a high use of spawn sites by marked individuals during the spawn period, and (4) changes in population distribution from winter to spawn seasons.

2.3 Study Area

The study was conducted in and around Baynes Sound, on the east coast of Vancouver Island (49.5° N, 124.8° W) (Figure 2.1). Baynes Sound is a wide, protected channel and the intertidal habitat is composed primarily of low-grade deltas and soft-bottomed tidal flats. The winter diet of scoters consists almost exclusively of clams (Bourne 1984, Lewis et al. 2007a). Annual herring spawn activity in the region generally starts in the first or second week of March. Although herring spawn events occur at a few locations within the Baynes Sound study area, most spawn events occur just outside of Baynes Sound at sites on the east coast of Denman Island, Hornby Island, and along the east coast of Vancouver Island south of Baynes Sound (DFO 2007).

The Department of Fisheries and Oceans (DFO) calculates a cumulative spawn habitat index (SHI) that represents the combined long-term frequency and magnitude of herring spawn events along each kilometer of coastline over time (DFO 2007). This measure of shoreline utilization by spawning herring is calculated as the product of the spawn shoreline length (m) and a spawn coefficient based on spawn width (m), number of egg layers, and percent cover, and is then pooled geographically. The total cumulative spawn habitat index for shoreline within the Baynes Sound study area is approximately one quarter of the spawn habitat index in the adjacent areas. Because herring spawn sites are generally located outside of the Baynes Sound wintering area and have a markedly higher frequency and magnitude of herring spawn activity, this study

area provides a good system for documenting the movement responses of wintering scoters to herring spawn.

2.4 Methods

2.4.1 Radio-telemetry

Surf scoters and white-winged scoters were captured in late fall during 2001-2003 using a modified floating mist-net system (Kaiser et al. 1995). Birds were banded and weighed, sex was determined by plumage characteristics (Iverson et al. 2003), and age class was estimated by bursal probing (Mather and Esler 1999). The birds were fitted with subcutaneous transmitters or implanted with internal coelomic VHF radios with external antennae following standard procedures (Mulcahy and Esler 1999). These radio types perform well for scoters with low mortality effects and good signal strength, accuracy, and retention (Iverson et al. 2006). Transmitters had an expected transmission period of up to 18 months. Over the three study years, radio transmitters were deployed on 116 surf scoters (2001 n=42, 2002 n=47, 2003 n=27) and 138 white-winged scoters (2001 n=56, 2002 n=34, 2003 n=48). Radio-marked scoters were tracked within Baynes Sound throughout the winter and spring. Each individual was located weekly or twice weekly when possible. At the beginning of herring spawn, the telemetry survey routes were expanded to include scoter concentrations along the east coast of Vancouver Island, Denman Island, and Hornby Island (Figure 2.2).

Fixes were obtained by determining the compass range of the null of a signal using a null/peak combiner (Kuechle 2005). Radio-telemetry was conducted by observers in two separate vehicles, each mounted with four-element Yagi antennae and programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN).

Simultaneous bearings were taken by the two observers to obtain bi-angulated locations. Error testing of the telemetry system indicated that observer bearings had a standard deviation of $\pm 4.2^\circ$ from the true bearing and a mean 90% error polygon of 0.07 km^2 ($\pm 0.004 \text{ SE}$). Given the size of the study area, these errors are relatively small and yield locations with adequate accuracy for analyzing movement and habitat use.

Telemetry bearings were processed using Location of a Signal (LOAS) software (ESS 2004). Biangulated locations were output from LOAS into ArcView 3.3 (Environmental Systems Research Institute 1999) to visually check for accuracy. The scoter location dataset was filtered to remove locations with non-intersecting bearings, locations that occurred significantly inland ($>100 \text{ m}$), and locations greater than 4 km from observers that may have been unreliable due to weak signal strength. The scoter location dataset was divided into winter and spawn seasons based on the date of spawn initiation for each study year (12 March 2002, 13 March 2003, 6 March 2004). Using the filtered dataset, all analyses of movement metrics were carried out in ArcView 3.3 using the Animal Movement extension (AME) (Hooge and Eichenlaub 1997).

2.4.2 Scoter distribution surveys

Surveys were conducted in Baynes Sound to evaluate seasonal variation in scoter abundance and distribution patterns. The study area (from Comox to Deep Bay) was divided into survey polygons approximately 1.5 km in length that extended 800 m from shore (Figure 2.1). Polygons were delineated according to habitat and anthropogenic characteristics of the environment. Counts were made using spotting scopes from one, two, or three observation points along the shore of each polygon. Surveys were conducted approximately biweekly from October to April during winters 2002-2003 and

2003-2004. Surveys were carried out only under good visibility conditions (i.e., surveys were suspended during fog, snow, heavy rain or winds exceeding 10 knots). Surveys were not conducted at herring spawn sites outside Baynes Sound.

2.5 Data Analyses

2.5.1 Movement metrics

The mean distance between consecutive locations, or interfix distance, was calculated using all locations for each individual using the “Location Statistics” function of AME (Kirk et al. 2008). Interfix distances during winter and spawn were calculated for any individual with three or more locations within a season (surf scoter n=66 winter, n=32 spawn; white-winged scoter n= 112 winter, n=51 spawn). We combined data across years based on the findings of Kirk et al. (2008) that winter movements within Baynes Sound were consistently small. In addition, this metric was calculated continuously for the winter and spawn seasons combined for individuals that had at least three locations in both winter and spawn seasons (surf scoter n= 28, white-winged scoter n= 48). The interseason distance, defined as the distance between the harmonic mean location (i.e., centre of activity) for each season (Smith et al. 1999), was calculated for individuals that had at least three locations in both winter and spawn seasons. The X and Y coordinates (easting and northing) of the harmonic mean location within each season were used to calculate the interseason distance (d) as:

$$d = [(X_{\text{winter}} - X_{\text{spawn}})^2 + (Y_{\text{winter}} - Y_{\text{spawn}})^2]^{1/2}$$

Least squares general linear models were used to evaluate variation in interfix distances in relation to season and individual attributes for both surf scoters and white-

winged scoters. An information theoretic approach to model selection (Burnham and Anderson 2002) was used to calculate Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for each model within a candidate set. The candidate model set used for each species separately consisted of the following models: season alone, individual (sex and age class) alone, season and individual additively, a season-individual interaction (season*sex*age), and a null model. The individual parameter always included both a sex variable (male or female) and an age variable (hatch-year or adult). The AIC_c value of each model was compared to that of the best-fitting model (ΔAIC_c) to assess the relative support for each candidate model. AIC_c weights, which indicate the relative support for each model within the candidate model set, were calculated. The statistical package SAS (SAS Institute 2003) was used to run general linear models.

2.5.2 Habitat use metrics

To estimate the fraction of scoters using spawn, the proportion of marked individuals present during the spawn season that were located at least once within specified distances of known herring spawn sites was determined. Shapefiles of spawn presence in the study area for 2002, 2003, and 2004 were obtained from the Department of Fisheries and Oceans, and buffers of 1 km and 2 km around these themes were created in ArcView 3.3. Scoter locations were selected and classified in relation to known spawn sites (≤ 1 km, ≤ 2 km, > 2 km) for each year.

The proportion of an individual's total number of locations during the spawn season that were within the vicinity of spawn using 1 km and 2 km buffers was determined to calculate an index of spawn use by individual scoters. Spawn use was

calculated for all individuals with three or more locations within the spawn season (surf scoter n= 32, white-winged scoter n=51).

Constancy metrics were calculated for marked scoters wintering in Baynes Sound to estimate the likelihood of movement to alternate habitats during winter, in contrast to measures of movement to herring spawn sites. A high constancy rate indicates a constant presence within the Baynes Sound study area. Individuals confirmed as either mortalities or radio-failures were excluded. The status (present or not detected) of each individual within the study area was determined for each week throughout the winter period (surf scoters n=60, white-winged scoters n=100). The fraction of marked individuals that were: (1) present in Baynes Sound every week, (2) not detected for one week only, or (3) not detected for two weeks or more were calculated. To calculate a mean constancy rate for each species, the proportion of “present” locations for each individual throughout the winter period was determined. To estimate the fraction of scoters that may have migrated from the study area (including Baynes Sound and spawning areas) entirely rather than moving to spawn sites, the fraction of individuals not located at any time during the spawn period was determined.

2.5.3 Numerical response

To evaluate seasonal variation in overall scoter numbers within the study area, the total number of surf scoters and white-winged scoters in all survey polygons for each survey for each winter and species was calculated separately. To infer the degree of movement away from Baynes Sound, and presumably to herring spawn sites, the percent change in scoter numbers between surveys immediately preceding and then immediately following spawn initiation was calculated.

2.6 Results

2.6.1 Movement response

Variation in interfix distance was strongly related to season; the season alone model received an AIC_c weight of 0.87 for both species (Table 2.1). There was little evidence that interfix distance varied by age or sex for either species. Both surf scoters and white-winged scoters moved much longer distances between consecutive observations during spawn than during winter (Table 2.2). Spawn season mean interfix distances were nearly 10 times greater than winter distances for surf scoters and more than 3 times greater for white-winged scoters. When interfix distances were calculated continuously for winter and spawn periods, both surf scoters and white-winged scoters showed a marked increase in interfix distances at the initiation of spawn (Figure 2.3), with several individuals from both species exhibiting increased movements just prior to spawn initiation. The difference between winter and spawn harmonic mean locations also differed by species, with surf scoters moving longer distances between seasons than white-winged scoters (Table 2.2). On average surf scoters moved more than 17 km, and white-winged scoters moved more than 10 km away from winter foraging sites to spawn locations. Therefore, the interseasonal movements of scoters (winter to spawn) were up to 10 times greater in distance than average winter movements.

2.6.2 Habitat use

The majority of individuals (78-91%) of both species were located close to spawn at least once during the spawn period, although surf scoters showed a slightly higher proportional use of spawn than white-winged scoters (Table 2.3). The proportion of individual locations within the vicinity of spawn differed by species; the mean individual

spawn use by surf scoters ($73 \pm 5\%$ of locations within 1 km, $82 \pm 4\%$ within 2 km) was higher than that of white-winged scoters ($53 \pm 4\%$ within 1 km, $60 \pm 4\%$ within 2 km).

Most individuals of both species were present in Baynes Sound every week (63% for both species), or not detected once (13% for both species) during winter (Table 4). The mean constancy rates were high for both surf scoters ($90 \pm 2\%$) and white-winged scoters ($92 \pm 2\%$). Only a small fraction of surf scoters (13%) and white-winged scoters (12%) were undetected during the spawn period, and it is unknown whether they moved beyond the monitoring area or the radios failed.

2.6.3 Numerical response

Survey totals of surf scoters and white-winged scoters within Baynes Sound showed generally high winter abundance followed by a decrease in numbers in spring (Figure 2.4). Herring spawn was first observed on 13 March 2003 and 6 March 2004 (DFO 2007). The abundance of surf scoters and white-winged scoters within Baynes Sound decreased markedly between the surveys just prior to and just following the initiation of spawn; surf scoter abundance decreased by 66% in 2002 and by 86% in 2003, while white-winged scoters decreased 78% in 2002 and 98% in 2003.

2.7 Discussion

Numerical and movement responses of both surf scoters and white-winged scoters were strongly related to the seasonal availability of abundant herring roe at spawn sites located near their wintering area. Both scoter species are abundant in Baynes Sound and show limited movements during the winter period. In comparison, both species moved greater distances during the spawn season, with surf scoters moving greater distances

than white-winged scoters. Some scoters exhibited increased movements just before spawn initiation, which may indicate that some individuals actively search for herring spawn during the spring. The increase in movement distance during the spawn period was interpreted as evidence of the long distance movements required to reach comparatively distant spawn sites, rather than increased movement while foraging within a spawn site. Sex and age classes were not important determinants of movements for either species, while the seasonal presence of herring spawn was the best-supported explanation for both scoter species.

In general, both scoter species showed a marked decrease in abundance in Baynes Sound following spawn initiation and this decrease in abundance was interpreted as the redistribution of wintering scoters to spawning areas adjacent to Baynes Sound. High constancy of use for both scoter species indicates that scoters wintering in Baynes Sound generally do not use the areas where herring spawn occurred in spring, and few scoters left the study area entirely during the spawn season. Although surveys were not conducted outside of Baynes Sound for this study, similar surveys in the region show that the decrease in scoter numbers in Baynes Sound is coincident with dramatic increases in scoter abundance at spawn sites along the east coast of Vancouver Island (Sullivan et al. 2002, CWS unpublished data). Telemetry surveys indicate that many of these large aggregations of scoters (> 20 000 scoters) at spawn sites are composed of not only redistributing local wintering scoters, but also migrant scoters arriving from wintering areas further south (CWS, unpublished data).

Surf scoters showed a stronger proportional response to spawn than white-winged scoters, with a greater fraction of the marked population located near spawn, and

individuals located proportionally more often close to spawn. Surf scoters also moved farther from winter foraging grounds than white-winged scoters to visit spawning sites. Because these species generally have high winter constancy rates and small winter home ranges (Kirk et al. 2008), these relocations to spawn events are clear evidence of a seasonal shift in movement patterns and habitat use.

Scoters in Baynes Sound feed primarily on clams during winter (Bourne 1984, Lewis et al. 2007a) and switch from their typical winter diet to a presumably more profitable food resource when it becomes available. Herring eggs are an easily accessible, high-energy, lipid-rich food item (Paul and Paul 1999) and may be used to build energy reserves prior to spring migration and reproduction (Bishop and Green 2001, Bond and Esler 2006, Willson and Womble 2006). Similarly, the lack of shell and small size of eggs presumably reduces handling time and digestion costs in comparison to bivalves (Speakman 1987, de Leeuw and van Eerden 1992, van Gills et al. 2003). The benefits of herring spawn events may range beyond direct nutritional value; scoters in Baynes Sound spent 50% less time foraging and decreased their dive rate when feeding on herring eggs (Lewis et al. 2007b). Further, herring spawn may allow for increases in non-foraging behaviours due to reduced feeding time (Rodway and Cooke 2001, Rodway et al. 2003, Žydelis and Esler 2005). Rodway et al. (2003) suggested that aggregating at herring spawn sites may provide opportunity for social interactions for harlequin ducks (*Histrionicus histrionicus*) and this may be true for other gregarious sea duck species.

