Spring migration routes and chronology of surf scoters (*Melanitta perspicillata*): a synthesis of Pacific coast studies

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Abstract: Understanding interconnectivity among wintering, stopover, and breeding areas of migratory birds is pivotal to discerning how events occurring in each might have a cross-seasonal effect on another. Such information can guide the location and timing of conservation efforts. Thus, we examined spring migration routes, chronology, and stopover use of 85 surf scoters (*Melanitta perspicillata* (L., 1758)) marked with satellite transmitters at four Pacific Flyway wintering sites: San Quintin Bay, Baja California; San Francisco Bay, California; Puget Sound, Washington; and Strait of Georgia, British Columbia. Eighty-three percent of marked scoters followed two main routes to the breeding area: a Southern Inland route involving staging in Puget Sound and Strait of Georgia and protracted inland migration, or a Northern Coastal route characterized by short movements along the Pacific coast of British Columbia and southeast Alaska with inland migration initiating from Lynn Canal and surrounding areas. Route choice was related to nesting site latitude in the Canadian Northern Boreal Forest. Data from birds tracked over 2 years indicated strong migration route fidelity, but altered chronology and stopover locations between years. Departure date varied by wintering site, but arrival and apparent settling dates were synchronous, suggesting individuals adjusted migration timing to meet an optimized reproductive schedule.

Résumé : La compréhension de l'interconnectivité entre les zones d'hivernage, d'arrêt et de reproduction chez les oiseaux migrateurs est essentielle si l'on veut voir comment les événements qui se passent dans chacune de ces zones peuvent avoir un effet lors d'une autre saison dans une autre zone. De telles informations pourraient orienter le choix des sites et du moment des interventions de conservation. Nous avons ainsi examiné les routes printanières de migration, leur chronologie et l'utilisation des points d'arrêt chez 85 macreuses à front blanc (*Melanitta perspicillata* (L., 1758)) munies d'émetteurs satellites à quatre sites d'hivernage sur la route de migration du Pacifique, la baie de San Quintin en Basse-Californie, la baie de San Francisco en Californie, Puget Sound au Washington et le détroit de Géorgie en Colombie-Britannique. Quatre-vingt trois pourcent des macreuses marquées suivent deux voies principales vers la zone de reproduction, une route du sud dans l'intérieur des terres comportant des arrêts à Puget Sound et au détroit de Géorgie avec une migration prolongée à l'intérieur des terres et une route côtière du nord caractérisée par de courts déplacements le long de la côte de la Colombie-Britannique et du sud-est de l'Alaska et une migration à l'intérieur des terres débutant au canal de Lynn et les environs. Le choix de route dépend de la latitude du site de nidification dans la forêt boréale du nord du Canada. Des données obtenues d'oiseaux marqués au cours de deux années indiquent une forte fidélité à la route de migration, mais la chronologie de la migration et les sites d'arrêt peuvent changer d'une année à l'autre. La date de départ varie en fonction du site d'hivernage, mais les dates d'arrivée et d'installation apparente sont synchronisées, ce qui laisse croire que les individus ajustent la chronologie de leur migration afin d'obtenir un calendrier optimal de reproduction.

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Introduction

Recent advances in the study of avian migration have underscored the important linkages between wintering, stopover, and breeding areas (Marra et al. 1998; Gill et al. 2001; Drent et al. 2003; Newton 2006), and the need to consider this interconnectivity in conservation planning (Mehlman et al. 2005). It is becoming increasingly clear that the timing of spring migration and quality of stopover sites can greatly influence reproductive success and female annual survival (Drent et al. 2006, 2007; Black et al. 2007), especially for arctic nesting species. Individuals are hypothesized to alter their migration strategies based upon decisions to minimize migration duration, maximize energy accumulation at stopovers, or avoid predation risk (Alerstam and Lindström 1990; Farmer and Wiens 1998, 1999; Vrugt et al. 2007), and ultimately optimize their fitness.

As techniques for studying migration improve (e.g., Webster et al. 2002), so too does our opportunity to examine individual migration strategies. For example, satellite telemetry has greatly advanced our ability to observe strategies of individuals under different climatic conditions (Miller et al. 2005) or across time (Berthold et al. 2002; Alerstam et al. 2006; Mosbech et al. 2006) at continental spatial scales. Understanding migration ecology from the basis of individual behavioral strategies allows us a powerful means of predicting the effects of future habitat changes by extrapolating individual responses to populations (Sutherland 1996; Atkinson et al. 2005). This is particularly important in the case of rapidly declining sea duck populations, many of which rely on habitats such as coastal waters and boreal lakes where resources are predicted to be altered dramatically as a result of climate change (Stewart et al. 1998; Harley et al. 2006).

Surf scoters (*Melanitta perspicillata* (L., 1758)) are sea ducks that winter along the Pacific and Atlantic coasts of North America and breed in low densities across the boreal forests of Alaska and Canada (Savard et al. 1998; Takekawa et al. 2010). Based on breeding and wintering area surveys, surf scoters have undergone long-term declines (Savard et al. 1998; Trost 2002; Nysewander et al. 2003), particularly in the western part of their range (Goudie et al. 1994; Hodges et al. 1996). Until lately surf scoters were one of the least studied waterfowl species in North America (Bellrose 1980; Savard et al.1998), and this lack of basic knowledge has hindered our ability to determine causes of decline.

Recent work has helped define the breeding range of Pacific coast surf scoters and has shown that birds from different wintering sites co-mingle across this area (Takekawa et al 2010). However, little is known about the timing of their spring migration and the routes that scoters follow from various Pacific coast wintering sites to the breeding grounds (see Savard et al. 1998). Individuals wintering in separate regions may experience variation in overwinter conditions that could differentially influence their subsequent migration timing or strategies and their breeding success, and this may ultimately translate into population-level effects (Gill et al. 2001; Newton 2004). Additionally, previous work with shorebirds has demonstrated how integrated observations of migratory populations and identification of broad regional patterns provide a much more complete picture of migration than do inferences based on observations from small segments of the population (Warnock and Bishop 1998; Farmer and Wiens 1999). Understanding how individual and regional migration strategies may influence the overall population will ultimately help direct management actions for conservation of surf scoters (Sea Duck Joint Venture (SDJV) Management Board 2001).[3]

We integrated data from satellite telemetry studies conducted at four major Pacific coast wintering sites to examine the spring migration strategies of individual surf scoters in western North America. These projects were initiated to examine migration from each wintering site separately; however, the similarities in timing and methodology of each project provided us with a unique opportunity to compare the routes and chronology of surf scoters wintering at different latitudes. Specifically, our objectives were to (*i*) establish primary spring migration routes of individuals from each wintering site; (*ii*) compare migration chronology among scoters from each wintering site, including arrival timing and settling dates at nesting sites in the Northern Boreal Forest; (*iii*) evaluate how winter body mass and wintering site departure timing relates to subsequent migration timing; and (*iv*) identify important stopover and staging areas.

## Materials and methods

Study area

We compiled migration data from surf scoters marked with platform transmitter terminals (PTTs) at four sites within their wintering range along the Pacific coast of North America (Fig. 1): San Quintin Bay, Baja California, Mexico (SQ; 116.0°W, 30.4°N); San Francisco Bay, California, USA (SF; 122.4°W, 37.8°N); Puget Sound, Washington, USA (PS; 122.4°W, 47.5°N); and Strait of Georgia, British Columbia, Canada (SG; 122.4°W, 49.3°N). While PS and SG are geographically close together, radio-marked birds from these sites tracked over the same time period as PTT-marked birds in the current study had high site fidelity to marking sites and maintained small home ranges over winter that rarely overlapped with each other (Kirk et al. 2008; J.R. Evenson and D.R. Nysewander, unpublished data; D. Esler, unpublished data). Because birds from these sites remained largely distinct from each other, our a priori assumption was that migration strategies could vary between them; thus, we chose to analyze data from these two marking sites separately. We examined spring migration chronology and routes along the Pacific coast from Baja San Quintin north to southeast Alaska, and through the Canadian provinces of British Columbia, Yukon Territory, and Alberta to the Northern Boreal Forest breeding areas of western Canada and eastern Alaska (Takekawa et al. 2010).

Capture and marking

We captured wintering surf scoters in floating mist nets using decoys (SQ, SF, PS, and SG; Kaiser et al. 1995) or

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[3] Sea Duck Joint Venture (SDJV) Management Board. 2001. Sea Duck Joint Venture Strategic Plan: 2001–2006. SDJV Continental Team. Unpublished Report, c/o USFWS, Anchorage, Alaska, USA, and Candian Wildlife Service, Sackville, N.B., Canada.

