Spatiotemporal associations between Pacific herring spawn and surf scoter spring migration: evaluating a 'silver wave' hypothesis

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ABSTRACT: Surf scoters *Melanitta perspicillata* are sea ducks that aggregate at spawning events of Pacific herring *Clupea pallasi* and forage on the eggs, which are deposited in abundance during spring at discrete sites. We evaluated whether migrating scoters followed a 'silver wave' of resource availability, analogous to the 'green wave' of high-quality foraging conditions that herbivorous waterfowl follow during spring migration. We confirmed that herring spawning activity began later in the year at higher latitudes, creating a northward-progressing wave of short-term localized food availability. Using satellite telemetry and aerial surveys, we documented the chronology of scoter spring migration and the use of stopover locations in relation to herring spawn timing and locations. We found that the migration chronology paralleled the northward progression of herring spawning events. Although there was considerable variability in the timing of both scoter migration and the initiation of herring spawning, the processes were related beyond a coincidental northward progression. During migration, 60% of the tracked scoters visited at least 1 spawn site, and those that used spawn sites were located on spawn sites for approximately one-third of their migration locations. Surf scoters showed close spatiotemporal associations with herring spawning events, confirming that the presence of herring spawn was a factor determining habitat use for many individuals. Surf scoters showed close spatiotemporal associations with herring spawning events, confirming that the presence of herring spawn was a factor determining habitat use for many individuals, a conclusion that is consistent with previous studies which used physiologically based metrics to evaluate the importance of herring spawn.

KEY WORDS: Habitat use · Herring spawn · *Melanitta perspicillata* · Migration · Satellite telemetry · Surf scoter

INTRODUCTION

Migrating animals face habitat and food resources that vary considerably over both time and space at 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 & Dierschke 2003, van der Graaf et al. 2006). Many

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 (Ryder 1970, Ankney & MacInnes 1978, Alisauskas & Ankney 1992, Warnock & Bishop 1998, Smith & Moore 2003, Morrison & Hobson 2004). Therefore, the timing of migration and the choice of stopover habitat can have population-level demographic consequences.

Migrating herbivorous birds are speculated to strategically time their migration to take advantage of the emergent spring growth of forage plants at stopover and staging sites (van der Graaf et al. 2006). This 'green wave' hypothesis posits that birds migrating from wintering areas to Arctic breeding areas follow the northward-progressing wave of emergent spring vegetation (Drent et al. 1978, 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).

The availability of other food resources for migrating animals may also vary temporally along a latitudinal gradient. In coastal ecosystems, many birds and mammals exhibit aggregative responses to ephemeral seasonal resource pulses, such as Pacific herring *Clupea pallasi* spawning events (Haegele 1993, Bishop & Green 2001, Sullivan et al. 2002, Womble et al. 2005). Across their range throughout the north Pacific Ocean, Pacific herring spawn from late winter to early summer, and in general, spawning is initiated later at higher latitudes. This general latitudinal progression of spawning events is probably the result of the initiation of spawning by sea temperatures >6°C (Haegele & Schweigert 1985). Herring spawning events are short-lived, with spawning activity occurring within a span of 3 to 6 wk in any given area, and the eggs hatch 1.5 to 3 wk after deposition (Haegele & Schweigert 1985, Hay 1985). Herring spawning events are typically limited to relatively sheltered inlets, bays, and estuaries (Haegele & Schweigert 1985). In the northeastern Pacific, despite the abundance of relatively protected shoreline along the coast of British Columbia (BC), Canada, and Southeast Alaska (SEAK), USA, spawning events are also highly localized, occurring on <2% of the entire BC coastline in a given year (Hay & McCarter 2007). It is likely that the proportion of shoreline used in SEAK is similar.

Spawning events provide food resources to a number of avian predators (Bishop & Green 2001, Sullivan et al. 2002, Rodway et al. 2003). Herring spawning activity occurs at generally the same time that many birds are migrating along 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 correspond to herring spawning locations and a northward-progressing spawn chronology. 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 & Esler 2005) but has not been considered on a migratory flyway scale.

Until recently, little was known about the migration patterns of many sea ducks, including the surf scoter *Melanitta perspicillata*. Recent work by De La Cruz et al. (2009) provides a thorough synthesis of Pacific surf scoter migration patterns, routes, and chronology. In general, most tracked scoters followed 2 major routes to the breeding area: either a southern inland route involving staging in southern BC or Washington State, followed by direct migration inland or a northern coastal route characterized by smaller movements along the Pacific coast of BC and SEAK, followed by inland migration from SEAK. During most of the year, scoters feed on bivalves and a variety of soft-bodied prey when in marine waters (Vermeer 1981, Anderson et al. 2008). Along the Pacific coast, surf scoters are known to congregate and forage at herring spawning events during late winter and early spring (Vermeer 1981, Vermeer et al. 1997, Sullivan et al. 2002, Lok et al. 2008). Proximity to herring spawn has been identified as a strong predictor of stopover habitat use (Lok et al. 2011). However, unlike other food resources, the silver wave of herring spawn is restricted to only a few weeks and along a very small proportion of the available coastline (Hay & McCarter 2007). This pattern has been speculated upon (Vermeer 1981, Savard et al. 1998), but no data have been available to test the silver wave hypothesis.