Harlequin ducks and Steller's eiders (*Polysticta stelleri*) modify their movements and food habits to use herring spawn (Rodway et al. 2003, Žydelis and Esler 2005). Although the aggregation of scoters at Pacific herring spawn sites is well documented

(Haegele 1993, Vermeer et al. 1997, Bishop and Green 2001, Sullivan et al. 2002), this is the only study that has quantified movement responses of individual scoters using radio-telemetry. The high fraction of both surf scoters and white-winged scoters located close to herring spawn sites and the greater distances moved during this time period suggest that herring spawn may be an important food resource for scoters in late winter. Vermeer et al. (1997) speculated that the fraction of a population using herring spawn sites may indicate the dependence of that population on spawn for acquiring energy. Surf scoters exhibited higher use of spawn sites and greater movement distances than white-winged scoters, indicating that herring spawn may be more important for this species. Compared to white-winged scoters, surf scoters appear to lose more body mass over winter (Anderson and Lovvorn 2008, E.M. Anderson, unpublished data), and are limited to smaller sizes of bivalves (E.M. Anderson, unpublished data). Consequently, the depletion of bivalve prey may limit the ability of surf scoters to meet energy requirements more than that of white-winged scoters. Species that deplete winter foods, such as surf scoters (Lacroix 2001, Kirk et al. 2007) may be more likely to rely on herring spawn for building energy reserves in late winter and early spring (Bond and Esler 2006), and those species that aggregate at herring spawn may depend on this resource for breeding in less resource rich areas (Žydelis and Esler 2005).

Late winter and spring migration habitat conditions are known to have important implications for waterfowl productivity. Energy intake and body mass often increase during the pre-breeding season, as an energy management strategy to help meet high costs of reproduction and migration (Alisauskas and Ankney 1992). The effects of habitat conditions and nutrient reserve levels during the pre-breeding season carry over to

subsequent stages of the annual cycle, and can influence variation in survival and reproductive success (Alisauskas and Ankney 1992, Anteau and Afton 2004, Reed et al. 2004).

Scoter populations have experienced numerical declines on both continental and regional scales (Goudie et al. 1994, Nysewander et al. 2004) and the causes for these declines are not known. Scoters are long-lived and have low reproductive outputs (Krementz et al. 1997) and these life history traits make them particularly sensitive to changes in the quantity and/or quality of their non-breeding habitats (Goudie et al. 1994, Esler et al. 2002). Variation in critical non-breeding habitat such as areas supporting herring spawn may have significant conservation implications. The Strait of Georgia herring stock is currently in reasonably good condition and consistently ranks highly for biomass within the province (DFO 2007), and is heavily used by many marine bird species. However, other traditional spawn sites in the Strait of Georgia have declined in numbers and shifted in distribution; birds are increasingly restricted to fewer spawn sites. In addition, herring stocks in nearby regions such as northern Puget Sound and the Strait of Juan de Fuca have experienced dramatic declines and the implications for the marine ecosystem are unclear (Stick 2005). Understanding the cross-seasonal links between the use of herring spawn during late winter and the energy requirements for migration and reproduction is critical for management and conservation of scoter populations, as well as other species that use herring spawn.

2.8 Acknowledgements

Funding and support for this project was provided by the Canadian Wildlife Service of Environment Canada and National Science and Engineering Council (NSERC)

strategic grant STPGP246079-01. We thank the Centre for Wildlife Ecology for providing scientific and logistic support. M. McAdie and D. Mulcahy performed the radio-transmitter implant surgeries. E. Anderson, B. Bartzen, T. Bowman, S. Coulter, R. Dickson, G. Grigg, S. Iverson, D. Lacroix, R. Lis, A. McLean, E. Sellentin, S. Wallace, and R. Žydelis helped capture scoters and provided field assistance. We thank all private landowners and shellfish farmers within Baynes Sound who granted us access to their properties during winter fieldwork. We thank K. Daniel and B. McCarter of DFO for assistance with the herring spawn data.

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Table 2.1 Summary of AIC results from general linear models assessing variation in mean interfix distance (km) for surf scoters and white-winged scoters during two seasons (winter and spawn) in Baynes Sound, BC. Individual (Indiv) models include sex and age as variables. Number of parameters includes +1 for intercept and +1 for model variance. Candidate models are listed by ΔAIC_c .

Model	Number of parameters	Surf Scoter			White-winged Scoter		
		ΔAIC_c	AIC_c	R^2	ΔAIC_c	AIC_c	R^2
Season	3	0.00	0.87	0.44	0.00	0.87	0.24
Season + Indiv	6	3.93	0.12	0.46	4.03	0.12	0.25
Season*Indiv	9	8.84	0.01	0.47	7.67	0.02	0.27
Null	2	54.87	0.00	0.00	43.27	0.00	0.00
Indiv	5	60.34	0.00	0.01	46.84	0.00	0.02

Table 2.2 Summary of movement metrics of surf scoters and white-winged scoters in Baynes Sound, British Columbia. Means are reported \pm SE.

Movement Metric		Surf scoter		White-winged scoter	
		Winter	Spawn	Winter	Spawn
Interfix distance (km)	mean	1.2 \pm 0.6	9.9 \pm 0.8	1.8 \pm 0.4	6.3 \pm 0.5
	range	0.2 - 12.6	1.2 - 31.2	0.2 - 18.1	0.5 - 36.7
	N	66	32	112	51
Interseason distance (km)	mean	17.7 \pm 1.9		10.4 \pm 1.6	
	range	0.3 - 33.8		0.3 - 42.3	
	N	28		48	

Table 2.3 Fraction of radio-marked surf scoters and white-winged scoters located close to active herring spawn sites in the Strait of Georgia, British Columbia, March and April 2002-2004.

Fraction of individuals (%)	N	Surf scoter			White-winged scoter		
		total	male	female	total	male	female
		57	41	16	87	50	37
Within 1 km of spawn		88	85	94	78	74	84
Within 2 km of spawn		91	88	100	81	78	84

Table 2.4 Fractions of radio-marked surf scoters (n = 60) and white-winged scoters (n = 100) located during the winter in Baynes Sound, British Columbia. Winter was defined as the time from capture (December) to the date of herring spawn initiation each spring (March).

Fraction of individuals (%)	Surf Scoter	White-winged Scoter
Present every week	63	63
Not detected 1 week	13	13
Not detected \geq 2 weeks	24	24

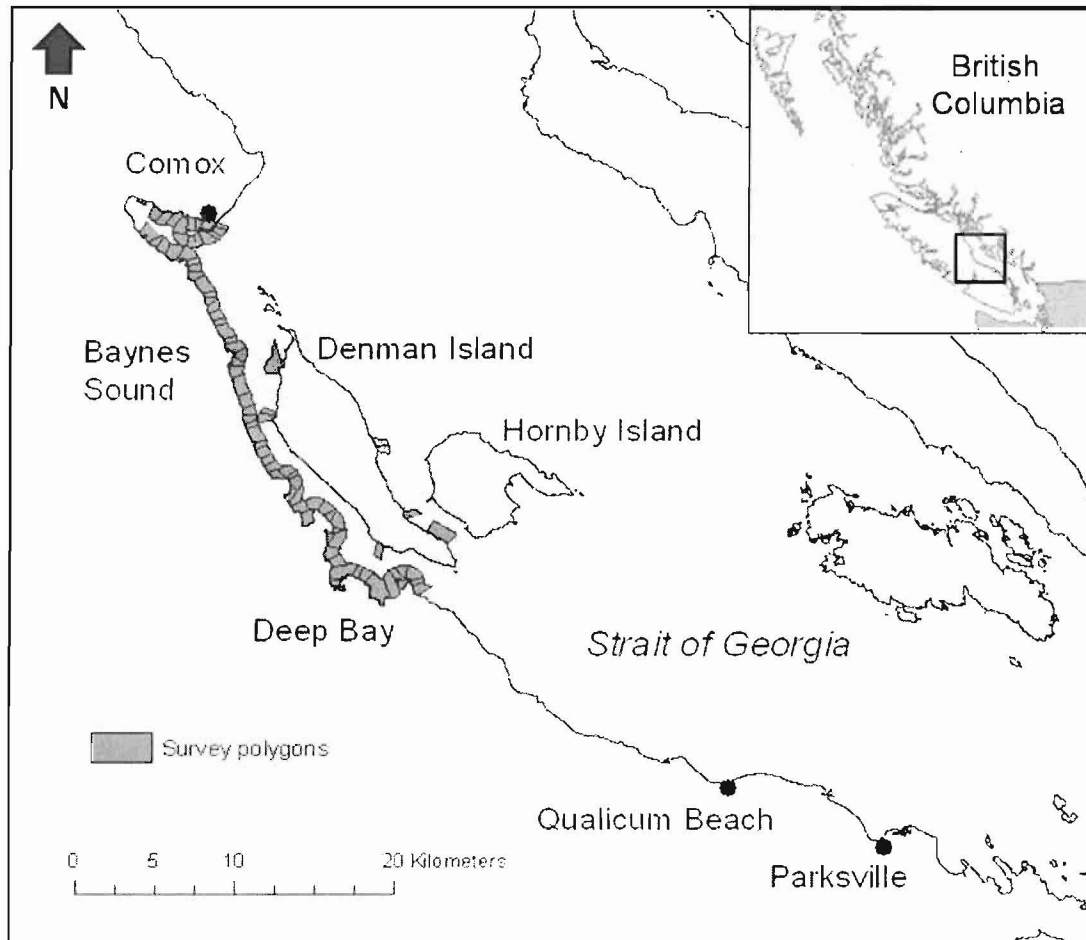


Figure 2.1 Baynes Sound study area and adjacent areas in the Strait of Georgia, British Columbia. Survey polygons are shaded to show the extent of the winter study area.

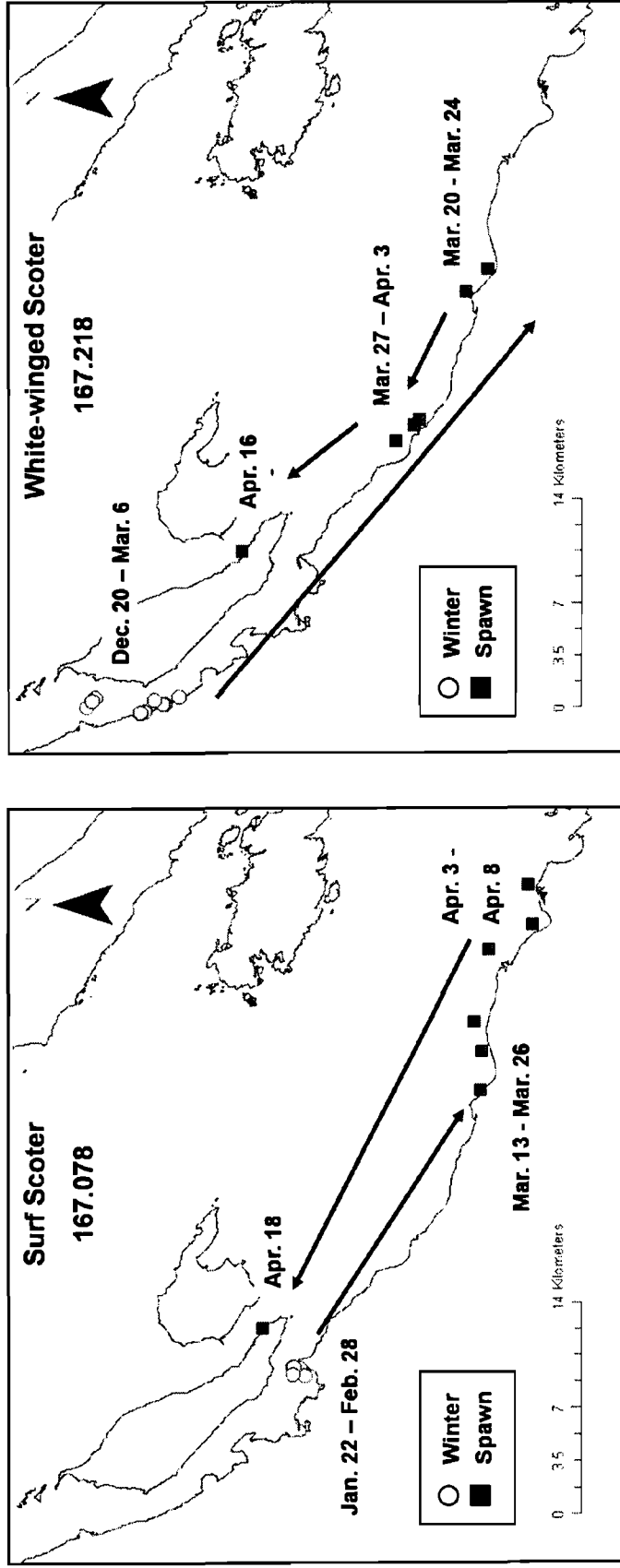


Figure 2.2 Examples of radio-telemetry locations and movements of representative surf scoter and white-winged scoter individuals during winter and spring in the Strait of Georgia, British Columbia, December – April 2003. Herring spawning started on 13 March 2003. Note that telemetry surveys were not conducted outside of the Baynes Sound study area during winter.

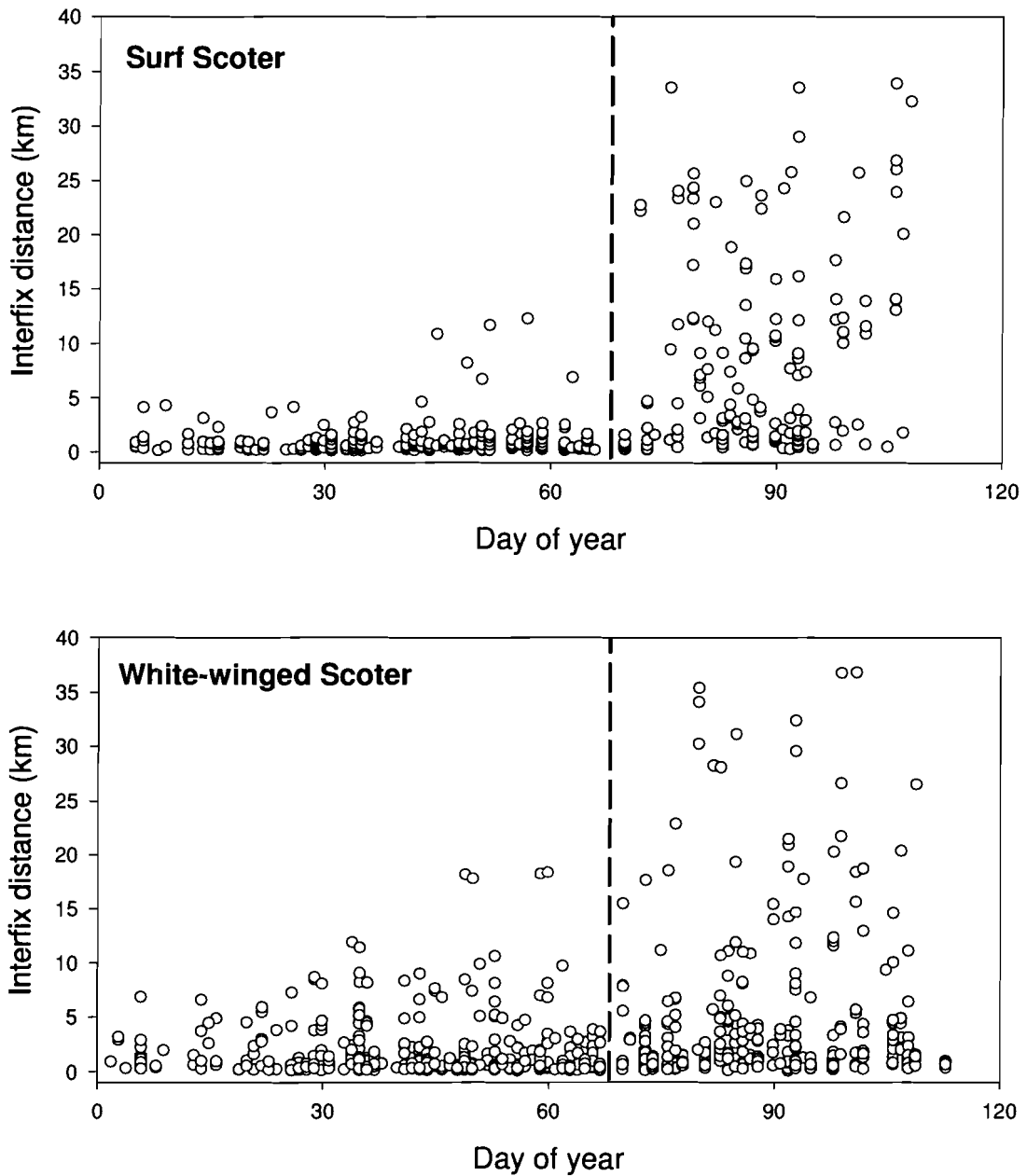


Figure 2.3 Interfix distances of all locations of surf scoters (28 individuals) and white-winged scoters (48 individuals) from January through April in 2002-2004, in the Strait of Georgia, British Columbia. The vertical dashed lines indicate the mean date of spawn initiation (day of year = 70) for the study years.