Fig. 1. Study site map showing winter marking sites (solid black polygons) and the locations and codes of the Pacific coast migration stop-over areas of surf scoters (*Melanitta perspicillata*) discussed in the text. We divided the spring migration route into these broad biogeographic migration areas to facilitate discussion of routes and to calculate mean stopover length of stay. From south to north the full names corresponding to the abbreviated codes are as follows: Coastal Migration Areas — San Quintin Bay (SQ), Baja California Coast (BC), Southern California Coast (SC), Central California Coast (CC), San Francisco Bay (SF), Northern California Coast (NC), Oregon Coast (OC), Columbia River Mouth (MC), Washington Coast (WC), Puget Sound (PS), Strait of Georgia (SG), Outer Vancouver Coast (VC), Queen Charlotte Sound (QC), Petersburg Southeast Alaska Coast (PK), Haines Southeast Alaska Coast (HK); Interior Migration Areas — Southern Inland British Columbia (SB), Central Inland British Columbia (CB), Northern Inland British Columbia (NB), Yukon Territory (YK), Lesser Slave Lake Alberta (LS), Cariboo Mountains Alberta (CM).
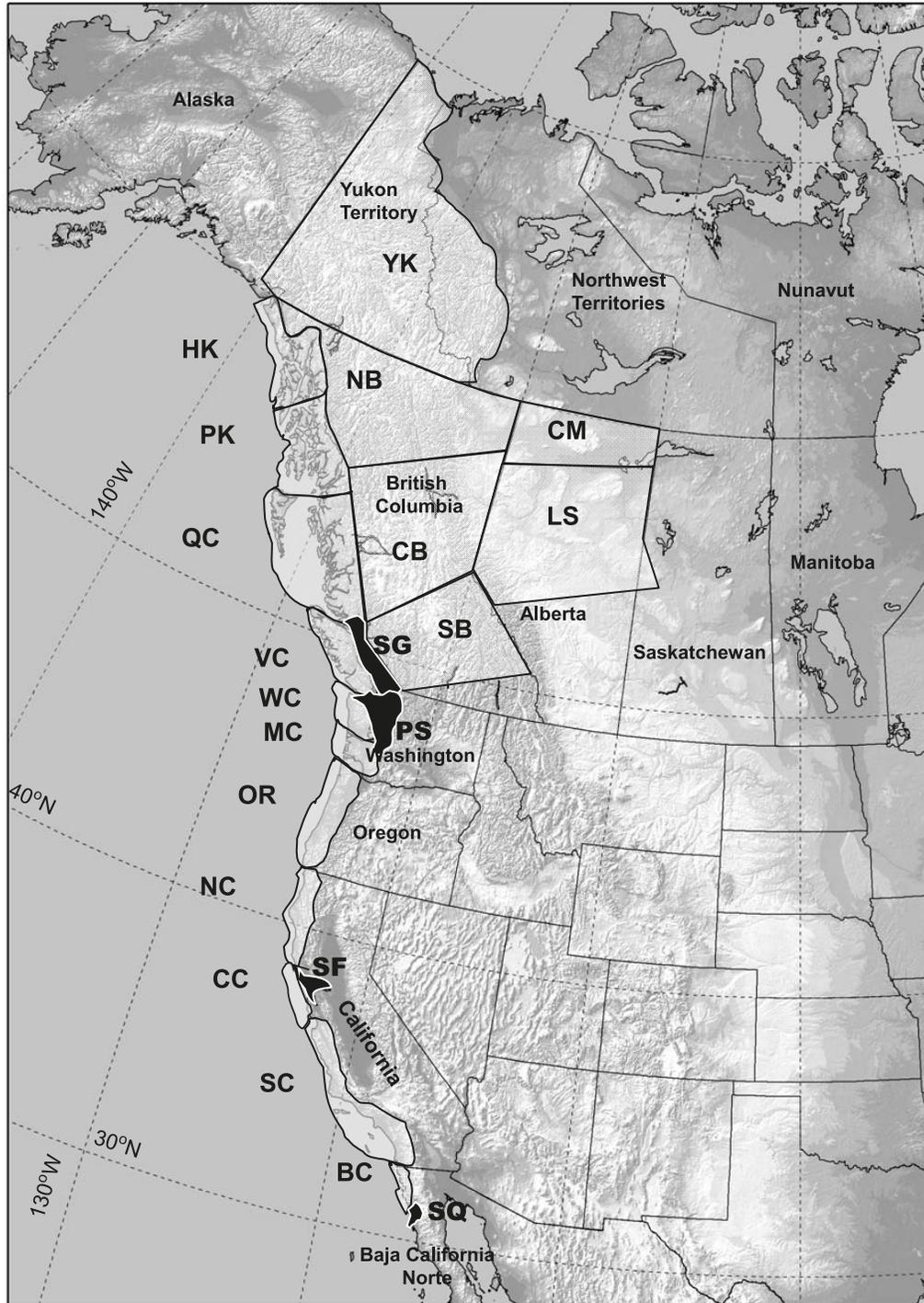
from small boats with a netgun (SQ and SF; Coda Enterprises, Inc., Mesa, Arizona, USA). Marking periods ranged from 8 to 27 February 2005 and 2006 in SQ; from 3 January to 27 February 2003, 2005, and 2006 in SF; from 20 November to 28 March 2003, 2004, 2005, and 2006 in PS; and from 1 to 30 November 2005 in SG. We banded, weighed, and measured each captured bird, used a combination of plumage characteristics and cloacal examination to determine sex, and estimated bursal depth to determine age (Mather and Esler 1999; Iverson et al. 2003). Coelomic implant transmitters with external antennas (38 g each, PTT-100; Microwave Telemetry, Inc., Columbia, Maryland, USA) were surgically implanted (Olsen et al. 1992; Korschgen et al.1996; Mulcahy and Esler 1999) in after 2nd year (ASY) male and female scoters. Implant transmitters are less disruptive and cause fewer behavioral modifications than external attachment methods for some wild waterfowl (Rotella et al. 1993; Hupp et al. 2003) and coelomic implant transmitters are preferred for scoters relative to other transmitter types when data are collected over a long period of time (Iverson et al. 2006). Marked birds were released after a recovery period of between 2 and 6 h. Sex of marked scoters varied at each marking site (Table 1); however, the majority of birds (84%) were adult female. All capture, handling, and marking of scoters was carried out under the guidance of the Animal Care and Use Committees at each investigator's institution or organization, with permits from California Department of Fish and Game, Canadian Wildlife Service, Washington Department of Fish and Wildlife, U.S. Fish and Wildlife Service, U.S. Geological Survey (USGS) Bird Banding Laboratory, and Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT).

Location data

All PTTs were programmed to transmit data for 6–8 h and turn off for 48–96 h, with the exception of two PTTs from PS that transmitted for 6 h and turned off for 144 h during spring migration. Transmitter signals were received by U.S. National Oceanic and Atmospheric Administration polar-orbiting weather satellites, and CLS America (Largo, Maryland) estimated transmitter location on the basis of Doppler shifts in transmitter frequencies. Location accuracy classes were determined based on satellite-to-PTT geometry, the number of transmissions received from the PTT, and the stability of the PTT transmission frequency during a satellite pass. For location classes (LC) 3, 2, 1, and 0, CLS America rated accuracy as <150, <350, <1000, and >1000 m, respectively. Accuracy was not provided for LC A (3 messages received by satellite), LC B (2 messages), and LC Z (latitude and longitude often provided if >1 message received). Data from each wintering site were compiled at the USGS Western Ecological Research Center and filtered using systematic plausibility tests of direction, distance, and rate of movement between locations (Douglas 2006). The filtering program was set to ensure that LC 1–3 locations were always retained. We used all filtered locations to calculate chronological dates; however, to plot overall migratory routes, we used a more restrictive filter (Douglas 2006) that chose the best location from every reporting cycle.

We used ArcMap version 9.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to plot and analyze the selected locations and delineate migration routes. We divided coastal and interior routes used by surf scoters into broad migration stopover and staging areas (Fig. 1; see legend for full area names) of similar biogeography along a latitudinal gradient. These migration areas were used to determine the numbers of scoters following identified routes and to facilitate discussion of differences in migratory strategies among individuals from different wintering sites.

Estimating migration duration and dates

Length of stay (LOS) in a particular migration area was estimated as the difference between the departure date from that area and the arrival date in that area plus one to account for the fact that the bird could have been present in the area both on the day of arrival and on the day of departure. Following Warnock and Bishop (1998), we defined a 2–7 day use of a migration area as a stopover event, and >7 days use of an area as a staging event. Staging areas have been defined as predictable locations with abundant feeding resources where birds can fatten significantly and have long lengths of stay (Skagen and Knopf 1994; Warnock and Bishop 1998); thus, we distinguished between these two events to identify important staging areas along migration routes.