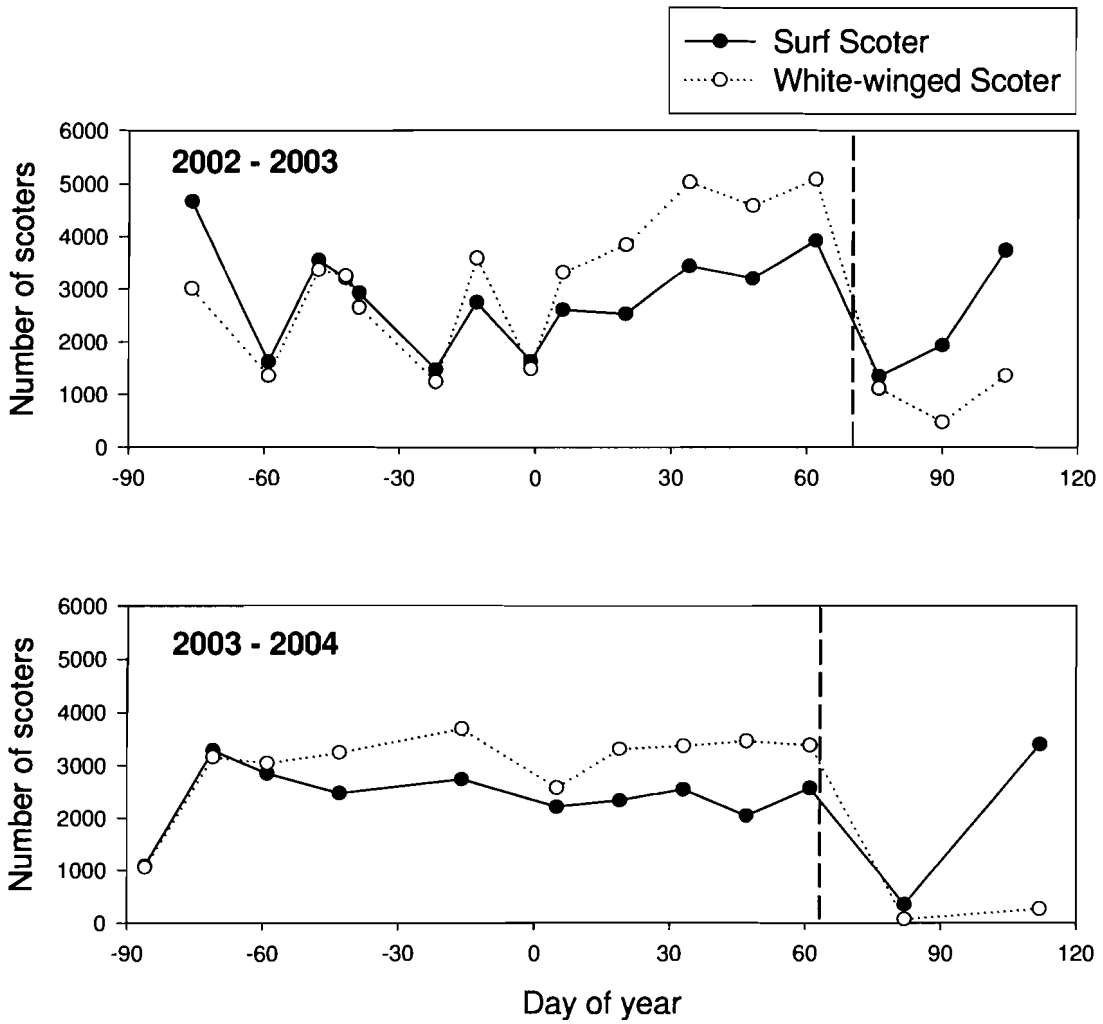


Figure 2.4 Abundance of surf scoters and white-winged scoters in Baynes Sound for surveys from October to April in 2002-2003 and 2003-2004. The vertical dashed line indicates the date of spawn initiation each year.

**CHAPTER 3 STOPOVER HABITATS OF SPRING
MIGRATING SURF SCOTERS IN SOUTHEAST
ALASKA**

3.1 Abstract

We used satellite telemetry to identify important stopover sites used by surf scoters migrating through southeast Alaska during spring. We then contrasted the habitat features of these sites to those of random sites to determine habitat attributes corresponding to use by migrating scoters. We identified 14 important stopover sites based on the use of satellite tagged surf scoters. Lynn Canal was identified as being an exceptionally important stopover site for surf scoters originating throughout the Pacific winter range; approximately half of the coastally-migrating surf scoters used this site, many for extended periods. The habitat attributes of important stopover sites were farther from the outer coast and closer to herring spawn sites than random sites, while physical shoreline attributes were generally poor predictors of site use. We conclude that the geography and resource availability within southeast Alaska provides unique and potentially critical stopover habitat for spring migrating surf scoters. Our work defines specific sites that deserve conservation consideration, as well as insights into the underlying mechanisms that make these habitats important.

3.2 Introduction

Many migratory birds acquire energy and nutrient reserves at spring stopover sites, and the availability and quality of resources at these sites may have implications for success during subsequent stages of the annual cycle (Ankney and MacInnes 1978, Alisauskas and Ankney 1992, Warnock and Bishop 1998, Smith and Moore 2003, Morrison and Hobson 2004). Several studies have described cross-seasonal effects of spring habitats on reproductive performance by migratory waterfowl (Lovvorn et al. 2003, Reed et al. 2004, Schmutz et al. 2006). Because spring stopover sites provide the energy and nutrients required for reproduction, it follows that population dynamics may be influenced by habitat quality at these sites.

Recent reviews and commentaries have highlighted the need for research addressing habitat use and resource availability along migration routes (Webster et al. 2002, Mehlman et al. 2005, Arzel et al. 2006, Drent et al. 2006). This requires identification of key sites used during spring migration, as well as an understanding of the habitat features that make these sites attractive to migrants. The importance of stopover sites has been defined by a number of criteria, often including the duration of stay (e.g., a brief stopover compared to longer term staging) or the relative value of a site for energy acquisition (Skagen and Knopf 1994, Farmer and Parent 1997, Warnock and Bishop 1998).

Little is known about the specific stopover sites used by surf scoters (*Melanitta perspicillata*) during spring migration along the Pacific coast. Identification of discrete areas used during spring migration has been previously limited by the large geographic

scale involved, the remoteness of areas used, the continuous nature of potential stopover habitat along the Pacific coast, and the lack of information about scoter distributions at this time of year. Habitat conditions and nutrient reserve levels during spring migration have been suggested as important factors affecting broad-scale and long-term population declines in other waterfowl (Anteau and Afton 2004). Scoter populations have been declining continent-wide (USFWS 1999, Nysewander et al. 2004) and this phenomenon could be similarly related to changes in spring stopover habitats. Hence, identification of key stopover sites and their associated habitat attributes are important for population management.

Satellite telemetry provides a useful and relatively unbiased tool for describing migration routes and identifying stopover sites over a large geographic range. We used satellite telemetry to track surf scoters using spring stopover sites in southeast Alaska. To identify potentially important stopover sites we considered migrant use, based on relative abundance and the frequency and consistency of use as a stopover site (Mehlman et al. 2005). In considering the habitat attributes that make these sites important, we considered intrinsic characteristics such as resource availability as well as geographical context, such as proximity to ecological barriers (Mehlman et al. 2005).

3.3 Study Area

The wintering range of surf scoters along the Pacific coast extends from Alaska to Baja California, Mexico (Savard et al. 1998). We compiled information from studies of surf scoters captured and marked at wintering areas throughout this range. These wintering areas included San Quintin Bay, Baja California, Mexico (116.0°W, 30.4°N); San Francisco Bay, California, USA (122.4°W, 37.8°N); Puget Sound, Washington, USA

(122.4°W, 47.5°N); and the Strait of Georgia, British Columbia, Canada (122.4°W, 49.3°N). In the spring, surf scoters migrate along the Pacific coast from these wintering areas to northern breeding areas throughout the inland boreal forest of western Canada and Alaska (Savard et al. 1998).

We considered all of southeast Alaska as our study area and examined stopover site use within this region (Figure 3.1). Southeast Alaska is comprised of a large, complex archipelago adjacent to a mountainous mainland. These landforms create an extensive network of protected waterways and nearshore marine areas that provide a wide variety of habitat types, and the region is a major migration route for many bird species in the Pacific Flyway.

3.4 Methods

3.4.1 Capture and marking

We captured surf scoters on their wintering grounds between November and March, 2002-2006, using a floating mistnet (Kaiser et al. 1995, Lewis et al. 2005), or a netgun (Mechlin and Shaiffer 1980). Birds were banded, weighed, and implanted with coelomic platform-transmitter-terminal (PTT) satellite-transmitters following standard procedures (Mulcahy and Esler 1999) (Table 3.1). This transmitter implantation method has been shown to perform well for scoters relative to other attachment methods (Iverson et al. 2006). The marked birds were released after a recovery period of at least 1 hour. PTT transmitters were programmed with duty cycles to transmit location data for 6-8 h and turn off for 48-96 h.

3.4.2 Location data

Satellite transmitter locations were obtained from the Argos data system, which estimated positions by calculating the Doppler-effect shift with receivers on National Oceanic and Atmospheric Administration (NOAA) weather satellites. We compiled the location data from all PTT-marked surf scoters and filtered the data spatially and temporally to select only coastal spring migration locations (Figure 3.1). PTT locations were classified by estimated accuracy and number of signals. For Location Classes (LC) 3, 2, 1, and 0, in which ≥ 4 messages are received by the satellite, Argos rates accuracy as <150 , 150-350, 350-1000, and >1000 m, respectively. Accuracy is not provided for LC A (3 messages), B (2 messages), and Z (latitude/longitude often provided if >1 message received). Location data usually included more than one useable location per bird in a transmission day; a single “Selected Location” for each bird per transmission day was chosen according to the criteria described in Miller et al. (2005), which favor locations with LC 3, 2 and 1, but recognize that accurate locations are obtained for a large proportion of detections within all Argos location quality classes. Although less conservative than filtering locations of lower location quality classes, this method allowed us to maximize the number of Selected Locations during the short migration period, and 91% of the Selected Locations were of LC 1 or higher.

3.4.3 Habitat data

We assembled Geographic Information System (GIS) data from existing data sources on shoreline habitat features of southeast Alaska that we considered to be potentially important predictors of surf scoter stopover habitat use. We assumed that the use of stopover sites was related to the habitat attributes of those sites, and that habitat

characteristics of used sites are related to habitat quality and profitability. In this habitat analysis, we used shoreline habitat attributes to represent environmental variables related to general resource availability throughout southeast Alaska. In addition to resource availability, we considered ecological context, such as the proximity to natural breaks and migration routes (Mehlman et al. 2005).

Habitat use by surf scoters during winter is well documented and strongly related to shoreline characteristics and associated bivalve prey distribution and densities (Žydelis et al. 2006). Shoreline habitat data were obtained from a shoreline ecosystem database compiled by Audubon Alaska and The Nature Conservancy (Albert and Schoen 2007). This dataset characterizes shoreline habitat within southeast Alaska using information from multiple sources, and integrates information about the physical characteristics, wave exposure, and bathymetry of the study area shoreline (Albert and Schoen 2007). The physical characteristics summarized for each shoreline segment included the maximum depth within 1 km of shore (depth), shoreline segment length (length), the maximum shoreline width between high tide and low tide (width), dominant substrate type (substrate), and an exposure index (exposure). Substrate was divided into 12 categories, including rocky shore/cliff, rock platform, rock with gravel beach, rock with sand and gravel, rock with sand beach, gravel beach, sand and gravel beach, sand and gravel flat, sand beach, tide flat, salt marsh, and no data. We considered the five categories containing rock as “rocky substrate” for our analyses. The exposure index is an estimate of wave energy based on the total area visible over water from each shoreline segment and increases with increased wave energy and exposure (Albert and Schoen 2007). In addition, we used this dataset to create a data layer representing the distance to the outer

coast of southeast Alaska by selecting the westernmost shoreline segments within the study area. This data layer was created to evaluate site use as a function of distance to the outer coast.

The presence of streams may influence prey distribution and provide fresh water for birds feeding on marine invertebrates (Nystrom and Pehrsson 1988). We obtained information on stream distribution within southeast Alaska from the USGS Hydrographic Dataset and created a layer that included only streams that intersect with the ocean.

During late winter and early spring, Pacific herring (*Clupea pallasii*) spawn along localized sections of shoreline within southeast Alaska. Surf scoters are known to aggregate at herring spawning sites and forage on abundant and energy-rich eggs (Haegele 1993, Vermeer et al. 1997, Bishop and Green 2001, Sullivan et al. 2002, Rodway et al. 2003), but its influence on stopover site use during spring migration has not previously been quantified. To evaluate site use as a function of distance to herring spawn sites, we compiled the distribution of major herring spawn locations in 2003-2006 from the Alaska Department of Fish and Game. The spawn distributions in all four years were combined into a single layer representing herring spawn distribution within all study years.

3.5 Data Analyses

3.5.1 Identification of important stopover sites

We used ArcGIS 9.1 (Environmental Systems Research Institute 2005) to analyze Selected Locations to determine migration stops on 1:250 000 digital charts. We defined a stopover event as the act of an individual stopping at a site for rest or refueling during migration. Spatially, stopover events were defined as a series of at least two consecutive

Selected Locations within 22 km of each other. This distance was based on the 95th percentile of mean distances between sequential locations for radio-marked surf scoters in late winter (Lok et al. In press), and was interpreted as a reasonable non-migratory movement distance within a site. To consider temporal use of sites, we subclassified stopover events as short stopovers if the site was used for 2-7 days and as staging stopovers if the site was used for >7 days (Warnock and Bishop 1998).

For each stopover event, we delineated an area of use for each individual by creating either a minimum convex polygon (≥ 3 locations) or a line (2 locations). The centroid of each area of use was calculated using the XTools Pro Extension for ArcGIS 9.1 (Data East 2007). Important stopover sites were defined as sites where the centroids of the areas of use of at least two individuals were within 5 km of each other. A 5 km distance was chosen to account for variation in PTT location accuracy and to encompass the areas of use of at least two individuals. Given the limited number of satellite-tagged individuals, we considered use by two individuals adequate to represent the selection and use of a specific site. A centroid of each important stopover site was calculated from the individual centroids of all areas of use within the 5 km radius.

3.5.2 Habitat attributes of important stopover sites

To identify habitat features associated with important stopover sites, we contrasted habitat attributes of 13 identified important sites with those of a set of 50 sites randomly distributed throughout the study area. A 5 km radius was selected to be large enough to encompass the locations of at least two individuals and the associated shoreline habitat, while being small enough identify a discrete area and minimize the overlapping of sites. Random plot centroids were created along the shoreline using the random

sampling tool in Hawth's Analysis Tools (Beyer 2004). Important stopover site centroids were fixed related to the shoreline using the snap to line tool. We created 5 km radius plots around both important stopover sites and random sites using the Buffer Wizard in ArcGIS 9.1. We then intersected GIS habitat layers with the plots and summarized the following shoreline characteristics for each plot: length, depth, width, exposure, percent rocky substrate, distance to outer coast, and distance to herring spawn. The mean weighted depth, width, and exposure were calculated by weighting each shoreline segment value by the length of the segment and dividing the sum of weighted segments by the total plot shoreline length. The percent rocky substrate within each plot was determined by calculating the length of all segments with a rocky substrate and dividing by the total shoreline length within the plot. We calculated the number of stream outlets within each plot. The distance to outer coast and distance to herring spawn were determined as the minimum distance from the centre of each plot to the outer coast or herring spawn layers, respectively.

We used logistic regression models to evaluate the use of stopover sites in relation to habitat characteristics in SAS (SAS Institute 2003). We examined the data for overdispersion, by calculating a variance inflation factor for the global model, but found that this was not a concern ($\hat{c} = 0.32$). We used an information theoretic approach to model selection (Burnham and Anderson 2002) and calculated Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for each model within a candidate set. For some models, we grouped physical shoreline characteristics into a "shoreline" suite of predictor variables, which included length, depth, width, exposure, streams and substrate. The candidate model set consisted of 14 models: (1) length (2) depth (3) width

(4) exposure (5) streams (6) rocky substrate (7) shoreline (8) coast (9) spawn (10) coast + spawn (11) coast + shoreline (12) spawn + shoreline (13) coast + spawn + shoreline and (14) a null model. We wanted to consider the relative effects of shoreline features individually, and to contrast the importance of physical shoreline features of used sites with food resource features (distance to spawn) and geographic features (distance to outer coast), in addition to considering additive combinations of physical attributes, resource availability, and geography. We compared the AIC_c value of each model to that of the best-fitting model (ΔAIC_c) to assess the relative support for each candidate model. We also calculated AIC_c weights (w_i), which indicate the relative support for each model within the candidate model set.

3.6 Results

3.6.1 Identification of important stopover sites

We documented a total of 72 stopover events for 37 individual satellite-marked birds in southeast Alaska (Figure 3.1). We identified 14 important stopover sites within southeast Alaska (Figure 3.2), which were used by 35 individual satellite-marked scoters in 62 stopover events (Table 3.2). Only 14% of the individual stopover events were not located within an identified important site, and the majority (95%) of all marked surf scoters visited at least one of these sites during spring migration. Important stopover sites were identified at Lynn Canal, Berners Bay, Eagle Harbor, Stephens Passage, Gastineau Channel, Young Bay, Tracy Arm, Seymour Canal, Hobart Bay, Eastern Passage, Vixen Inlet, West Behm Canal, Klawock Inlet, and Annette Island (Figure 3.2). We identified the area of Lynn Canal, including Chilkat Inlet, Chilkoot Inlet, and Taiya Inlet, as a single important stopover and staging site although it did not strictly meet our criteria.

We were unable to identify a distinct 5 km radius circumscribing this important stopover site due to the very high number of overlapping areas of use (22 stopover events, 17 individuals) and instead considered the entire area a single important site. Because of the unique nature of this area, and the inability to define it as a discrete stopover site, we did not include it in the habitat analysis.

Temporally, stopovers events were identified as 35 short stopover events (27 individuals) and 37 staging stopover events (32 individuals) (Table 3.2). Approximately half (49%; $n=37$) of the marked surf scoters in this study made staging stopovers within southeast Alaska. The majority of individuals (54%) both stopped (2-7 days) and staged (> 7 days) at least once in southeast Alaska, while 19% only stopped and 27% only staged. Most of the identified important sites were used in at least two years, and three of the sites were used in at least three study years (Table 3.2).

3.6.2 Habitat attributes of important stopover sites

Stopover site use was strongly related to small distances from herring spawn and to greater distance from the outer coast. Within the candidate model set, the coast + spawn model best explained stop site use ($w_i= 0.97$), with no other model receiving strong support (Table 3.3). Models with the highest ΔAIC_c values included distance to coast and distance to spawn parameters. This suggests that the distance from the outer coast and distance from herring spawn provided the best explanation of the variation between stopover and random sites.

Important stopover sites were located an average of less than 10 km away from spawn sites while random sites were located more than 50 km away (Table 3.4). Eight of the identified important stopover sites (Berners Bay, Young Bay, Seymour Canal, Hobart

Bay, Vixen Inlet, West Behm Canal, Klawock Inlet, and Annette Island) have well documented herring spawn activity in recent history. On average, important stopover sites were located approximately twice as far away from the outer coast as random sites. Stopover sites also tended to contain fewer streams and to be more exposed than random sites, although these parameters contributed far less to model fit than herring spawn and distance to outer coast.

3.7 Discussion

We identified 14 important stopover sites for spring migrating surf scoters in southeast Alaska. The majority of the marked surf scoters in this study made multiple stopovers within southeast Alaska, indicating that this region is heavily used and likely important for migrating scoters. Most marked individuals stopped at identified important stopover sites, and a single site, Lynn Canal, was used for stopovers by approximately half of the marked surf scoters from throughout the Pacific wintering range. Most of the identified important stopover sites were used in at least two years, indicating reasonably consistent use between years, which suggests that specific sites are used for stopovers. We are confident that the migration patterns of the marked scoters are indicative of stopover site use by surf scoters in general, given the gregarious nature of scoters. Radio-telemetry and survey observations in 2005 and 2006 confirm that southeast Alaska is used by tens of thousands of surf scoters during spring migration (E. Lok, Simon Fraser University, unpublished data).

We found a very strong relationship between scoter stopover sites and the combination of decreasing distance to herring spawn sites and increasing distance to the outer coast. Herring spawn availability may be an important habitat attribute because it is

an easily accessible and energy-rich food source (Paul and Paul 1999) that coincides with the need for abundant energy for fueling migration and subsequent reproduction (Bishop and Green 2001, Bond and Esler 2006, Willson and Womble 2006). Increased distance from the outer coast may be important for several reasons. Much of the herring spawning activity in southeast Alaska occurs along the inner coast, and scoter habitat use may mirror habitat use by spawning herring. Although we found that physical shoreline attributes were generally poor predictors of site use within southeast Alaska during spring, habitat use by surf scoters during winter is related to shoreline characteristics and associated bivalve prey distribution and densities (Žydelis et al. 2006). Recent habitat mapping in southeast Alaska indicates that the distribution of blue mussels is more continuous in regions closer to the mainland coast (ShoreZone Program 2006), which would provide predictable food resources for scoters. From a migratory perspective, the inside coast is more sheltered, and may provide access to preferred migration pathways inland.

Stopover sites throughout southeast Alaska were used for both short stopovers and longer duration staging, and most individuals both stopped and staged. Overall, stopover site use appears to be influenced by multiple factors, suggesting that that not all spring migration habitats serve the same stopover function and the aggregate value of these sites must be considered (Mehlman et al. 2005). The frequent and consistent use of Lynn Canal by large numbers of individuals indicates that it is an important stopover site for migrating surf scoters. More individuals staged here than at any other site, suggesting that this site may serve more as a longer term staging site than a short term stopover stepping stone. Many of the used sites are well documented herring spawn sites;

however, Lynn Canal was a particular exception in that there was no documented herring spawn within the site during the study years, having experienced marked declines in herring stocks in recent years (Willson and Womble 2006). Geographical context may be an important factor in the use of Lynn Canal as a stopover and staging site, given its location as the most northeastern waterway in southeast Alaska. This region is likely a natural break for scoters to take advantage of abundant marine resources and gauge weather conditions before turning inland to migrate into the boreal forests of northern Canada.

Aggregations of birds, such as the scoters within Lynn Canal during spring migration, are vulnerable to stochastic natural events and human activity impacts (Ford et al. 1982). Of the 14 sites we have identified as important stopovers for surf scoters, only Berners Bay has been identified as an Important Bird Area (IBA) (Audubon 2008). Given the large numbers of scoters from throughout the Pacific surf scoter population using this specific area during such an important period in their annual cycle, scoters in this region may be particularly vulnerable to events such as contaminant spills.

The strong relationship between important stopover sites and herring spawn emphasizes the need for integrating the management of herring fisheries with the management of sea ducks. Several herring stocks in southeast Alaska have decreased to levels that are no longer commercially viable (Willson and Womble 2006). The identification of Berners Bay as an IBA is largely based on its importance to numerous species that depend on the Pacific herring runs which were once widespread throughout Lynn Canal, but which now occur mainly in Berners Bay (Audubon 2008). Understanding the importance of herring spawn during stopover and staging and the

energy requirements for migration and reproduction is critical for management and conservation of scoter populations, as well as other species that use this ephemeral spring resource.

3.8 Acknowledgements

This study was funded by the Sea Duck Joint Venture. This work was conducted following guidance from Animal Care and Use Committees and with permits from California Department of Fish and Game, Canadian Wildlife Service, U. S. Fish and Wildlife Service, USGS Bird Banding Laboratory, Simon Fraser University, and Washington Department of Fish and Wildlife. Funding was provided by the USGS Western Ecological Research Center Coastal Ecosystems Program with support from the Calfed Ecosystem Restoration Program.

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Table 3.1 Summary of surf scoters marked with platform transmitter terminal (PTT) satellite transmitters in 2003-2006 from four wintering areas: San Quintin Bay, Baja California, Mexico (SQ), San Francisco Bay, California, USA (SF), Puget Sound, Washington, USA (PS), and Strait of Georgia, British Columbia (SG). Transmitters deployed that did not leave wintering areas are not included. Numbers in parentheses denote the total number of birds used for stopover analyses. Individuals that migrated inland directly, died, or experienced radio failure were not included in stopover analyses.

Year	Wintering Area			
	SQ	SF	PS	SG
2003	0	8 (5)	0	0
2004	0	0	7 (2)	0
2005	2	9 (2)	16 (5)	8 (5)
2006	3 (3)	11 (8)	11 (7)	0
Total	5 (3)	28 (15)	34 (14)	8 (5)

Table 3.2 Migration stopover sites of satellite marked spring migrating surf scoters in southeast Alaska during 2003 – 2006.
Sites are ordered by latitude from north to south.

Stopover Site	Coordinates	Individuals	Total	Stopover events		Years of use
				2-7 days	≥7 days	
Lynn Canal	59.138°N, 135.342°W	17	22	15	7	2003, 2005, 2006
Berners Bay	58.778°N, 134.972°W	2	2	2	0	2003, 2006
Eagle Harbor	58.481°N, 134.827°W	2	2	0	2	2005, 2006
Stephens Passage	58.242°N, 134.654°W	2	2	2	0	2005, 2006
Gastineau Channel	58.205°N, 134.319°W	7	7	0	7	2003, 2005, 2006
Young Bay	58.187°N, 134.548°W	2	2	1	1	2003, 2006
Tracy Arm	57.796°N, 133.558°W	2	2	0	2	2003, 2006
Seymour Canal	57.657°N, 133.917°W	2	2	2	0	2006
Hobart Bay	57.442°N, 133.501°W	2	2	1	1	2005, 2006
Eastern Passage	56.426°N, 132.230°W	2	2	1	1	2003, 2006
Vixen Inlet	55.851°N, 132.092°W	3	3	3	0	2004, 2006
West Behm Canal	55.576°N, 131.876°W	4	4	4	0	2003, 2006
Klawock Inlet	55.521°N, 133.192°W	2	2	1	1	2005
Annette Island	55.092°N, 131.335°W	8	8	7	1	2003, 2004, 2005, 2006

Table 3.3 Summary of AIC results from logistic regression models assessing habitat variation in relation to whether plots were surf scoter stopover sites or random points. Shoreline models include length, depth, width, exposure, streams, and percent rocky substrate. Number of parameters includes +1 for intercept. Candidate models are listed by ΔAIC_c

Model	Number of parameters	ΔAIC_c	AIC_c	w_i	McFadden's R^2
coast + spawn	3	0.00	28.27	0.97	0.66
spawn	2	7.70	35.97	0.02	0.51
spawn + coast + shoreline	9	10.30	38.57	0.01	0.73
spawn + shoreline	8	13.72	41.98	0.00	0.63
coast + shoreline	8	23.61	51.88	0.00	0.48
coast	2	26.11	54.37	0.00	0.22
streams	2	33.86	62.13	0.00	0.10
exposure	2	33.88	62.15	0.00	0.10
length	2	37.23	65.50	0.00	0.04
shoreline	7	37.77	66.04	0.00	0.22
null	1	37.94	66.21	0.00	-
width	2	39.61	67.88	0.00	0.01
rocky substrate	2	40.03	68.29	0.00	0.00
depth	2	40.08	68.34	0.00	0.00

Table 3.4 Habitat attributes of important stopover sites of spring-migrating surf scoters in comparison to random sites. Attributes are summarized by 5 km radius plots. Averages are reported with 95% CI.