We defined the departure date from a wintering site as the median date between the last location at the wintering site and the first location in a new migration area (Fig. 1). Similarly, we estimated departure date from coastal to inland areas as the median date between the last coastal location and the first interior location. Breeding ground arrival date was estimated as the median date between last interior location and first location in the breeding range as defined by the distribution of the marked population (see Takekawa et al. 2010). We used the median date between arrival in the breeding area and the first day a bird was located in an apparent nesting area (typically an area <20 km²) where it remained for ≥25 days (following Takekawa et al. 2010) as the settling (nest initiation) date for females. Paired males typically leave females about 3 weeks after arriving to breeding lakes (Savard et al. 1998); thus, we used males in our calculation of settling date only if they remained in an apparent nesting area for ≥21 days. For some birds, breeding area arrival date was the same as the settling date if the first location in the breeding area was in the apparent nesting area for that bird. Finally, we estimated total migration duration as the difference between the settling date and the wintering site departure date plus 1 day to include both the departure day and the arrival day in the calculation. We present all dates in ordinal, or day of year, format as specified by the International Organization for Standardization.

Statistical analysis

We used linear regression (PROC REG; SAS Institute Inc. 2005) to model the relationship between body mass at time of capture and wintering site departure date of scoters from PS and SF. We did not adjust mass for structural size to obtain an estimate of body condition, given that recent work shows using unverified body condition indices provides no improvement over using body mass alone to predict

Table 1. Summary of surf scoters (*Melanitta perspicillata*) marked with satellite transmitters (platform transmitter terminal; PTTs) in 2003–2006 from four different wintering sites: San Quintin Bay, Baja California, Mexico (SQ); San Francisco Bay, California, USA (SF); Puget Sound, Washington, USA (PS); and Strait of Georgia, British Columbia, Canada (SG).

	SQ		SF		PS		SG		
Year	Male	Female	Male	Female	Male	Female	Male	Female	Total
2003	0	0	0	8	0	0	0	0	8
2004	0	0	0	0	4	3	0	0	7
2005	0	2	0	9	2	14	4	4	35
2006	0	3	0	12 (5)	2	8 (5)	0	0	35
Total	0	5	0	34	8	30	4	4	85

Note: Numbers represent scoters that departed from wintering areas in each year. The number of birds that produced 2 years of data during any part of spring migration is shown in parentheses.

condition and can actually lead to reduced predictability of fat stores in some species (Schamber et al. 2009). Therefore, in the absence of a verified condition index for scoters, we felt that the best practice was to use body mass for our regression analysis. We also only used birds marked during January and February and excluded those marked in the fall, because earlier marked birds may fluctuate substantially in mass over the winter. Nearly all males were marked during the fall, and we excluded the few males marked in spring ($n = 5$) and conducted this analysis only on females. For all individuals, we used linear regression to model the relationship between wintering site departure and migration duration, coastal departure latitude, breeding area arrival date, and settling date, as well as to examine coastal departure latitude, which marks the beginning of interior migration, in relation to final nesting latitude.

We used one-way ANOVA (PROC GLM; SAS Institute Inc. 2005) to determine if departure, arrival, and settling dates, stopover LOS, and migration duration varied by wintering site. We also compared these variables within each wintering site among birds using different migration routes. For these analyses, we combined data across years and sexes because sample sizes were not large enough to permit consideration of these variables (Table 1). Statistical analyses were performed with SAS version 9.1 (SAS Institute Inc. 2005), and we used the Tukey–Kramer method to make multiple comparisons among wintering sites while preserving type I error. The significance value for all tests was $\alpha < 0.05$.

Results

Location data

We used location data from all birds that departed their wintering sites and progressed in a northward direction ($n = 85$; see Table 1). As migration progressed, the sample size decreases owing to transmitter failure or battery drain, as well as scoter mortality ($n = 1$ confirmed mortality). Of the 85 birds that left wintering areas, we tracked 74 throughout the entire breeding season. We received a total of 33 081 locations between 1 February and 15 June from 2003 to 2006, but 1.6% of these were discarded as outliers by the plausibility filtering program. The remaining locations were categorized as LC 3 (16.7%), LC 2 (16.6%), LC 1 (18.5%), LC 0 (12.5%), LC A (15.9%), LC B (18.1%), and LC Z (1.8%).

Migration strategies

Routes

Scoters from all wintering sites used coastal migration routes (Figs. 2*a*–2*d*) and used several areas for stopovers. North of Puget Sound, most scoters traveled along the interior passages of large coastal islands (Strait of Georgia, Queen Charlotte Sound, and Hecate Strait, British Columbia; the Inside Passage, Alaska) with the exception of seven SF scoters that used the western edge of Vancouver Island, British Columbia.

The majority of scoters from all four marking sites followed two main routes from the point of PS and SG onward. Forty-two percent of all birds migrating inland followed a Southern Inland route, in which they began their migration inland from PS and lower SG areas. Scoters using the Southern Inland route sometimes staged in PS or SG, and typically displayed a protracted inland migration. Forty-one percent of all birds that migrated inland used a Northern Coastal route, flying along the coast of British Columbia and southeast Alaska, usually making frequent stops, and finally departing for inland migration from the northern end of the Inside Passage of southeast Alaska (Figs. 2*a*–2*d*, Table 2). A smaller number used an Intermediate Coastal route in which they made some coastal stopovers and migrated inland from various river mouths and deltas within the Queen Charlotte Sound and Petersburg Southeast Alaska migration areas (13%; Figs. 2*a*–2*d*, Table 2). In addition, two scoters continued farther north and began their interior migration near the Copper River Delta, Alaska (144.6°N, 60.2°W) and from Cook Inlet, Alaska (152.7°N, 60.2°W; Figs. 2*a*, 2*b*). One SQ scoter migrated interior from the mouth of the Columbia River, Washington (124.2°N, 46.7°W); however, its PTT stopped transmitting in Southern Central British Columbia. Routes taken by these three birds were termed Other (Table 2).

Among wintering sites, mean coastal departure latitude for inland migration did not vary ($F_{[3,74]} = 2.50$, $P = 0.066$). However, the Northern Coastal route was the single most common path for scoters marked in SQ (50%), SF (53%), and SG (50%; Table 2). Fifty-six percent of PS marked scoters used the Southern Inland route to the breeding area (Table 2). For scoters from all of the marking sites, coastal departure latitude was positively related to final nesting latitude (PROC REG: $F_{[1,74]} = 57.05$, $P < 0.0001$, $r^2 = 0.44$; Fig. 3).

Fig. 2. Migration routes of surf scoters (*Melanitta perspicillata*) marked at four Pacific coast wintering sites: (*a*) Strait of Georgia (SG), (*b*) Puget Sound (PS), (*c*) San Francisco Bay (SF), and (*d*) San Quintin Bay (SQ). Routes depicted include those of all birds that made a complete migration from wintering site to the Northern Boreal Forest breeding area. Colored arrows in *a* represent the Southern Inland (blue), the Intermediate Coastal (clear), and the Northern Coastal (yellow) routes.
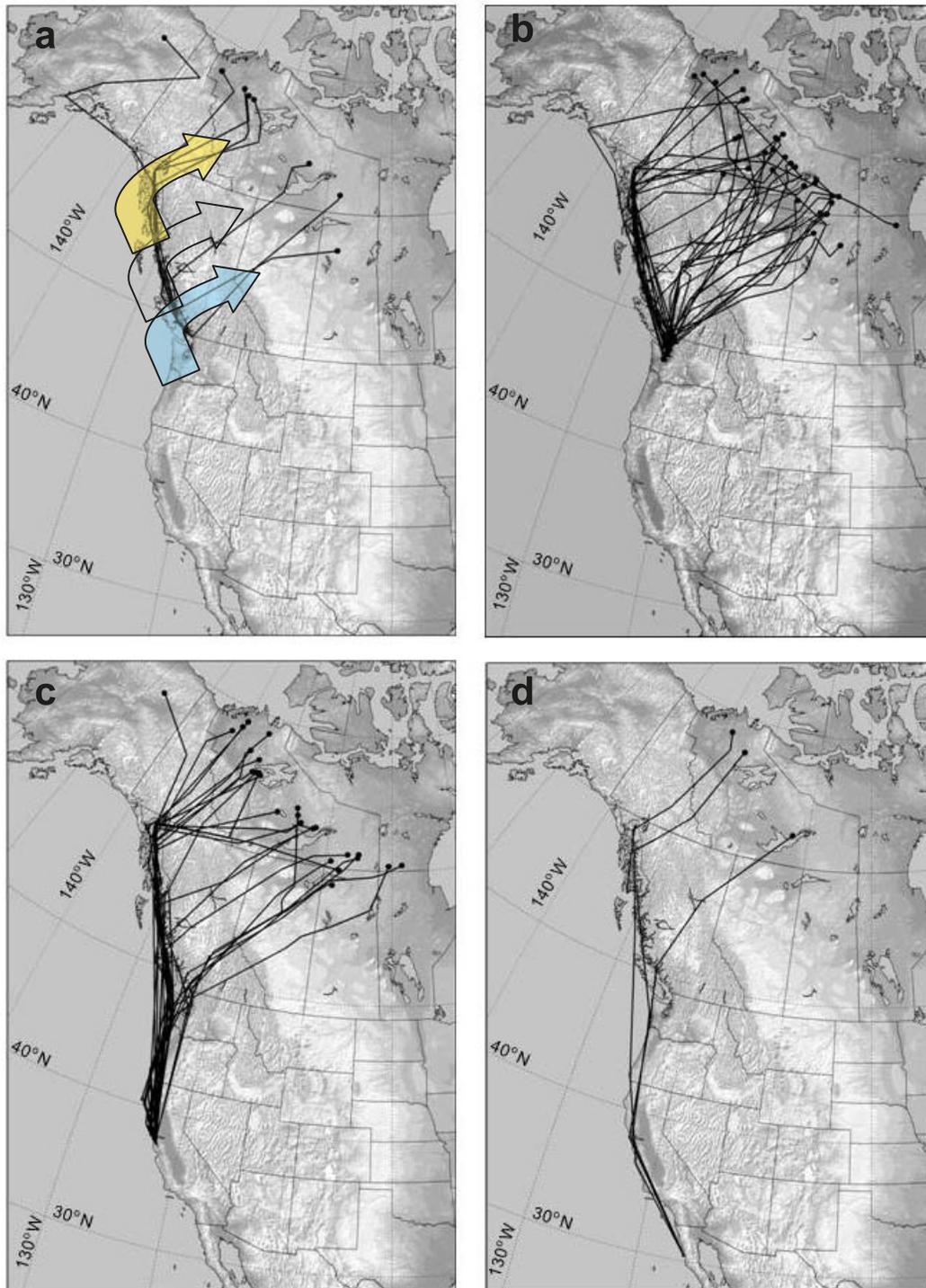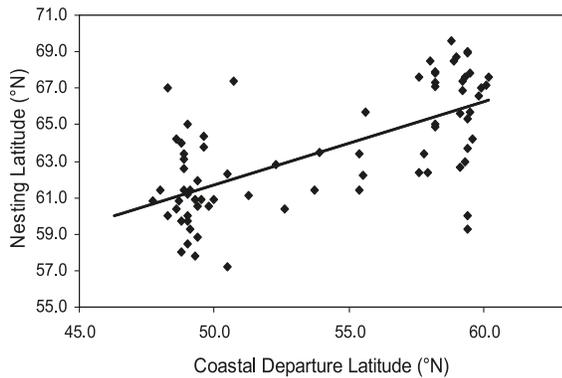