Predictor variable	Units	Stopover sites		Random sites	
		Average	Range	Average	Range
Distance to herring spawn	km	8.2 ± 6.2	.01 - 30.3	47.2 ± 7.9	4.5 - 145.8
Distance to outer coast	km	88.2 ± 17.8	30.1 - 124.8	45.7 ± 9.8	0 - 144.4
Depth	m	79.5 ± 27.7	22.9 - 186.7	79.1 ± 19.8	1.7 - 309.5
Width	m	118.6 ± 47.9	29.7 - 264.7	153.5 ± 54.6	27.0 - 779.8
Length	km	28.9 ± 7.6	3.0 - 54.0	40.4 ± 7.9	6.4 - 163.8
Rocky substrate	%	48.3 ± 13.9	3.4 - 78.3	50.1 ± 7.8	0.9 - 99.1
Streams	number	8.5 ± 3.5	0 - 20	19.9 ± 6.1	0 - 109
Exposure index		212.5 ± 17.2	172.1 - 274.1	171.1 ± 16.3	100.0 - 298.3

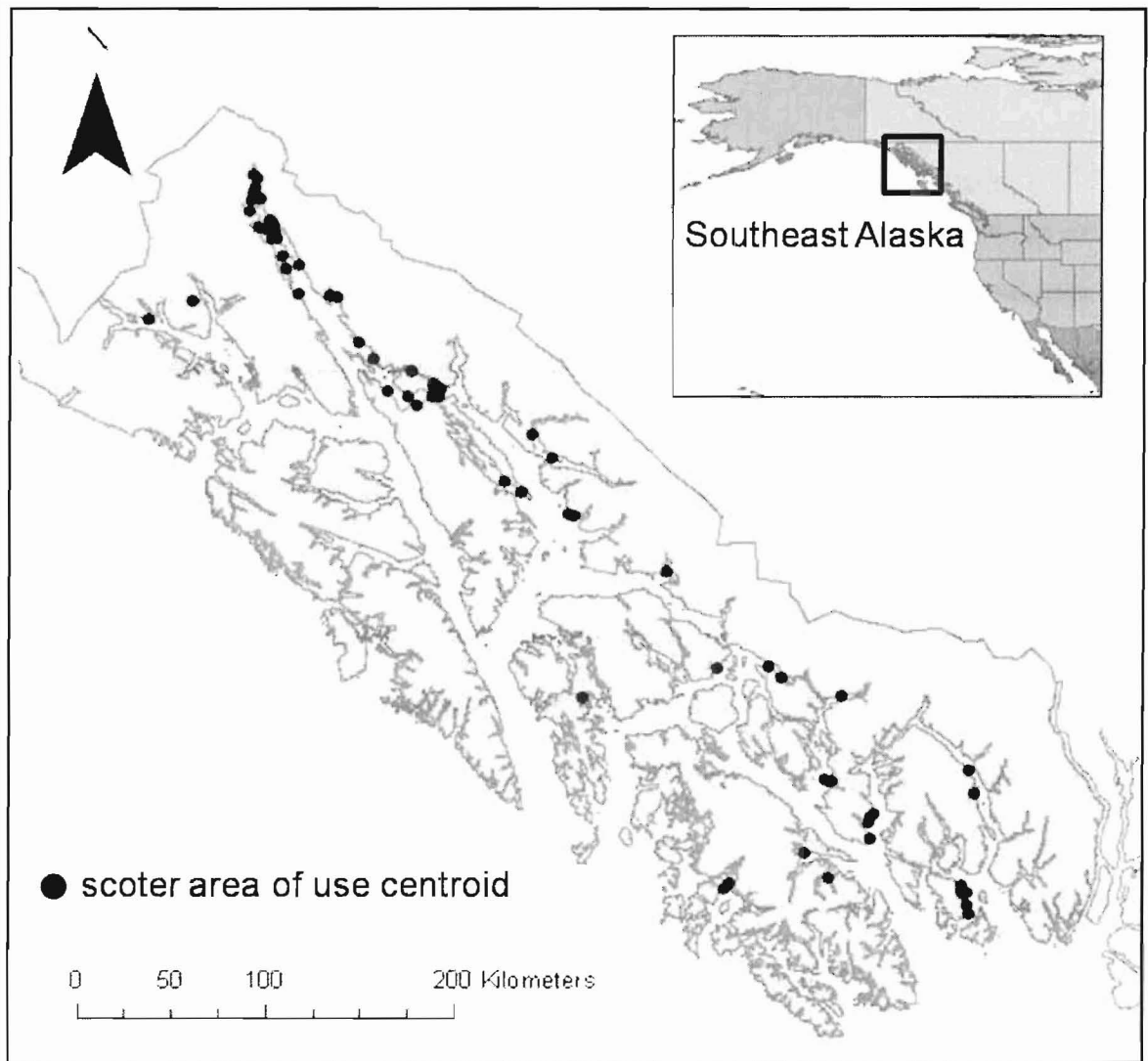


Figure 3.1 Centroids of stopover areas of use (n=72) of 31 satellite-marked spring migrating surf scoters in southeast Alaska, 2003-2006. An area of use is defined as series of at least two consecutive selected locations (representing a location on a single day) within 22 km of each other.

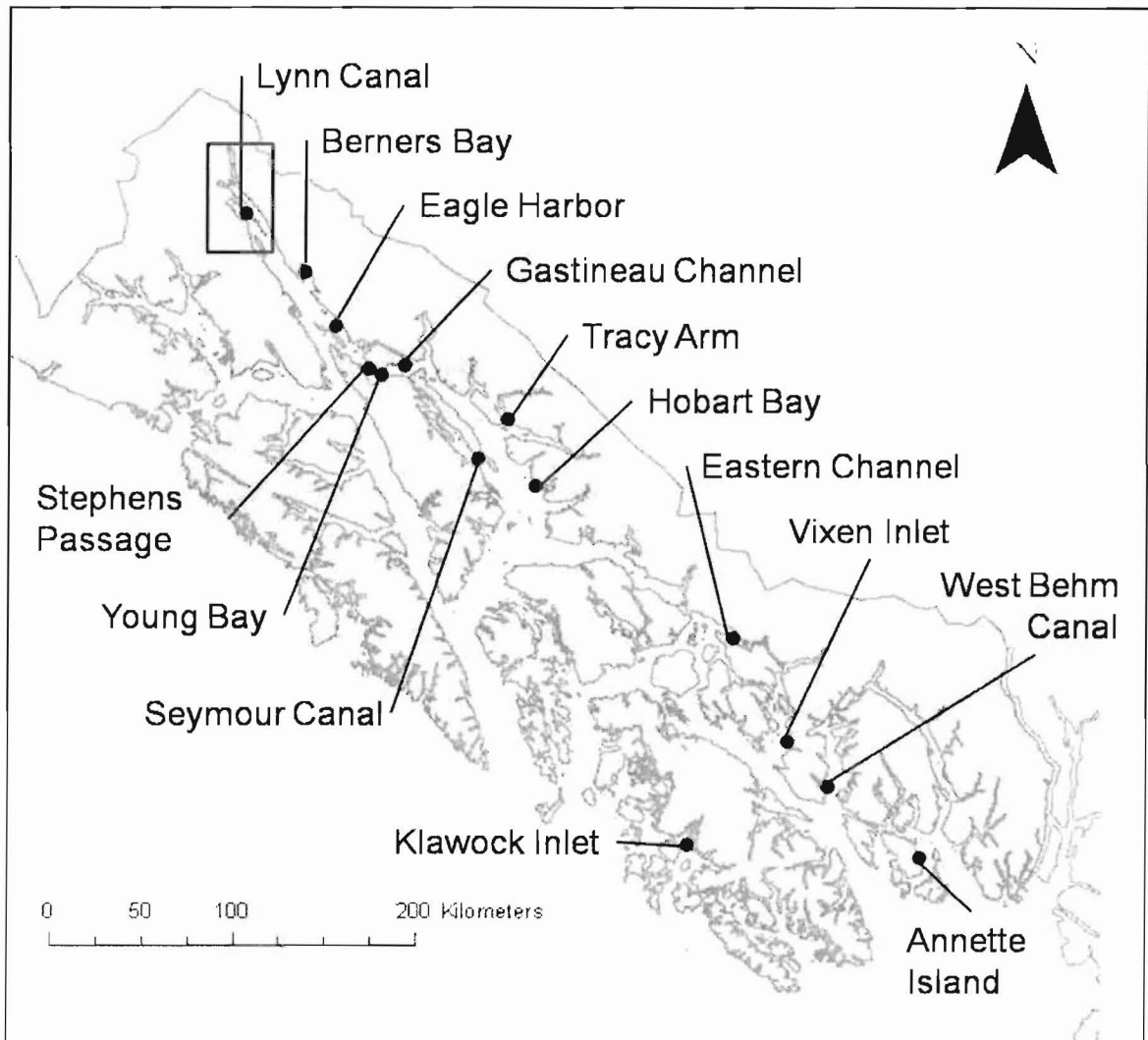


Figure 3.2 Important stopover sites of satellite-marked spring migrating surf scoters in southeast Alaska, 2003 – 2006. The box highlights northern Lynn Canal, which is a unique and very heavily used stopover area.

**CHAPTER 4 SPATIOTEMPORAL ASSOCIATIONS
BETWEEN PACIFIC HERRING SPAWN AND SURF
SCOTER SPRING MIGRATION: EVALUATING A
“SILVER WAVE” HYPOTHESIS**

4.1 Abstract

Surf scoters (*Melanitta perspicillata*) are known to aggregate at spawning sites of Pacific herring (*Clupea pallasii*) and forage on the eggs, which are deposited in great abundance in intertidal and shallow subtidal zones along a small proportion of available coastline. We considered this relationship on a continental scale, by determining whether the phenology of scoter spring migration and their selection of stopover locations corresponded to herring spawn timing and locations; in other words, we evaluated whether scoters follow a “silver wave” of resource availability that influences when and where they choose to migrate. We found strong support for a basic assumption of the silver wave hypothesis, specifically that herring spawn activity initiates later in the year at higher latitudes, creating a northward-progressing wave of short-term localized food availability. We compared locations of satellite-tagged surf scoters with spawn availability and found that surf scoter migration generally coincided with the northward progression of herring spawn within the study years, although there was considerable variability in timing of both scoter migration and herring spawn initiation. At a continental scale, the majority of tagged scoters visited at least one spawn site during migration, and those that used spawn sites were located at spawn sites for approximately a third of their migration period. On a regional scale, surf scoters showed strong spatiotemporal associations with herring spawn sites, confirming that the presence of herring spawn was an important factor determining habitat use during spring migration for many individuals. Although the distribution and timing of spawning activity appears to explain only some of the variation in continental migration strategies, herring spawn is clearly an important resource for many spring-migrating surf scoters.

4.2 Introduction

Migrating animals face habitat and food resources that vary considerably in both time and space, across local, regional, and continental scales. The timing of migration and the choice of habitats are shaped by spatiotemporal variation in resource availability, and migrating animals are known to adopt optimal migration strategies in light of this variation (Ottich and Dierschke 2003, van der Graaf et al. 2006). Migratory birds acquire energy and nutrient reserves at spring stopover sites, and the availability and quality of resources at these sites can have implications for success during subsequent stages of the annual cycle (Ankney and MacInnes 1978, Alisauskas and Ankney 1992, Warnock and Bishop 1998, Smith and Moore 2003, Morrison and Hobson 2004). Therefore, the timing of migration and the choice of stopover habitat may be closely linked with temporally varying resource availability, which in turn can have population-level demographic consequences.

Migrating herbivorous birds are speculated to strategically time migration phenology to take advantage of emergent spring growth of forage plants at stopover and staging sites (van der Graaf et al. 2006). This green wave hypothesis posits that birds travel along a corridor while migrating from wintering areas to arctic breeding areas to follow the wave of emergent spring vegetation at higher latitudes (Owen 1980). Stopover site use by some migrating waterfowl appears to be closely linked to peaks in forage biomass and quality during spring (van der Graaf et al. 2006).

Other food resources for migrating animals may vary temporally in availability along a latitudinal gradient. In coastal ecosystems, many birds and mammals exhibit aggregative responses to ephemeral seasonal resource pulses, such as Pacific herring

(*Clupea pallasii*) spawning events (Haegele 1993, Bishop and Green 2001, Sullivan et al. 2002, Womble et al. 2005). On a global scale, Pacific herring spawn from late winter to early summer, and in general, spawn initiates later at higher latitudes. This general latitudinal progression of spawning events is probably the result of spawning being initiated by sea temperatures greater than 6° C (Haegele and Schweigert 1985). Herring spawn events are short-lived, with spawning activity occurring within a span of 3-6 weeks in any given area, and eggs hatching in 1.5 to 3 weeks from deposition (Haegele and Schweigert 1985, Hay 1985). Herring spawn events are also highly localized, occurring on less than 2% of the entire BC coastline in a given year (Hay and McCarter 2007).

These events provide food resources to a number of avian predators (Bishop and Green 2001, Sullivan et al. 2002, Rodway et al. 2003). Herring spawning activity occurs at generally the same time that many birds are migrating up the coast to northern breeding areas. Therefore, we propose a “silver wave” hypothesis, analogous to the green wave hypothesis for herbivorous birds, which posits that migration timing and habitat choice by migrating birds would correspond to herring spawn locations and a northward-progressing spawn phenology. Use of these ephemeral and energy-rich herring spawn resources has been documented for both birds and mammals on local and regional scales (Rodway et al. 2003, Womble et al. 2005, Žydelis and Esler 2005), but has not been considered on a continental or migratory scale.

Along the Pacific coast, many sea ducks, including surf scoters (*Melanitta perspicillata*) are known to congregate at herring spawn sites during late winter and early spring (Vermeer 1981, Vermeer et al. 1997, Sullivan et al. 2002, Lok et al. In press).

However, spring migration ecology is poorly documented for surf scoters, and little is known about the specific habitat attributes that determine use of staging and stopover sites during spring migration (Savard et al. 1998), although proximity to herring spawn has been identified recently as a strong predictor of stopover and staging habitat use (Chapter 3). Unlike the green wave of resource availability for herbivorous birds, herring spawn availability is restricted in both time and to a relatively small spatial distribution, as herring spawn occurs on a very small proportion of available coastline (Hay and McCarter 2007). Because surf scoters are only able to use herring spawn at specific sites for short periods of time, the distribution and timing of herring spawn could potentially influence the temporal and spatial patterns of surf scoter migration, i.e., the “silver wave” hypothesis. This pattern has been speculated (Vermeer 1981, Savard et al. 1998), but data to address the silver wave hypothesis have not been previously available.

We considered the timing and stopover locations of spring-migrating surf scoters in relation to the timing and location of Pacific herring spawn to consider whether the silver wave hypothesis is a reasonable explanation for observed migration strategies. We investigated a basic assumption of the silver wave hypothesis, specifically whether the timing of Pacific herring spawn activity progressed northward along the British Columbia (BC) and southeast Alaska (SEAK) coasts through time, using existing herring spawn data sets from fisheries agencies along the coasts of BC and SEAK. Although this progression has been described on a global scale (Haegerle and Schweigert 1985), this relationship had not been documented on a smaller continental scale. Second, we documented migration patterns of marked surf scoters using satellite telemetry and contrasted those patterns with availability of spawn at a broad scale. Finally, we

evaluated spatiotemporal relationships between herring spawn activity and surf scoters at a regional scale within 3 sites in SEAK, using survey data.

4.3 Study Area

The wintering range of surf scoters along the Pacific coast extends from Alaska to Baja California, Mexico (Savard et al. 1998b). We compiled information on spring migration from surf scoters originating from several areas throughout this wintering range, including San Quintin Bay, Baja California, Mexico (116.0°W, 30.4°N), San Francisco Bay, California, USA (122.4°W, 37.8°N); Puget Sound, Washington, USA (122.4°W, 47.5°N); and the Strait of Georgia, British Columbia, Canada (122.4°W, 49.3°N). In spring, surf scoters migrate along the Pacific coast from these wintering areas to inland breeding areas throughout the boreal forest of western Canada and Alaska (Savard et al. 1998). The coasts of British Columbia and southeast Alaska are variable, from exposed west aspect shores of the Pacific Ocean to very sheltered fjords and tidewater glaciers along protected inside passages. The coast of British Columbia and southern part of southeast Alaska is characterized by extensive networks of islands and protected bays and channels, while the northern part of southeast Alaska is comprised of numerous long fjords and several large soft-bottomed river deltas. Although herring spawning has historically occurred along approximately 20% of the BC coast (DFO 2007), most spawning is concentrated in a few areas and is localized to approximately 2% of the coast in a given year (Hay and McCarter 2007).

4.4 Methods

4.4.1 Captures and marking

We captured surf scoters on wintering grounds between November and March, 2002-2006, using a floating mistnet (Kaiser et al. 1995, Lewis et al. 2005), or a net shot from a netgun (Mechlin and Shaiffer 1980). Birds were implanted with platform-transmitter-terminal (PTT) satellite-transmitters (Table 4.1) following standard procedures (Mulcahy and Esler 1999). This radio implantation method has been shown to perform well for scoters relative to other attachment methods (Iverson et al. 2006). Tagged birds were released after a recovery period of at least 1 hour. PTT transmitters were programmed with duty cycles to transmit location data for 6-8 h and turn off for 48-96 h.

4.4.2 Location data

Satellite transmitter locations were obtained from the Argos data system, which estimated positions by calculating the Doppler-effect shift with receivers on National Oceanic and Atmospheric Administration (NOAA) weather satellites. We compiled the location data from all PTT-tagged surf scoters and filtered the data spatially and temporally to select only coastal spring migration locations, which we defined as those locations occurring along the coastline of BC and SEAK. PTT locations are classified by estimated accuracy and number of signals. For Location Classes (LC) 3, 2, 1, and 0, in which ≥ 4 messages are received by the satellite, Argos rates accuracy as <150, 150-350, 350-1000, and >1000 m, respectively. Accuracy is not provided for LC A (3 messages), B (2 messages), and Z (latitude/longitude often provided if >1 message received). Location data usually included more than one useable location per bird in a transmission

day so a “Selected Location” for each transmission day was selected according to the criteria described by Miller et al. (2005). These criteria favor locations with LC 3, 2 and 1, but recognize that accurate locations are obtained for a large proportion of locations within all Argos location quality classes. Although less conservative than filtering locations of lower location quality classes, this method allowed us to maximize the number of Selected Locations during the short migration period.

4.4.3 Aerial surveys

We conducted aerial surveys to document the distribution and abundance of surf scoters both before and during the spawning/migration period in 2006. Surveys were conducted along the shoreline in three regions in SEAK; Ketchikan, Juneau, and Haines (Figure 4.1). All three areas were surveyed once prior to herring spawning initiation (1 April 2006 to 2 April 2006). During the spawning/migration period, the Ketchikan region was surveyed twice (20 April 2006 and 24 April 2006), the Juneau region was surveyed once (8 May 2006), and the Haines region was surveyed twice (9 May 2006 and 15 May 2006). Surveys were conducted in a Cessna 185 or Heliocourier with an experienced survey pilot and passenger side observer between 0900 h and 1600 h. Surveys followed the shoreline at altitudes of 150-200 m and flight speeds of <200 km/hour. Survey routes varied in shoreline length between regions (Ketchikan - 540 km, Juneau - 463 km, Haines- 394 km) and survey duration varied accordingly. We used digital marine charts (NOAA 1:250,000) to record locations of all observed surf scoters; groups were recorded as a single location with an estimate of group size. Groups of <100 were counted individually; larger group were estimated by 10s, 100s, or 1000s, depending on the size of the group.

4.4.4 Herring spawn data

We created a database documenting the distribution and timing of major herring spawn events along the BC and SEAK coast in 2003-2006 using existing data from Department of Fisheries and Oceans (DFO) and the Alaska Department of Fish and Game (ADFG). The DFO Pacific Herring Geographic Bulletin dataset is available online (DFO 2007) and reports the timing and magnitude of herring spawning in 101 management sections along the BC coast. The dataset also includes the centroid position for each section, which is determined by calculating the mean latitude and longitude coordinates using all the recorded spawning events within the section (Figure 4.1). The mean spawn date was considered the most representative spawn date of the majority of spawning herring in a section (B. McCarter, Department of Fisheries and Oceans, personal communication). We compiled the location and timing of herring spawning within similar management sections within SEAK from the ADFG and unpublished sources (J. Womble, National Park Service, unpublished data). For continental scale analyses, we considered spawn distribution and timing for BC and SEAK combined. For regional scale analyses, we compiled Geographic Information Systems (GIS) coverages of herring spawn distribution within SEAK during the study years.

4.5 Data Analyses

4.5.1 Spawn progression and migration patterns

We examined the underlying assumption of the silver wave hypothesis that Pacific herring spawning activity along the BC and Alaska coast progresses northward through spring, with spawning activity initiating later at higher latitudes, potentially providing a progressive wave of short-term food availability. We used least squares

general linear models to evaluate variation in latitude of herring spawning activity along the BC and SEAK coasts in relation to the day of year (doy) and year. We included the day of year variable as an indicator of seasonal progression, where 1 January = 1, while the year variable and day of year by year interactions were included to account for potential inter-annual variation in this relationship. We used SAS (SAS Institute 2003) for statistical analyses. We used an information theoretic approach to model selection (Burnham and Anderson 2002) and calculated Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for each model within a candidate set. The candidate model set consisted of the following models: (1) day of year (doy) (2) year (3) doy + year (4) doy + doy*year (5) doy + year + doy*year and (6) a null model. We compared the AIC_c value of each model to that of the best-fitting model (ΔAIC_c) to assess the relative support for each candidate model. We calculated AIC_c weights (w_i) to compare the relative support for each model within the candidate model set, and calculated R^2 values to indicate overall model fit. Finally, we calculated model-averaged parameter estimates and unconditional standard errors based on Akaike weights for all candidate models (Burnham and Anderson 2002).

For the silver wave hypothesis to be supported, we would expect a general correspondence between herring spawn availability and scoter locations, assuming the basic premise that herring spawn progresses northward over time is correct. To evaluate this, we compared the temporal and spatial patterns of herring spawn availability with scoter locations. Estimates of average spawn latitude for each date were calculated from model-averaged parameter estimates based on Akaike weights (Burnham and Anderson 2002) across the models in the candidate set describing the relationship of herring spawn

date by latitude (above). We then regressed the latitude of observed scoter locations against estimates of the average latitude of herring spawn for the date of each bird location; under the silver wave hypothesis, we would expect a positive relationship, with a slope of approximately 1, indicating that the scoters are following the progression of herring spawn availability exactly.

4.5.2 Spawn site use metrics

The silver wave hypothesis predicts that, in addition to a general latitudinal correspondence between locations of migrating scoters and herring spawn. We recognize that a single mean date for each spawning event does not fully represent herring spawn availability over time and space, so we plotted scoter locations against herring spawn availability to illustrate the spatiotemporal overlap between herring spawn availability and migrating scoters. There should be close spatial correspondence between scoter locations and sites with available herring spawn. Unlike the green wave for herbivorous birds, in which resource availability occurs in a broad swath related to latitude, herring spawn occurs at small, spatially discrete sites, so the silver wave hypothesis requires confirmation that these specific sites are used by migrating birds. We evaluated this prediction at two geographic scales.

Continental scale - The satellite telemetry location data were imported into ArcGIS 9.1 (Environmental Systems Research Institute 2005) to create a map of surf scoter spring migration locations and herring spawning locations. Because spawning activity varied in both time and space, we filtered location data both spatially and temporally. We considered spawn site use along the entire BC and SEAK coast. We created buffers of 22 km radius around documented spawning locations using the Buffer

Wizard in ArcGIS 9.1. We considered a location at a spawn site if it was within 22 km of the centroid of an active spawn management section. The 22 km radius is based on the 95th percentile of mean interfix distances for radio-tagged surf scoters in late winter when herring spawn is available (Lok et al. In press). Once the data were spatially selected, we filtered the data temporally by comparing the date of the scoter location to the mean date of spawning within that management section. Locations were only considered at an active spawn if the date was on, or within, 21 days following the mean spawning date. We chose a period of 21 days to account for the presence of eggs from 1.5 – 3 weeks after deposition and the possibility of spawning events initiating after the mean spawning date within a management section. Locations at active spawn sites were used to calculate metrics of spawn site use by scoters. Metrics included the number of individuals located at spawn sites, the proportion of an individual's locations at spawn sites, the number of spawn sites visited by an individual, and the proportion of all locations at spawn sites. Previous work has shown that Lynn Canal (59.138°N, 135.342°W), within the Haines region of SEAK, is a highly used stopover and staging site for migrating surf scoters during the study years, despite not having any spawning activity during the study years (Chapter 3). To account for the apparent alternative function of this unique area, we calculated the same metrics for all locations in BC and SEAK excluding those in Lynn Canal.

Regional scale - Aerial survey data were imported into ArcGIS 9.1 to create a map of surf scoter group locations, scoter abundance, and herring spawn distribution within each survey region (Ketchikan, Juneau, and Haines). We categorized surveys as before spawning and during spawning based on the timing of herring spawn activity

within each survey area and the dates of surveys. We calculated several metrics of habitat use before and during spawning. We calculated the density of scoters within the survey areas before and during spawning activity, and weighted scoter locations by group size to calculate a mean distance of individual scoter locations to herring spawn sites. To account for variation in the proportion of coastline with available spawn, we calculated a density of scoters per km of available spawn. In addition, we used the Buffer Wizard in ArcGIS 9.1 and created a buffer of 1 km around documented spawning locations to determine the number and proportion of scoters within 1 km of herring spawn sites.

4.6 Results

4.6.1 Spawn progression and migration patterns

Variation in the latitude of spawning activity was clearly related to the day of year and year (Figure 4.2). Within the candidate model set, the day of year + day of year*year model was the most strongly supported model ($w_i = 0.55$, $R^2 = 0.61$), with the day of year + year model receiving slightly more than half the support of the most strongly supported model ($w_i = 0.32$, $R^2 = 0.61$) (Table 4.2). These findings provide strong support for the underlying assumption of the silver wave hypothesis that herring spawning activity along the Pacific coast initiates later in the year at higher latitudes. Across all years, the regression equation describing herring spawn latitude as a function of day of year alone was herring spawn latitude = $41.73 (\pm 0.67) + 0.12 (\pm 0.01) * \text{doy}$. In addition, we found that this relationship varied somewhat inter-annually. Model-averaged parameter estimates and unconditional standard errors describing the average latitude of herring spawning activity are shown in Table 4.3.

We compared the latitude of PTT-tagged surf scoter locations to the predicted latitude of spawning activity for the same day of year for all study years combined. We found that the predicted spawn latitude explained some of the variation in surf scoter latitude ($R^2=0.21$). The relationship between predicted spawn latitude and surf scoter latitude was positive but less than 1 (surf scoter latitude = $19.11 (\pm 2.65) + 0.64(\pm 0.05) \cdot \text{predicted spawn latitude}$). This indicates that surf scoter locations do not follow spawning activity exactly, showing a delayed progression up the coast in comparison to herring spawn activity.

4.6.2 Spawn site use metrics

Continental scale - When we considered a broader date range of spawn availability, we found that the patterns of surf scoter spring migration only somewhat paralleled that of northward herring spawn availability (Figure 4.3). However, the majority of PTT-tagged surf scoters were located at spawn sites at least once. Of 51 individuals located within BC and SEAK, 31 (60%) were located at a spawn site at some point during spring migration. We found that the mean (\pm SE) proportion of an individual scoter's locations located at spawn sites was $33 \pm 4\%$. On average surf scoters visited 2.1 ± 0.6 spawn sites during coastal spring migration through BC and SEAK. Overall, 24% of scoter locations were located at spawn sites. When we considered only locations outside of Lynn Canal we again found that 31 of 51 individuals were located at a spawn sites, and the number of individuals and mean number of spawn sites visited by an individual did not change. However, we found that the proportion of an individual's locations located at a spawn site was larger ($42 \pm 4\%$), and the proportion of all locations at spawn sites was 31%.

Regional scale - In general, use of all 3 survey regions was relatively low prior to the spring migration period, and very high during the spawning/migration period, with over 100,000 scoters observed in the Haines region during surveys in May (Table 4.4). The mean distance to spawn sites also varied by survey area, with scoters in the Ketchikan and Juneau regions showing marked decreases in distance to spawn between pre-spawn and spawn surveys, while scoters in the Haines region showed little change in distance to spawn (Table 4.4). The use of spawn sites varied markedly between survey areas (Table 4.4). Scoters showed strong responses to spawn availability in the Ketchikan area, with the majority (90-99%) of scoters in this area located within 1 km of spawn sites. Fewer (49%) surf scoters were located at spawn sites in the Juneau region, and an even lower proportion (3-15%) were observed at spawn sites in the Haines area. However, when the amount of coastline with available spawn was considered in calculating scoter densities, scoters showed the strongest response to spawn availability in the Haines region, where scoter numbers were the highest and the amount of available coastline with spawn was the smallest (Table 4.5).

4.7 Discussion

We found several lines of support for the silver wave hypothesis, which suggests that surf scoter spring migration timing and stopover locations are adjusted to some degree to correspond to availability of abundant food resource represented by herring spawn. Data consistent with the silver wave hypothesis include our finding that herring spawn activity initiates later in the spring at higher latitudes, creating a northward progression of food availability for scoters. We found that the northward progression of herring spawn activity was strongly related to the day of year, indicating that spawn

availability is a reasonably predictable seasonal resource during migration on a broad scale. A study of the variation in the temporal and spatial availability of herring spawn along the BC coastline found that the reliability and timing of herring spawn events are quite variable from year to year at small geographic scales, but become increasingly predictable at broader geographic scales (Willson and Womble 2006). Because herring eggs are available to predators for up to three weeks after spawn initiation (Haegele and Schweigert 1985, Hay 1985), herring eggs are available for several weeks at multiple locations throughout the spring, creating generally continuous availability of spawn along the coast during spring. This means that variation in herring spawn timing and distribution may have less observable implications for highly mobile consumers of spawn, such as birds (Willson and Womble 2006). Pre-migratory surf scoters show increased movements in response to herring spawn at a local scale (Lok et al. In press) and are presumably capable of moving in search of spawn at larger scales, particularly during migration.