Individual scoters most commonly initiated inland migration from river mouths and sounds, and interior routes usually followed a north to northeast orientation to nesting sites (Figs. 2*a*–2*d*). All birds following the Southern Inland route traveled across the Fraser River Plateau in the Central In-land British Columbia migration area (see Fig. 1) and then through the Lesser Slave Lake or Cariboo Mountain migration areas, en route to nesting sites in the Northwest Territories and Saskatchewan. Scoters following the Northern Coastal route traveled through the mountains in Northern In-

Table 2. Percentage and number of surf scoters (*Melanitta perspicillata*) from each Pacific coast wintering site (San Quintin (SQ), San Francisco Bay (SF), Puget Sound (PS), Strait of Georgia (SG)) that followed each migratory route to the breeding area.

Wintering site	n	Southern Inland	Intermediate Coastal	Northern Coastal	Other
SQ	4	25 (1)	0	50 (2)	25 (1)
SF	30	33 (10)	13 (4)	53 (16)	0
PS	36	56 (20)	14 (5)	28 (10)	2 (1)
SG	8	25 (2)	12.5 (1)	50 (4)	12.5 (1)
Overall	78	42 (33)	13 (10)	41 (32)	4 (3)

Fig. 3. Scatterplot chart depicting the relationship between coastal departure latitude and ultimate nesting site latitude of Pacific coast surf scoters (*Melanitta perspicillata*). The linear regression equation describing the fit of the line is $y = 0.4544x + 39$, $r^2 = 0.4353$.

Fig. 4. Cumulative proportion of surf scoters (*Melanitta perspicillata*) departing over time for spring migration from four Pacific coast wintering sites: (*a*) Strait of Georgia (SG), (*b*) Puget Sound (PS), (*c*) San Francisco Bay (SF), and (*d*) San Quintin Bay (SQ). Mean departure dates are represented by vertical black lines and median dates by vertical gray lines. Departure dates ranged from 20 February to 30 May, and mean departure date from SF was significantly earlier than mean departure date from PS ($F_{[3,84]} = 4.64$, $P = 0.005$).
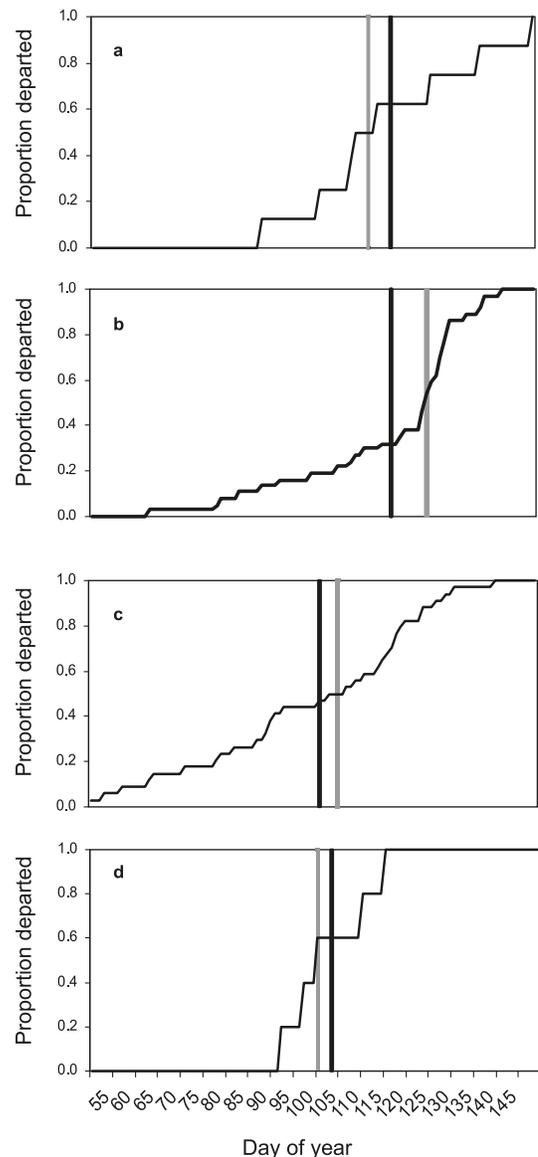

land British Columbia and Yukon Territory to nesting sites in the Northwest Territories. Fifty-six percent of scoters departing on the Northern Coastal route left from the Taiya Inlet, north of Haines, Alaska. These birds mainly traveled through Chilcoot and White Pass into Northern Inland British Columbia and across Yukon Territory mountain ranges to nesting sites at or north of the Great Bear Lake in the Northwest Territories (Figs. 2*a*–2*b*). Scoters departing from lower latitudes near Haines or from the Queen Charlotte Sound and Petersburg Southeast Alaska migration areas traveled through Central Inland British Columbia and the Cariboo Mountain areas, or through Northern Inland British Columbia and Yukon Territory to reach their nesting areas.

Chronology

Mean winter departure date was variable among sites, but was significantly different only between SF and PS ($F_{[3,84]} = 4.64$, $P = 0.005$; Figs. 4*a*–4*d*, Table 3). Departure dates ranged from 20 February (SF 2006) at the earliest to 30 May (SG 2005) at the latest (Figs. 4*a*–4*d*, Table 3). We found that body mass was significantly related to female winter departure date, and lighter birds left wintering sites later (PROC REG: $F_{[1,44]} = 10.62$, $P = 0.002$, $r^2 = 0.18$; Fig. 5).

Mean departure date from the coast to inland migration corridors was significantly different only between SF and PS ($F_{[3,74]} = 4.69$, $P = 0.005$; Table 3) such that PS birds departed earlier than SF birds. Breeding area arrival dates did not vary significantly among wintering sites ($F_{[3,71]} = 2.55$, $P = 0.063$; Table 3). We found no significant difference in settling dates among wintering sites ($F_{[3,70]} = 2.01$, $P = 0.121$). The mean difference between arrival and
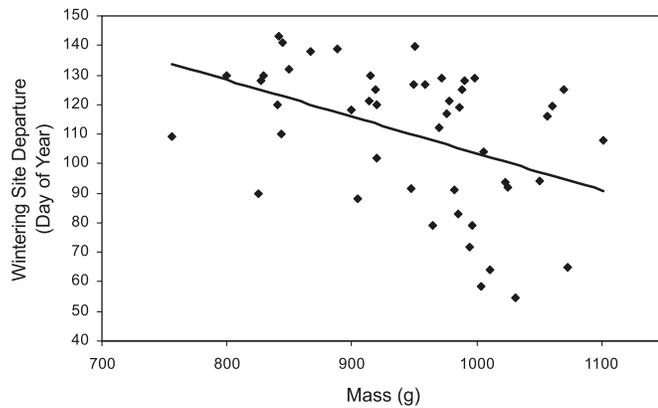
Table 3. Wintering site departure, coastal departure for inland migration, breeding area arrival, and settling ordinal dates by wintering site (San Quintin (SQ), San Francisco Bay (SF), Puget Sound (PS), Strait of Georgia (SG)) and migration strategy (Southern Inland, Intermediate, Northern Coastal) for Pacific coast surf scoters (*Melanitta perspicillata*).