We found that surf scoter migration generally coincided with the northward progression of herring spawn within the study years, but did not follow the same pattern exactly. The temporal and spatial patterns of herring spawn availability explained only part of the variation in surf scoter spring migration locations. Not all individuals used spawn sites, and not all locations of other individuals were at spawn sites. We must consider the possibility that our metrics of the association between scoters and spawn may be minimum estimates, as not all spawn sites along the entire coast can be documented with complete certainty, and there are often smaller subsequent spawning events after the mean spawn date for a management section (Haegele and Schweigert

1985). However, we found that there was considerable use of spawn sites during migration; the majority of PTT-tagged surf scoters used herring spawn sites at some point during migration, despite the very small proportion of coastline used by spawning herring. There is evidence of disproportionately high use of spawn relative to the very small amount of spawn along the coast for spawn use metrics at both continental and local scales. In particular, regional scale data showed that when spawn was available, it was used heavily, as evidenced by the high densities of scoters at the small amount of available herring spawn sites in the Haines region. This generally supports the silver wave hypothesis, but suggests that herring spawn availability is not the only important factor driving scoter migration strategies and site use.

The spatial and temporal availability of resources influences stopover site use and migration timing (Ottich and Dierschke 2003, van der Graaf et al. 2006). For highly mobile scoters, the generally continuous availability of herring spawn sites and abundant alternative foraging habitat likely gives them increased flexibility in modifying migration timing and site use. Surf scoters may be using a combination of stopover sites that provide varying habitat resources (Chapter 3). Very high numbers of surf scoters were observed in Lynn Canal during spring, despite the lack of herring spawn in the area during the study years and the use of this area may be due to the unique geographic setting. Lynn Canal is the most northeastern area of southeast Alaska, and likely provides a natural break and stopover area along their coastal migration route before they turn inland to breed (Chapter 3). When we considered spawn use along the coast excluding Lynn Canal, we found increasing support for spawn site use in other areas along the migration route. This suggests that herring spawn availability along the coast may be

more important for stopovers along the migration route (Chapter 3), and that not all spring migration habitats serve the same resource function (Mehlman et al. 2005). It is also important to consider that the herring populations in Lynn Canal have declined markedly in recent history, and that herring spawn availability in this area has been reduced to a small fraction of the former distribution (Willson and Womble 2006), when it occurs at all.

Marine birds are generally recognized to be responsive to spatial and temporal variation in prey availability (Weimerskirch et al. 1994, Ainley et al. 1996, Guillemette and Himmelman 1996, Litzow et al. 2002, Żydelis et al. 2006) and to adjust their foraging efforts and locations in response to ephemeral or novel prey (Marston et al. 2002, Christie and Reimchen 2005, Lacroix et al. 2005, Lewis et al. 2007b, Lok et al. In press). However, to our knowledge, this is the first documentation of spatiotemporal relationships between migrating marine birds and the ephemeral food resource represented by spawning marine fish. We suspect that this phenomenon may occur in other bird taxa, particularly because many types of marine birds are known to aggregate at spawn sites to forage either on congregated adult fish or the spawn (Haegele 1993, Vermeer et al. 1997, Bishop and Green 2001, Sullivan et al. 2002). Herring eggs are an easily accessible, high-energy, lipid-rich food item (Paul and Paul 1999) and may be used to build energy reserves prior to and during spring migration and reproduction (Bishop and Green 2001, Bond and Esler 2006, Willson and Womble 2006). Species that deplete winter foods, such as surf scoters (Kirk et al. 2007, Lewis et al. 2007a) might rely on herring spawn for acquiring energy reserves in late winter and early spring (Bond and Esler 2006), and species that aggregate at herring spawn may depend on this resource for

breeding in less resource rich areas (Žydelis and Esler 2005). Vermeer (1997) speculated that the fraction of a population using herring spawn sites could indicate the dependence of that population on herring spawn for acquiring energy. The availability and quality of resources during spring migration may have implications for success during subsequent stages of the annual cycle (Ankney and MacInnes 1978, Alisauskas and Ankney 1992, Warnock and Bishop 1998, Smith and Moore 2003, Morrison and Hobson 2004). Several studies have described cross-seasonal effects of spring habitats on reproductive performance by migratory waterfowl (Lovvorn et al. 2003, Anteau and Afton 2004, Reed et al. 2004, Schmutz et al. 2006) and, because these sites provide the energy and nutrients required for reproduction, it follows that population dynamics may be influenced by habitat conditions during spring migration.

Variation in non-breeding habitat such as areas supporting herring spawn may have important conservation implications. Herring spawn sites are heavily used by many marine bird and mammal species (Haegele 1993, Sullivan et al. 2002, Willson and Womble 2006). However, traditional spawn sites in many areas have declined in numbers and shifted in distribution, and species are increasingly restricted to fewer spawn sites (Stick 2005, Willson and Womble 2006). Understanding the cross-seasonal links between the use of herring spawn during late winter and the energy requirements for migration and reproduction is critical for management and conservation of scoter populations, as well as the many other species that use herring spawn.

4.8 Acknowledgements

This study was funded by the Sea Duck Joint Venture. This work was conducted following guidance from Animal Care and Use Committees and with permits from

California Department of Fish and Game, Canadian Wildlife Service, U. S. Fish and Wildlife Service, USGS Bird Banding Laboratory, Simon Fraser University, and Washington Department of Fish and Wildlife. Funding was provided by the USGS Western Ecological Research Center Coastal Ecosystems Program with support from the Calfed Ecosystem Restoration Program. We acknowledge the Department of Fisheries and Oceans, the Alaska Department of Fish and Game, and J. Womble for herring spawn data. We thank pilots L. Bennett and D. Doyon for aerial survey expertise. B. Meredith, P. Doherty, S. Heintz, and D. Douglas all provided valuable ground support and knowledge in Alaska. We acknowledge Environment Canada Science Horizons Program for financial support, and the Centre for Wildlife Ecology at Simon Fraser University for financial and logistical support.

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Table 4.1 Summary of surf scoters marked with platform transmitter terminal (PTT) satellite transmitters in 2003-2006 from four wintering areas: San Quintin Bay, Baja California, Mexico (SQ), San Francisco Bay, California, USA (SF), Puget Sound, Washington, USA (PS), and Strait of Georgia, British Columbia (SG). Transmitters deployed that did not leave wintering areas are not included. Numbers in parentheses denote the total number of birds used for herring spawn use metrics. Individuals that migrated inland directly, died, or experienced radio failure during migration were not included in analyses.

Year	Wintering Area			
	SQ	SF	PS	SG
2003	0	8 (7)	0	0
2004	0	0	7 (2)	0
2005	2 (1)	9 (8)	16 (5)	8 (6)
2006	3 (3)	11 (9)	11 (10)	0
Total	5 (4)	28 (24)	34 (17)	8 (6)

Table 4.2 Summary of AIC results from general linear models assessing variation in spawning activity latitude of Pacific herring along the coasts of British Columbia and southeast Alaska, 2003-2006. Number of parameters (K) includes +1 for intercept and + 1 for model variance. Candidate models are listed by ΔAIC_c . Note that AIC_c weights (w_i) sum to 1 and indicate the relative support for each candidate model.

Model	Parameters (K)	AIC_c	ΔAIC_c	w_i	R^2
doy + doy*year	6	228.18	0.00	0.55	0.61
doy + year	6	229.26	1.08	0.32	0.61
doy	3	232.11	3.93	0.08	0.59
doy + year + doy*year	9	232.87	4.69	0.05	0.61
null	2	406.05	177.87	0.00	n/a
year	5	410.31	182.12	0.00	0.01

doy = day of year (1 January = 1)

Table 4.3 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SEU) of weighted parameter estimates calculated from all candidate models of herring spawn activity latitude along the coasts of British Columbia and southeast Alaska, 2003-2006. Day of year is scaled so 1 January = 1.

Parameter ^a	Summed w_i	Weighted parameter estimate	SE _U
Intercept	1	41.43	0.77
day of year (doy)	1	0.13	0.01
Year			
2003	0.37	-0.13	0.43
2004	0.37	-0.08	0.27
2005	0.37	0.14	0.25
doy*2003	0.60	-0.01	0.00
doy*2004	0.60	0.00	0.00
doy*2005	0.60	0.00	0.00

^a We set categorical variable year 2006 as a reference value in all candidate models

Table 4.4 Summary of spawn site use metrics for surf scoters observed during aerial surveys in three regions in southeast Alaska, April – May 2006.

Metric	Survey area	Pre-spawn surveys	Spawn surveys
Number of scoters observed	Ketchikan	729	77,860
	Juneau	2,442	51,160
	Haines	452	-
Fraction of scoters within 1 km of spawn (%)	Ketchikan	28%	98%
	Juneau	3%	49%
	Haines	0%	-
Mean distance to spawn site (km)	Ketchikan	7.3	0.4
	Juneau	21.9	9.5
	Haines	52.9	-
		42.0	55.5

Table 4.5 Densities of surf scoters observed during aerial surveys in three regions (Ketchikan, Juneau, and Haines) in southeast Alaska, April-May 2006

Surf scoter density	Ketchikan	Juneau	Haines
<i>% surveyed shoreline with spawn</i>	7.3	5.8	1.8
Pre-spawn survey	1.3	5.3	1.1
Spawn survey	144.1	306.0	359.0
Spawn survey density at spawn sites	1937.9	938.7	2904.5

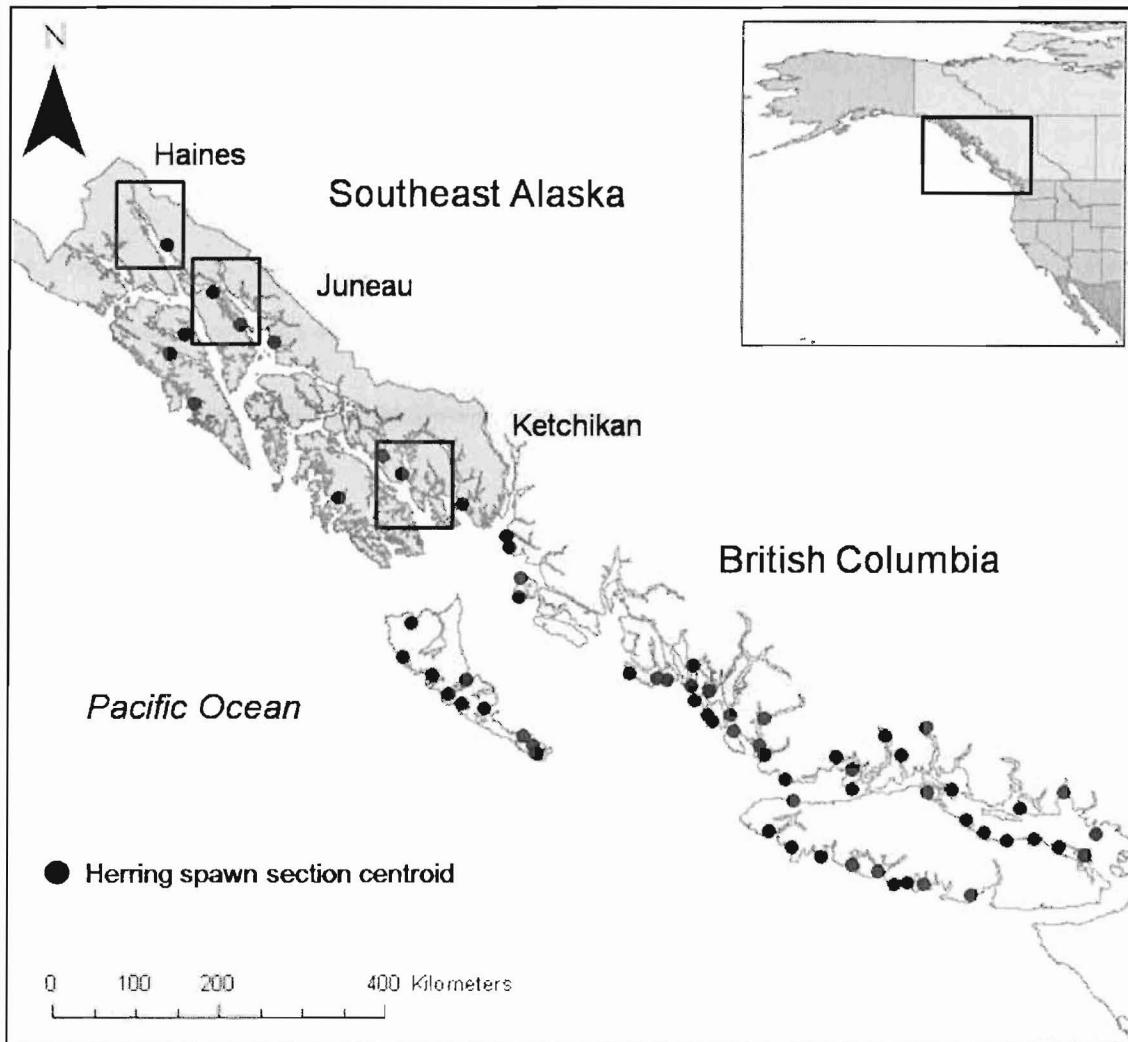


Figure 4.1 Pacific herring management section centroids along the coasts of British Columbia and southeast Alaska. Only sections that had documented spawning activity from 2003 to 2006 are shown. Survey regions are highlighted by boxes; note that not all coastline within highlighted regions was surveyed.

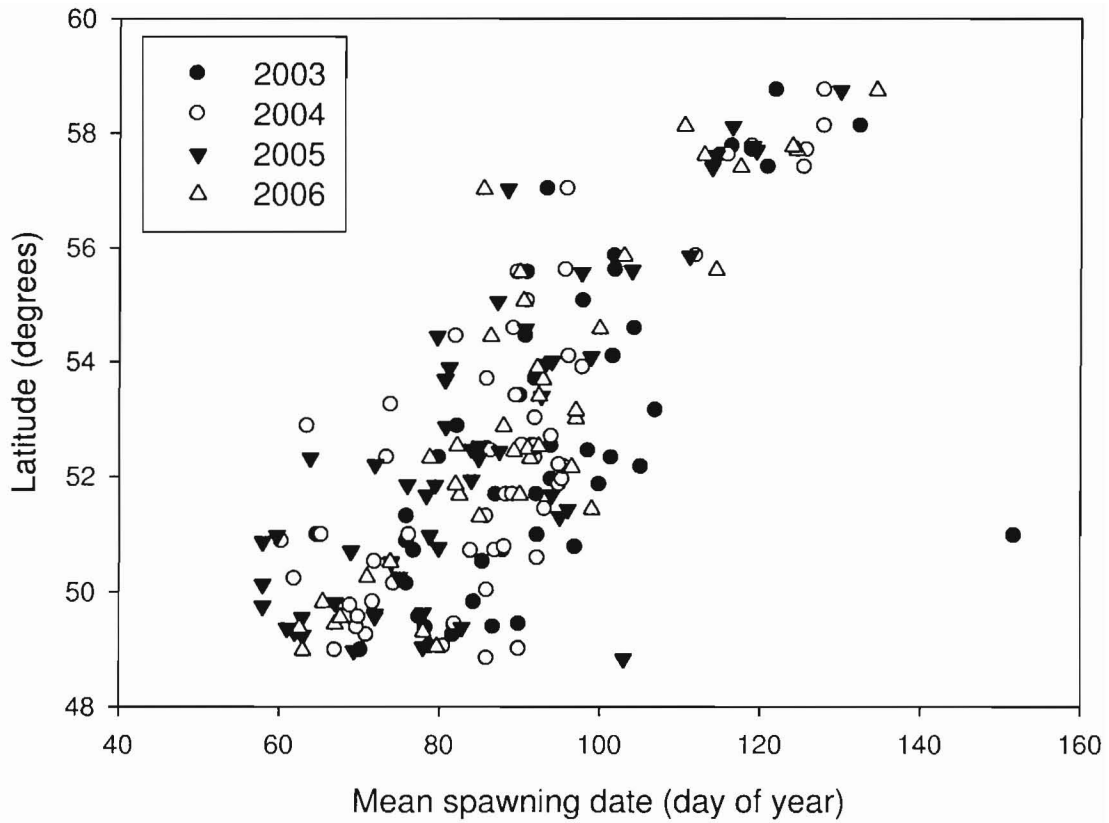


Figure 4.2 Latitude and mean spawning date for all management sections with documented Pacific herring spawning activity along the British Columbia and southeast Alaska coasts from 2003-2006.

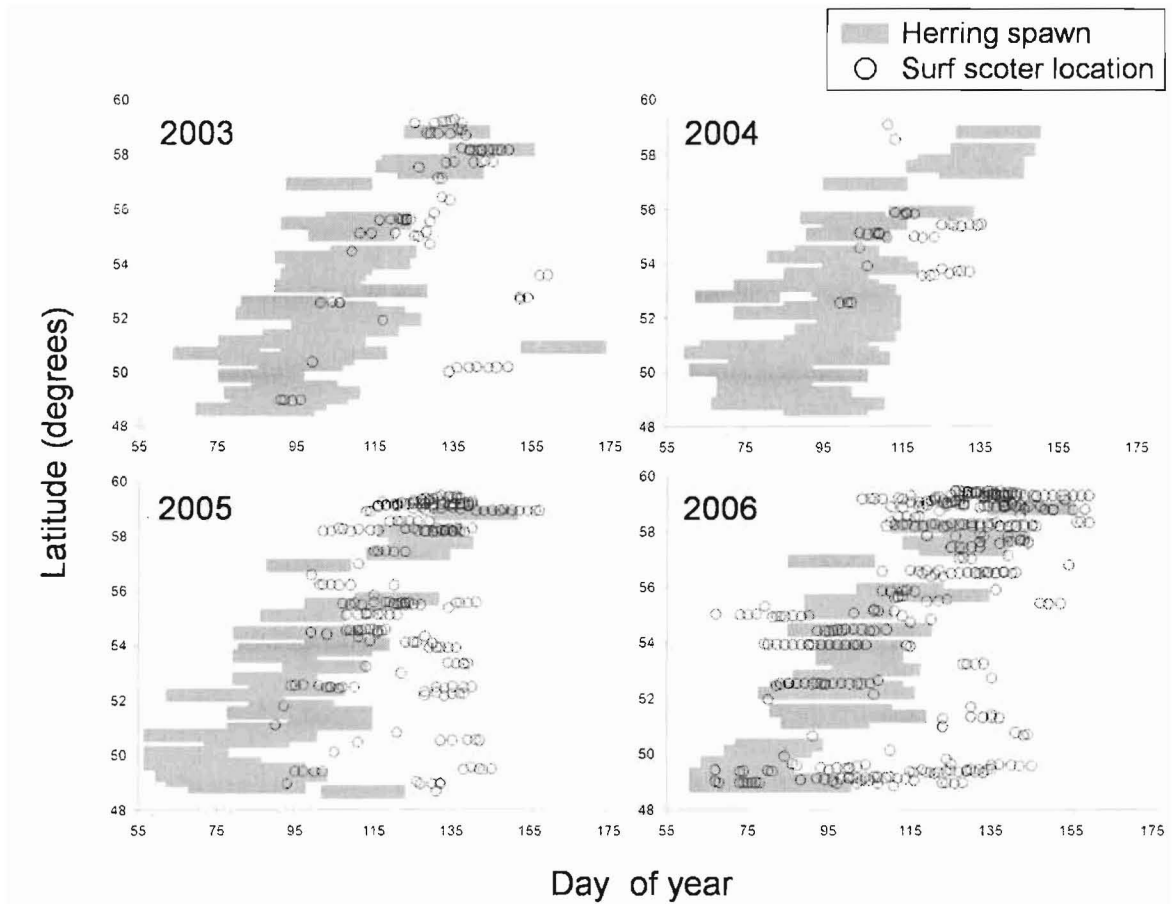


Figure 4.3 Comparison of herring spawn availability and locations of PTT-tagged surf scoters along the coasts of British Columbia and southeast Alaska, 2003-2006. Herring spawn availability (shaded area) was determined by spawn times and estimates of the time before eggs hatch (mean spawn date + 21 days).

CHAPTER 5 GENERAL CONCLUSIONS

5.1 Thesis Summary

Waterfowl acquire energy and nutrient reserves for migration and reproduction at spring migration stopover areas (Ankney and MacInnes 1978, Krapu 1981, Alisauskas and Ankney 1992, Gauthier et al. 2003, Reed et al. 2004, Schmutz et al. 2006), and therefore spring migration habitat conditions can have important implications for waterfowl productivity. Along the Pacific coast, surf scoters (*Melanitta perspicillata*) and white-winged scoters (*M. fusca*) are known to congregate and forage at Pacific herring (*Clupea pallasii*) spawning sites during late winter and early spring (Vermeer 1981, Vermeer et al. 1997, Sullivan et al. 2002), and it has been speculated that scoters migrate northward in association with the northward progress of herring spawn (Vermeer 1981, Savard et al. 1998). In this thesis, I investigated site use of scoters during late winter and spring migration, with particular emphasis on the use of herring spawn at multiple geographic scales. First, I documented movement and habitat use of wintering radio-tagged surf scoters and white-winged scoters in relation to herring spawn prior to spring migration. Second, I identified important stopover and staging sites of migrating surf scoters, as well as the habitat attributes of these sites. Third, I considered the spatiotemporal associations of migrating surf scoters with herring spawn availability at regional and migratory scales. The results and implications of these efforts are described below.

In the Strait of Georgia, British Columbia, herring spawn events in late winter provide a short-term pulse of abundant and energy-rich food. In Chapter 2, I documented the movement and site use of wintering surf scoters and white-winged scoters before and during the period of herring spawn activity. I found that both scoter species exhibited relatively small movements during winter (interfix distances of 1.2 – 1.8 km, surf scoters and white-winged scoters respectively), but altered their behaviour markedly when herring spawn occurred, moving considerably farther with interfix distances of 6.3 km (white-winged scoters) and 9.9 km (surf scoters). Most (78-91%) individuals of both species visited herring spawn sites at least once, and the majority (60-82%) of telemetry locations were within 2 km of spawn sites during the herring spawn. Surf scoters and white-winged scoters moved from a wintering area with stable resource availability (Lewis et al. 2007a) to areas with ephemeral but abundant food resources. I conclude that scoters altered their movements to take advantage of herring spawn, and the large proportion of individuals using herring spawn suggests that this resource may be potentially important for pre-migratory scoters.

Habitat use by surf scoters during spring migration has not been previously studied in detail. In Chapter 3, I identified important stopover and staging sites used by surf scoters migrating through southeast Alaska from their wintering areas along the Pacific Coast. Based on locations of satellite transmitter marked surf scoters, I identified 14 important stopover and staging sites. One site, Lynn Canal, was determined to be an exceptionally important stopover and staging site for surf scoters from throughout their Pacific winter range; approximately half of the coastally migrating surf scoters used this site for stopover or staging. I compared the habitat attributes of stopover and staging sites

to randomly selected sites, and found that smaller distances to herring spawn sites and greater distances to the outer coast were strong predictors of site use, but physical shoreline habitat characteristics were poor predictors. I conclude that the availability of herring spawn and the geographical context within southeast Alaska defines selected and potentially important stopover and staging habitat for spring migrating surf scoters.

Given that herring spawn distribution was a strong predictor of surf scoter stopover and staging site use, I considered the spatiotemporal associations of migrating surf scoters with herring spawn availability along the British Columbia and southeast Alaska coasts (Chapter 4). I evaluated a silver-wave hypothesis, which predicts that surf scoters follow the availability of herring spawn northward along the coast during spring migration. I found strong support for the assumption that herring spawn activity initiates later in the year at higher latitudes, creating a wave of short-term localized food availability. I also found that surf scoter migration, based on locations of scoters marked with satellite transmitters, generally coincided with the northward progression of herring spawn. On a continental scale, the majority of marked scoters visited at least one spawn site during migration, and those that visited spawn sites were located at spawn sites for approximately a third of their migration locations. At a regional scale, surf scoters showed strong spatiotemporal associations with herring spawn sites, confirming that the presence of herring spawn may be an important factor in determining habitat use during spring migration. Although the distribution and timing of spawning activity does not explain all of the variation in continental migration strategies, herring spawn is a potentially important resource for many migrating surf scoters.

I found that scoters show strong spatiotemporal associations with herring spawn along the coasts of British Columbia and southeast Alaska throughout the late winter and spring. Although not all individuals visited spawn sites, the vast majority of individuals make use of this seasonal resource pulse when it is available, suggesting that it is a valuable seasonal resource. In considering herring spawn availability as a predictor of stopover and staging site use, herring spawn appears to be closely associated with site use during migration, but is not the only factor determining which sites are used. Similarly, herring spawn availability does not appear to drive surf scoter migration strategies, but appears to be used considerably when it is available along the migration route. Collectively, these studies show high use of herring spawn both before and during spring migration, and suggest that herring spawn is an important resource at a potentially sensitive time of the annual cycle.

This information contributes to general knowledge about surf scoter spring migration strategies, and will contribute to ongoing studies of body mass variation in relation to areas, seasons, and spawn occurrence. Habitat use of late spring-staging and migrating surf scoters may have important implications for understanding the cross-seasonal effects of habitat conditions and nutrient reserve levels on populations, and may have habitat management implications. By identifying used and presumably important spring habitats, this work defines specific sites that deserve conservation consideration, and provides insights into the underlying mechanisms that make these habitats important.

5.2 Future Directions

The strong associations of surf scoters with herring spawn sites both before and during migration suggest that herring spawn is likely an important resource for surf

scoters. However, use of this resource does not necessarily indicate that it is required. Therefore, further investigations of the influence of herring spawn on demographic attributes such as reproductive performance or survival are needed. There is evidence for body mass optimization in sea ducks prior to migration (Bond and Esler 2006), and surf scoters show marked increases in body mass both before and during spring migration (E. Anderson, University of Wyoming, unpublished data). Studies of harlequin ducks (*Histrionicus histrionicus*) indicated that nutrients from herring spawn are not allocated into egg production (Bond et al. 2007), however, the nutrients derived from herring spawn are most likely used for migration and during other stages of reproduction. Species that deplete winter foods, such as surf scoters (Lacroix 2001, Kirk et al. 2007) may be more likely to rely on herring spawn or other alternative prey for building energy reserves in late winter and early spring (Bond and Esler 2006). The benefits of herring spawn events may extend beyond nutritional value; scoters in Baynes Sound showed reductions in foraging time and decreased their dive rate when feeding on herring eggs (Lewis et al. 2007b), allowing for increases in non-foraging behaviours. Even if herring spawn is not directly responsible for the mass gain or nutrients used in clutch formation, the presence of an abundant and easily available food may facilitate other important components of the annual cycle such as courtship, pairing, incubation, and brood-rearing (Rodway et al. 2003).

There is need for further investigation into other factors that influence surf scoter migration strategies. There are numerous habitat attributes other than herring that may influence choice of stopover and staging sites that I was unable to address, and identifying the importance these attributes would provide greater information about

habitat use during spring. For example, sea duck distribution in winter is strongly related to bivalve distribution (Esler et al. 2000, Žydelis and Esler 2005, Žydelis et al. 2006), and this likely has implications for stopover and staging site use. This may be of particular importance in an area such as Lynn Canal, which is used heavily by scoters but has shown marked declines in herring spawn availability (Willson and Womble 2006). Scoters there are likely consuming mussels, and distribution and quality of mussel beds make dictate habitat use and condition of scoters in that important staging area. Also, safety and predator distributions are increasingly recognized as affecting shorebird migration strategies and this could influence migration strategies in sea ducks.

5.3 Management Implications and Recommendations

I found that surf scoter stopover and staging site use is strongly predicted by herring spawn availability, but that geographical context is also a strong predictor of stopover site use. This suggests that the use of spring migration habitats is influenced by multiple factors. As a result, the management and conservation of spring migration habitat requires the management of individual identified stopover sites, the aggregate value of multiple spring migration habitats, and the resources that make these sites attractive to migrants.

Identifying stopover sites for conservation recognition – I identified 14 important stopover sites within southeast Alaska, and the majority of marked surf scoters used one or more of these sites for both short stopovers and staging. This suite of stopover sites presumably has habitat value beyond the sum of its parts. I recommend that the data that identify important sites and habitat attributes (Chapter 3) be disseminated to agencies and organizations that identify, prioritize, and support initiatives that result in the

identification of important conservation areas for birds and marine coastal habitat. These organizations include the U. S. Fish and Wildlife Service, Alaska Department of Fish and Game (ADFG), U.S. Forest Service, National Park Service, and BirdLife International and its partner agencies, including Audubon.

In particular, Lynn Canal was identified as a particularly important stopover and staging area, as it was used by many scoters (>100 000 on a single day) from multiple wintering areas, many for more than 7 days. Lynn Canal is the most northeastern waterway in southeast Alaska, likely making this site a natural break for scoters to take advantage of abundant marine resources before turning inland to the boreal forests of northern Canada to breed. This region may also provide increased access to preferred routes inland. From a management and conservation perspective, this should make Lynn Canal a high priority for identification as a site of conservation concern. From survey estimates, this region may support almost a third of the global population of surf scoters for several weeks in May (Chapter 4), and fits several of the criteria for a globally important Important Bird Area under BirdLife International guidelines.

Identifying sites for risk management - Concentrations of birds in a very small area are at greater risk for catastrophic events such as contaminant spills (Ford et al. 1982). Lynn Canal and surrounding areas are heavily used during spring and summer by numerous tourism cruise ships, and the high numbers of birds congregated in this small area during this time period increases the risk of such events. I recommend that stopover site and survey data that highlights areas and times of higher risk should be distributed to agencies that manage contaminant spill response to aid in designing response plans in areas that are potentially critical for surf scoters and other species.

Managing important resources - Given the use of herring spawn by scoters, the management of sea ducks should be closely tied to management of Pacific herring. Declines and distributional shifts in herring stocks and traditional spawn sites means that the species that use herring spawn are increasingly restricted to fewer spawn sites (Stick 2005, Willson and Womble 2006). The management and conservation of herring spawn sites is likely important for not only surf scoters, but also the numerous other species of birds and mammals that use these sites (Haegele 1993, Sullivan et al. 2002, Willson and Womble 2006). I recommend communication and data sharing with fisheries agencies create management plans and objectives that include sea ducks as important consumers of herring spawn.

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