Wintering site	Route	Winter departure		Coastal departure		Arrival		Settling		Difference between arrival and settling	
		Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n
SQ	Southern Inland	111.0	1	144.0	1	149.0	1	151.0	1	2.0	1
	Intermediate Coastal	—		—		—		—		—	
	Northern Coastal	108.5±7.5	2	148.8±3.8	2	154.5±5.5	2	161.8±3.8	2	7.3±1.8	2
	Overall*	103.8±4.2AB	5	144.6±3.2AB	4	152.7±3.7	3	158.2±4.2	3	5.5±2.0	3
SF	Southern Inland	104.8±7.0	10	136.4±2.4	10	145.4±2.1	10	149.0±2.1	10	3.6±1.0	10
	Intermediate Coastal	103.3±11.1	4	139.0±3.9	4	142.0±3.3	4	146.5±3.3	4	4.5±1.6	4
	Northern Coastal	100.1±5.6	16	143.6±1.9	16	145.5±1.7	15	147.5±1.7	15	2.0±0.8	15
	Overall*	100.5±4.2A	34	140.6±1.5A	30	145.0±1.2	29	147.9±1.2	29	2.9±0.6	29
PS	Southern Inland	128.8±3.4a	20	130.9±1.3a	20	142.6±1.3	20	148.2±2.4	19	5.2±1.8	19
	Intermediate Coastal	103.8±6.8b	5	134.8±2.6a	5	143.8±2.6	5	148.3±1.9	4	5.3±3.4	4
	Northern Coastal	112.1±4.8b	10	142.5±1.8b	10	144.8±1.9	9	151.2±3.4	9	6.4±2.7	9
	Overall*	118.2±3.1B	8	134.8±1.2B	38	143.2±1.0	35	149.8±1.7	34	6.4±1.3	34
SG	Southern Inland	144.0±4.4a	2	144.0±3.2	2	149.0±4.0	2	150.0±4.5	2	1.0±1.3	2
	Intermediate Coastal	127.0	1	143.0	1	144.0	1	149.0	1	5.0	1
	Northern Coastal	109.0±3.1b	4	138.3±2.2	4	139.8±2.9	4	142.5±3.2	4	2.8±0.9	4
	Overall*	117.5±7.0AB	8	140.4±1.6AB	8	143.1±2.1	8	145.4±2.1	8	2.3±0.7	8

Note: We compared chronology among wintering sites and reported differences in the Overall row using uppercased letters. We also compared chronology by strategy within wintering areas and reported differences using lowercased letters under each wintering site. The absence of letters indicates no significant differences.

*Sample size (n) for each Overall category includes birds that began migration but stopped transmitting before beginning inland migration. These birds were never assigned a migration strategy and thus are not included in calculations of means by strategy. In addition, because of the small sample size (n = 3), we did not calculate means for the Other migration strategy; however, scoters using this strategy were included in the calculation of overall means.

Fig. 5. Scatterplot chart depicting the relationship between the unadjusted body mass of female surf scoters (*Melanitta perspicillata*) and departure date across all wintering sites. The linear regression equation describing the fit of the line is $y = -0.1243x + 227.75$, $r^2 = 0.1833$.

settling at apparent nesting sites ranged from 2.3 ± 0.7 days (SG) to 6.4 ± 1.3 days (PS) and did not differ among birds from all wintering sites ($F_{[3,70]} = 2.36$, $P = 0.078$; Table 3). Wintering site departure date was positively related to breeding area arrival date and to settling dates (PROC REG; arrival: $F_{[1,74]} = 8.33$, $P = 0.005$, $r^2 = 0.10$; settling: $F_{[1,73]} = 8.58$, $P = 0.005$, $r^2 = 0.11$); however, it was not related to coastal departure date for interior migration (PROC REG: $F_{[1,77]} = 0.75$, $P = 0.39$, $r^2 = 0.01$).

We also compared chronology by migration route within each wintering site (Table 3). We excluded Other migration routes because of the small number of birds using them ($n = 3$). We found significant differences in chronology by route for PS and SG birds only. Birds from both areas using the Northern Coastal route departed the wintering area significantly earlier than those using the Southern Inland route or, in the case of PS, Intermediate Coastal routes (PS: $F_{[2,32]} = 7.68$, $P = 0.002$; SG: $F_{[2,4]} = 21.11$, $P = 0.008$). PS scoters using the Northern Coastal route departed the coast for inland migration significantly later than PS birds following the Southern Inland and Intermediate Coastal routes ($F_{[2,32]} = 13.58$, $P < 0.0001$).

Migration duration and stopover areas

The total duration of spring migration by individuals ranged from 1.5 days (PS 2006) to 90.5 days (SF 2006) across all years and wintering sites. The mean total duration of migration differed significantly only between PS and SF scoters ($F_{[3,70]} = 4.64$, $P = 0.005$); SF scoters took longer to migrate compared with PS scoters (Table 4). The mean duration of coastal migration was significantly shorter for PS birds compared with SF birds, but was not different among any of the other wintering sites ($F_{[3,74]} = 9.22$, $P < 0.0001$; Table 4). The duration of inland migration was significantly longer for PS scoters compared with birds from SQ, SF, and SG ($F_{[3,70]} = 8.71$, $P < 0.0001$; Table 4). We found positive relationships between winter departure date and total migration duration (PROC REG: $F_{[1,73]} = 381.04$, $P < 0.0001$, $r^2 = 0.84$), marine migration duration (PROC REG: $F_{[1,77]} = 443.15$, $P < 0.0001$, $r^2 = 0.85$), and inland migration duration (PROC REG: $F_{[1,73]} = 4.74$, $P = 0.032$, $r^2 = 0.06$).

Individuals made between 0 and 9 stopovers at coastal areas, and between 0 and 5 stopovers at inland areas. The mean number of coastal migration areas in which scoters stopped was significantly different among wintering sites ($F_{[3,75]} = 10.41$, $P < 0.0001$), and SQ birds had the greatest number of stops in migration areas (Table 4, Fig. 6). In contrast, we did not find any difference in the number of stops in inland migration areas among wintering sites ($F_{[3,70]} = 1.99$, $P = 0.123$; Table 4). Mean LOS at coastal migration areas was significantly longer for SF compared with PS scoters ($F_{[3,75]} = 5.89$, $P = 0.001$; Table 4). There were no differences in mean LOS at inland migration areas among scoters from each wintering site ($F_{[3,70]} = 1.92$, $P = 0.134$). Length of stay at coastal migration areas decreased with later winter departure dates from all wintering sites (PROC REG: $F_{[1,77]} = 82.47$, $P = 0.0001$, $r^2 = 0.52$); however, we found no relationship between length of stay at inland migration areas and departure dates from all wintering sites (PROC REG: $F_{[1,73]} = 0.00$, $P = 0.95$, $r^2 = 0.00$).

Among migration stopover areas that we defined on the lower Pacific coast (below Puget Sound; Fig. 1), the largest number of birds stopped along the Oregon coast ($n = 23$, 59% of SQ and SF migrants; Fig. 6). Although individuals stopped in each general migration region that we identified, SQ birds mainly used three lower Pacific coast areas for staging (Baja California Coast, San Francisco Bay, Oregon coast), whereas SF birds staged only in central California (Fig. 6). Puget Sound and outer Vancouver Coast were used as staging areas only by SF scoters. Above the Strait of Georgia, each stopover area was used by scoters from all wintering areas (Fig. 6), with the exception that PS and SQ scoters stopped but did not stage in Queen Charlotte Sound. Of migration areas available to scoters from all winter marking sites, Haines Southeast Alaska had the greatest use ($n = 39$) and the longest mean LOS (mean $\pm$ SE: SQ = 31.5 $\pm$ 11.6 days; PS = 13.89 $\pm$ 2.46 days; SG = 21.24 $\pm$ 1.75 days) for birds from all marking areas except SF. All SF scoters that staged in PS used the Southern Inland route and stayed 27.6 $\pm$ 6.4 days in PS. SF scoters that used the Northern Coastal route staged in the Haines Southeast Alaska migration area for 19.6 $\pm$ 1.89 days. All but two scoters that arrived in the breeding area made at least one stop at an interior migration area. Overall, Lesser Slave Lake had the greatest use of any single interior migration area, with 24 (31%) of all inland migrating birds stopping in this area. Stopover sites on the Fraser River Plateau (Southern Inland British Columbia and Central Inland British Columbia combined) were used by 34 (44%) of all birds. For scoters using the Northern Coastal route, Yukon Territory was the most heavily used stopover site. Twenty-one birds (27% of all inland migrating birds, 66% of birds migrating from Haines Southeast Alaska) stopped in the Yukon Territory migration area, but only PS birds staged in this area (Fig. 6).

Route fidelity

We obtained 2 years of migration data for 6 female surf scoters (SF = 3, PS = 3) in the spring of 2005 and 2006. All six birds followed very similar routes in both years (Fig. 7) with some differences in the number of stopover
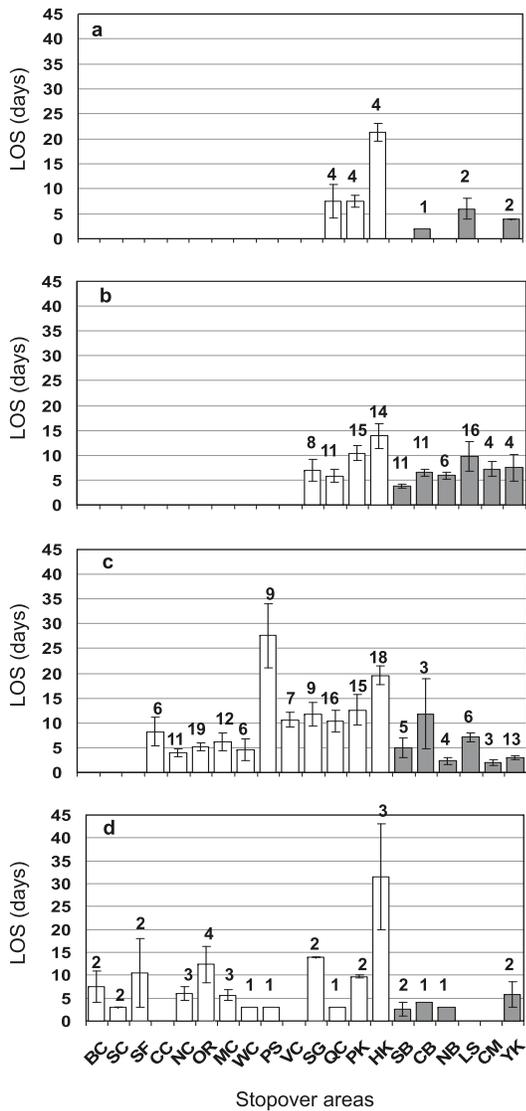
Table 4. Migration duration, number of stops in migration areas, and length of stay (LOS) by wintering site (San Quintin (SQ), San Francisco Bay (SF), Puget Sound (PS), Strait of Georgia (SG)) and migration strategy for Pacific coast surf scoters (*Melanitta perspicillata*).

| | | Total duration (days) | | Coastal | | | | | | Inland | | | | | |
| | | | | Duration (days) | | Stops | | LOS (days) | | Duration (days) | | Stops | | LOS (days) | |
Wintering site	Route	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*
SQ	Southern Inland	41.0	1	33.0	1	2.0	1	16.5±3.2	1	8.0	1	2.0	1	3.5±1.6	1
	Intermediate Coastal	—	2	—		—		—		—		—		—	
	Northern Coastal	54.3±11.3		40.3±11.3	2	5.0±0.0	2	8.1±2.3	2	14.0±0.0	2	2.5±0.5	2	5.4±1.1	2
	Overall*	49.8±7.9AB	3	38.1±4.9AB	4	4.0±0.7A	4	10.6±2.2AB	4	12.0±2.0A	3	2.3±0.3	3	4.8±0.9	3
SF	Southern Inland	45.2±6.3	10	31.6±5.8	10	2.6±0.4a	10	15.6±3.0	10	13.7±1.3a	10	2.7±0.2a	10	6.3±1.4	10
	Intermediate Coastal	44.3±10.0	4	35.8±9.1	4	5.0±0.6b	4	7.4±4.8	4	8.5±2.0ab	4	1.8±0.4ab	4	4.1±2.2	4
	Northern Coastal	49.0±5.2	15	43.5±4.6	16	3.9±0.3b	16	12.3±2.4	16	5.0±1.1b	15	1.3±0.2b	15	3.3±1.2	15
	Overall*	47.0±3.6A	29	38.5±3.4A	30	3.7±0.3AB	30	12.7±1.8A	30	8.4±1.1A	29	1.8±0.2	29	4.4±0.8	29
PS	Southern Inland	19.7±3.1a	19	1.1±3.0a	20	0.3±0.2a	20	1.2±0.9a	20	18.6±1.8a	19	3.0±0.3a	19	5.7±1.2	19
	Intermediate Coastal	51.1±6.1b	5	31.0±6.0b	5	3.8±0.4b	5	8.1±1.7b	5	20.2±3.6a	5	2.2±0.5b	5	8.6±2.3	5
	Northern Coastal	42.1±4.5b	9	30.4±4.3b	10	2.8±0.3b	10	10.7±1.2b	10	9.9±2.7b	9	1.2±0.4b	9	7.8±1.7	9
	Overall*	31.4±3.3B	34	14.7±3.4B	36	1.6±0.3C	36	5.0±1.0B	36	16.3±1.5B	34	2.4±0.2	34	6.6±0.9	34
SG	Southern Inland	7.0±3.7	2	0.0±0.0	2	0.0±0.0	2	0.0±0.0	2	7.0±1.9	2	1.5±0.4	2	3.8±0.5	2
	Intermediate Coastal	23.0	1	16.0	1	1.0	1	16.0±2.6	1	7.0	1	2.0	1	3.0±0.67	1
	Northern Coastal	34.5±2.6	4	29.3±1.8	4	2.8±0.2	4	11.0±1.3	4	5.3±1.3	4	1.3±0.3		3.4±0.3	4
	Overall*	28.9±5.9AB	8	22.9±6.0AB	8	2.1±0.6BC	8	8.8±2.1AB	8	6.0±0.8A	8	1.6±0.3		3.2±0.3	8

Note: We compared durations and stops among wintering sites and reported differences in the Overall row using uppercased letters. We also compared chronology by strategy within wintering areas and reported differences using lowercased letters under each wintering site. The absence of letters indicates no significant differences.

*Sample size (*n*) for each Overall category includes birds that began migration, but stopped transmitting before beginning inland migration. These birds were never assigned a migration strategy and thus are not included in calculations of means by strategy. In addition, because of the small sample size (*n* = 3), we did not calculate means for the Other migration strategy; however, scoters using this strategy were included in the calculation of overall means.

Fig. 6. Mean length of stay (LOS) in migration stopover areas by surf scoters (*Melanitta perspicillata*) from four Pacific coast wintering sites: (*a*) Strait of Georgia (SG), (*b*) Puget Sound (PS), (*c*) San Francisco Bay (SF), and (*d*) San Quintin Bay (SQ). Open bars represent coastal migration areas and shaded bars represent inland migration areas. Error bars represent 1 SE and numbers above each bar indicate the number of birds that stopped in that migration area.

Discussion

Use of routes

We integrated satellite telemetry data from surf scoters marked at four wintering sites on the Pacific coast of North America to identify spring migration routes and chronology. We identified Southern Inland and Northern Coastal migration routes used by 83% of surf scoters. The route followed by an individual had a strong influence on chronology and stopover sites, and therefore its migration strategy. Use of these routes, as shown by comparing inland departure latitudes, was independent of wintering sites in which scoters were marked. However, there was a clear relationship between departure latitude for inland migration and ultimate nesting site latitude. Given that strong female natal philopatry exists for many sea ducks (Goudie et al. 1994; Eadie et al. 1995; Pearce et al. 2005), and nesting site fidelity has been demonstrated for surf scoters (Takekawa et al. 2010), nesting site may play a large role in determining the migration route used by Pacific Coast surf scoters. Avian migrants are known to alter their overall migration routes to adjust for variation in winter and spring resources (Catry et al. 2004) or regional weather conditions (Alerstam et al. 2006), but in our study surf scoters with data spanning two consecutive years showed strong fidelity to overall migration routes and made slight alterations in chronology at stopover sites.

Energetics and predation risks by route

Factors determining migration strategy selection include time, energy, and risk of mortality (Alerstam and Lindstrom 1990). Given the short ice-free nesting period in the Northern Boreal Forest breeding area (Takekawa et al. 2010), surf scoters may be expected to maximize their energy gains during migration (Alerstam and Lindström 1990; Farmer and Wiens 1998, 1999) and migrate with significant capital investment for self maintenance or egg production (Klaassen et al. 2006). Annual route fidelity such as what we found in surf scoters may confer advantage to individuals who gain local knowledge about stopovers that have predictable food resources and about predators along the route (Rohwer 1992; Bauer et al. 2008). Between the two main migration routes observed in this study, prey type, value, and predictability, as well as risk of predation, may differ greatly.

Scoters taking the Southern Inland route staged (SQ, SF birds) or remained (PS, SG birds) in the Puget Sound and Strait of Georgia until mid-May. During spring, surf scoters are known to aggregate at spawning sites of Pacific herring (*Clupea pallasi* Valenciennes in Cuvier and Valenciennes, 1847), where they consume lipid-rich, energetically profitable roe (Bishop and Green 2001; Sullivan et al. 2002; Lewis et al. 2007; Anderson et al. 2009). Spawning tapers off at most sites in mid-April when the first SQ and SF migrants are arriving to the region, although spawning at historically large spawn sites such as Cherry Point, may occur through the end of June (Stick 2005). Scoters that use the Southern Inland route could be relying on the once predictable, but now declining (Stick 2005) spawn to accumulate resources before turning inland. However, in a recent study, very few radio-marked surf scoters responded to spring herring spawn events within Puget Sound (J.R. Evenson and D.R. Nysewander, unpublished data), and additional work

areas used and LOS (Table 5). During the 2nd year, transmitters provided fewer locations; thus, we could not be certain that all stopovers were represented. Migration chronology was different between years for each bird, although settling dates were remarkably similar for PS birds. One PS scoter both departed its wintering area and arrived in the breeding area within a day of the previous year (Table 5). Additionally, four of the birds arrived and settled in the breeding area simultaneously during both of the years they were tracked (Table 5). These four birds represented both PS and SF wintering areas and both the Southern Inland and the Northern Coastal routes.

Table 5. Migration duration, number of stopovers, length of stay (LOS), and chronology for six female surf scoters (*Melanitta perspicil-*

Wintering site	PTT No.	Year	Route*	Total duration (days)	Winter departure (ordinal date; days)	Coastal Stopover No.	LOS (days)
SF	55912	2005	SI	27.0	132.0	4	4.8
		2006	SI	26.0	115.5	2	8.3
	55914	2005	NC	52.0	92.0	4	12.3
		2006	NC	27.0	125.5	2	10.5
	55919	2005	SI	33.0	125.0	4	5.0
		2006	SI	65.0	80.5	1	45.0
PS	43888	2005	NC	14.0	129.0	1	8.0
		2006	NC	79.0	64.0	4	19.5
	53978	2005	SI	22.0	127.0	0	0.0
		2006	SI	37.5	112.0	1	14.5
	53980	2005	SI	18.0	126.0	0	0.0
		2006	SI	16.0	125.0	0	0.0

*Route names: NC, Northern Coastal; SI, Southern Inland.

in this area shows that scoters may be in part relying on epifaunal invertebrate prey during late winter and spring (Anderson et al. 2008).

It is unclear why birds that follow the Southern Inland route choose to stage during inland migration, instead of remaining on the coast for a longer period of time. Depletion of spawn or alternate benthic and epibenthic prey (Kirk et al. 2007; Anderson et al. 2008) could be one factor spurring inland migration. Prey availability in high-latitude freshwater lakes may be less predictable than in coastal waters because of their ephemeral nature (Piersma 2003). However, thawing of lower to mid-latitude lakes in areas such as the Fraser River Plateau occurs as early as March (Calbick et al. 2004) and emerging aquatic invertebrates could provide an abundant source of prey for staging scoters migrating during April and May. Predators encountered inland may be less predictable than those on the coast. While predation of scoters and other waterfowl from raptors is prevalent in coastal waters (Todd et al. 1982; Savard et al. 1998), birds migrating across land may encounter a more diverse array of predators including mammalian predators. However, birds using freshwater lakes may also have more cover from predators available, thereby reducing their risk of predation (Lind 2004) compared with birds in open coastal waters.

In contrast to the Southern Inland route strategy, there is some evidence that individuals using the Northern Coastal route may be following a "silver wave" of herring spawn resources up the Pacific coast to their final staging site. Lok (2008) found that the phenology of scoter migration along some areas of the British Columbia and southeast Alaska coasts was tied to Pacific herring spawning activity, which occurs in a northward, latitudinal progression over the course of spring. Lok (2008) also identified areas farther from the mainland coast and closer to herring spawns as important habitat for migrating scoters. This may reflect a strategy of balancing use of sites with highly predictable prey sources with those that are more protected from aerial predators (Schmaljohann and Dierschke 2005; Bauer et al. 2008; Pomeroy et al. 2008). If migration routes are predicated on nesting site latitude, then scoters following the Northern Coastal route may be obliged to obtain all their

capital energy stores from coastal resources such as roe or benthic prey before turning inland. The most direct inland path to nesting sites in the northern part of the breeding area takes individuals over subarctic mountain ranges where access to thawed, freshwater lakes with abundant prey items may be limited.

Chronology

To maximize their fitness, migrants time their migration based on body condition and proximate cues in their environment (Weber et al. 1998). We found that poor individual condition, as measured by female body mass at time of marking, did have a significant, although slight, negative influence on departure time from the wintering site. Furthermore, at all wintering sites, individual scoters departing earliest had longer total migration durations, longer mean LOS at stopover sites, arrived earliest to the breeding areas, and settled at nesting sites slightly earlier than later departing birds. Birds that depart late from wintering sites may have a hard time correcting for poor timing en route to breeding areas. Studies of barnacle geese (*Branta leucopsis* (Bechstein, 1803)) and American redstarts (*Setophaga ruticilla* (L., 1758)) have also shown that birds departing from wintering areas earliest are the earliest breeders, suggesting that optimal reproductive fitness for some species has its basis in the wintering ground (Marra et al. 1998; Prop et al. 2003; Black et al. 2007).

Among wintering sites and migration routes, mean arrival dates to the breeding area were remarkably similar. Birds from all wintering sites and using all routes settled at nesting sites less than a week after arrival to the breeding area. Thus, wintering site and migration route taken did not seem to confer a greater ability to arrive on time and initiate nesting on the breeding area. However, our results do suggest a strong selective pressure on timing of arrival. Arrival time is an important element of competition among migratory birds (Newton 2006), as individuals who arrive earlier begin breeding earlier (Nilsson and Persson1994), lay more eggs (Dalhaug et al. 1996), and show the highest fledging success (Brinkhof et al. 1993). Surf scoters are one of the most northerly nesting duck species (Goudie et al. 1994), and re-

lata) migrating along the Pacific coast in two consecutive years.

Departure		Inland Stopover			Settling	
Ordinal date (days)	Latitude (°N)	No.	LOS (days)	Arrival (ordinal date; days)	Ordinal date (days)	Latitude (°N)
151.0	49.8	2	3.5	155.5	158.0	60.5
132.0	49.4	2	4.3	136.0	140.5	60.5
141.0	59.3	1	2.0	143.0	143.0	67.6
146.5	57.6	1	5.0	151.5	151.5	67.6
145.0	50.0	4	3.0	150.0	157.0	60.9
125.5	49.3	2	9.5	137.5	144.5	60.9
136.0	57.6	1	6.0	142.0	142.0	62.4
142.0	57.9	0	0.0	142.0	142.0	62.4
127.0	48.3	3	7.0	141.0	148.0	60.0
126.5	49.0	2	11.0	130.5	148.5	60.0
126.0	48.7	3	5.7	141.0	143.0	60.8
125.0	47.7	2	7.5	140.0	140.0	60.8

production in arctic and subarctic nesting species may be particularly sensitive to arrival timing given the limited number of ice-free days available for nesting (Hupp et al. 2006; Takekawa et al. 2010). We could not determine if marked birds that appeared to be nesting successfully produced broods, thus it is not clear if wintering site or route use had implications for ultimate reproductive success.

Chronology data for six spring migrants across 2 years provided additional evidence of the ability of individuals to adjust their strategy depending on changing conditions. While in each year these birds followed the same route to the same nest sites, timing of departure from wintering site and coast were highly variable. During both years, Southern Inland migrants had longer inland migrations than scoters following the Northern Coastal route. Four individuals arrived and settled to nesting areas on the same day, and three birds did this during both years. Individuals may have been able to adjust their migration timing in relation to weather or variable foraging conditions en route to arrive at the breeding area within the same narrow breeding window each year (Farmer and Wiens 1999; Drent et al. 2003).

Stopover ecology

Individually marked birds in our study made short "hops" or slightly longer "skips" (Piersma 1987) between stopover sites along the coast. Individuals that migrated along the coast used at least one stopover site, but this increased with distance traveled. Making series of short flights such as this is energetically cheaper than covering the distance in long flights, and may indicate the availability of good stopover habitat resources (Piersma 1987). North of their wintering sites, scoters used each of the broad coastal stopover areas that we delineated, with the exception that SQ birds did not stop in two areas. On the lower coast below Puget Sound, the San Francisco Bay, the Central California coast, and Oregon coast were used as staging areas. Little is known about habitat use and foraging ecology of scoters during spring migration at sites along this stretch of the lower Pacific coast. Scoters are likely not foraging on herring roe in California, as spawns in this region occur prior to the initiation of migration. For example, the peak of herring spawn in San

Francisco Bay is in January, and most spawn events are completed by March (California Department of Fish and Game 2005). However, on the Oregon coast, herring spawning can last through April (Haegele and Schweigert 1985) and may be available to migrating scoters.

Once migrants reach PS and latitudes north of this migration area, LOS at stopover sites increases dramatically and it is unclear what factors drive this change. Lok (2008) provide evidence that migrating scoters make prolonged visits to herring spawn sites at these latitudes, but they also found scoter use of spawn varied and birds did not respond to all spawn sites. The two coastal areas that had the greatest number of staging individuals and the longest LOS were the Puget Sound and Haines Southeast Alaska migration areas. Both are the final stopover areas before inland migration for the majority of Pacific coast surf scoters that use the Southern Inland and Northern Coastal routes. These areas historically have supported very large herring spawns (Stick 2005; Lok 2008), the timing of which corresponds with the migration of scoters. However, in both areas, herring populations have declined dramatically in the past several years (Stick 2005; Willson and Womble 2006).

Regardless of the source of food in these areas, studies of arctic-nesting birds have established the critical importance of the final staging area before take-off to breeding areas for building capital income (Drent et al. 2003; Prop et al. 2003). An extended stay in the Lynn Canal region within the Haines Southeast Alaska migration area to accumulate energy stores may be valuable for scoters using the Northern Coastal route, as the largely mountainous path they take to the breeding area seems to present limited opportunities to stop at thawed lakes for foraging. Instead, these birds migrate inland rapidly, making few stops and arriving shortly before initiating nesting. The strategy of scoters using the Southern Inland route allows them time to forage at more southern interior sites. Several inland stopover areas were used by a large number of individuals, but staging was most prevalent in the Fraser River Plateau (encompassed by the Southern Inland British Columbia and Central Inland British Columbia migration areas) and in the Lesser Slave Lake area. These areas are characterized by lower elevation river

Fig. 7. Repeated migratory routes for six individual female surf scoters (*Melanitta perspicillata*) from two wintering sites (Puget Sound (PS), San Francisco Bay (SF)) followed by satellite transmitter during the springs of 2005 and 2006. Solid lines represent first journeys (2005) and broken lines indicate second journeys (2006). Circles represent stopover sites in 2005, whereas squares represent stopovers in 2006.
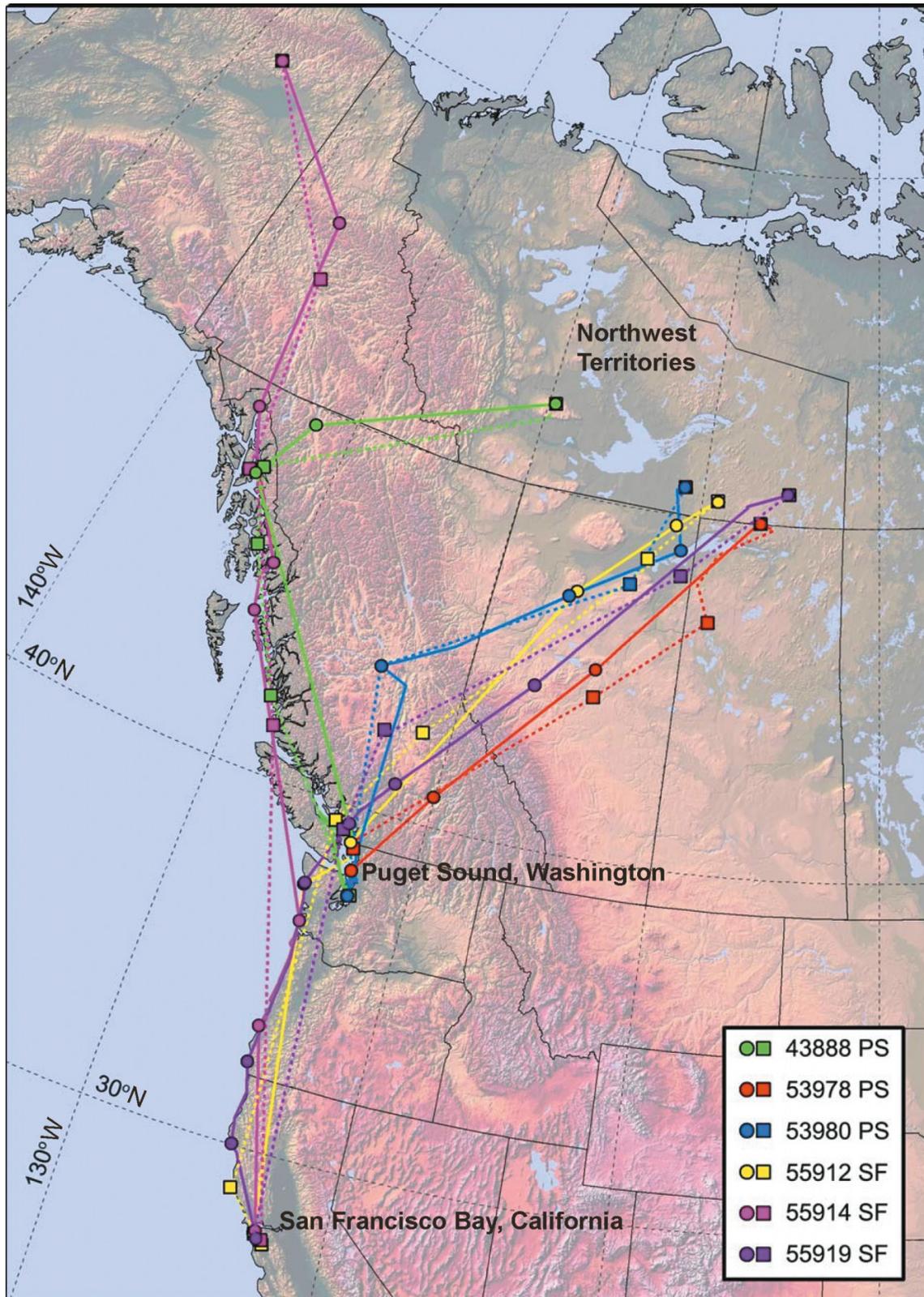
drainages and lakes, as opposed to other more mountainous stopover areas. Scoters have been observed using freshwater lakes during migration (Savard et al. 1998), and several individuals in this study staged at the same large lakes on the Fraser River Plateau.

Conservation implications and future research

Conservation of migratory birds requires a complete understanding of year-round geographical ranges and habitat requirements (Webster et al. 2002). Until recently, very little was known about the life history of the surf scoter, including connectivity between wintering sites and breeding areas (Sea Duck Joint Venture (SDJV) Management Board 2001)[3]. Results from our effort to delineate spring migration of surf scoters indicate that individual scoters do not follow specific routes to the breeding area based on their wintering site. However, our study does show that different migratory routes confer unique migratory strategies and have strong latitudinal relationships to nest sites. Given these relationships, it seems possible to examine whether or not one migratory route is more advantageous than another by looking at reproductive success of individuals at different latitudes.

It should also be possible to use stable isotope ratios in somatic tissues and eggs to determine if marine or freshwater reserves accumulated during spring migration play a bigger role in the body condition and reproduction of individuals taking one route over another (Gauthier et al. 2003; Schmutz et al. 2006; Yerkes et al. 2008). These methods would be useful in discerning the effects of climate change and habitat loss on scoters following coastal or inland strategies. As a result of climate change, migratory birds have been shown to alter their migration phenology in an attempt to match changing temperatures or prey phenology (Cotton 2003; Drever and Clark 2007). Temperature change could alter spawning timing of Pacific herring or the emergence of invertebrates in freshwater lakes, and thus could affect birds disproportionately depending on their migration strategy.

Our study underscores the importance of the Puget Sound, Strait of Georgia, and Lynn Canal as final coastal staging areas for the majority of Pacific coast surf scoters. In addition to these and other specific southeast Alaska coastal staging sites already deemed significant to migrating surf scoters (see Lok 2008), our broader view of scoter migration routes highlights the need to better understand the role and importance of stopover areas in California and on the Oregon coast. Similarly, inland lakes and drainages on the Fraser River Plateau, British Columbia, and in northern Alberta were identified as key staging areas for migrating scoters, but little is known about their resource value for this species. Use of these stopover areas should be further evaluated to identify specific areas that may be important to conserve.

Acknowledgements

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