We examined the timing and stopover locations of spring-migrating surf scoters in relation to Pacific herring spawn to test whether observed migration patterns are consistent with the silver wave hypothesis. First, we investigated a basic assumption of the silver wave hypothesis: whether the timing of Pacific herring spawning activity progressed northward along the BC and SEAK coasts through the spring months within the studied years. Second, we documented migration patterns of surf scoters using satellite telemetry and contrasted these patterns with the availability of herring spawn. Finally, we used survey data to assess whether surf scoters were specifically associated with herring spawning events at 3 areas in SEAK.

MATERIALS AND METHODS

Study area

The wintering range of surf scoters along the Pacific coast extends from Alaska to Baja California, Mexico (Savard et al. 1998). All data were collected from spring-migrating surf scoters originating from several areas throughout this wintering range: San Quintin Bay (SQ), Baja California, Mexico (30.4° N, 116.0° W); San Francisco Bay (SF), California, USA (37.8° N, 122.4° W); Puget Sound (PS), Washington, USA (47.5° N, 122.4° W); and the Strait of Georgia (SG), British Columbia, Canada (49.3° N, 122.4° W). In the 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, De La Cruz et al. 2009, Takekawa et al. 2011). Habitats along 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 BC and southern part of SEAK have extensive networks of islands and protected bays and channels, while the northern part of SEAK has numerous long fjords and several large soft-bottomed river deltas. Although ~20% of the BC coast has been used for herring spawning at some time (DFO 2008), most spawning is concentrated and localized to roughly 2% of the coast in a given year (Hay & McCarter 2007).

Herring spawn data

We created a database documenting the distribution and timing of major herring spawning events along the BC and SEAK coast from 2003 to 2006 using existing data from the 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 2008) and reports the timing and magnitude of herring spawning in 101 management sections which cover the entire BC coast each spawning season. The dataset also includes the centroid position for each section, which is determined by calculating the mean latitude and longitude coordinates of all the recorded spawning events within the section (Fig. 1). The dataset reports the earliest date of spawning (min. date) and latest date of spawning (max. date) within a year for each section. The mean spawning date was considered the most representative date of the majority of spawning herring in a section (B. McCarter pers. comm.). We compiled the location and timing of herring spawning within similar management sections of SEAK from the ADFG and unpublished sources (J. Womble unpubl. data). For analyses of platform-transmitter-terminal (PTT) scoter locations, we considered spawning distribution and timing for BC and SEAK combined. For aerial survey analyses, we compiled geographic information system (GIS) coverage of herring spawning event distribution within SEAK during the study years.
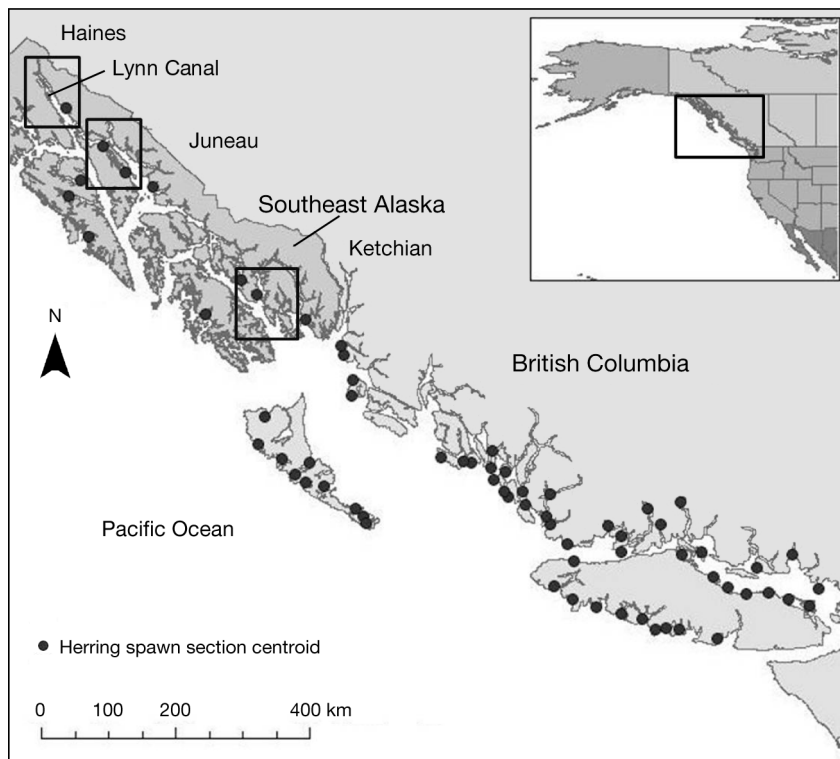

Fig. 1. Pacific herring *Clupea pallasi* management section centroids along the coasts of British Columbia and southeast Alaska. Only sections that had documented spawning activity from 2003 to 2006 are shown. Survey regions are highlighted by boxes; note that not all coastline within highlighted regions was surveyed

Captures and fitting of transmitters

We captured surf scoters on wintering grounds between November and March in 2002 to 2006 using a floating mistnet (Kaiser et al. 1995, Lewis et al. 2005), or a net shot from a netgun (Coda netgun, Coda Enterprises). The birds were implanted with PTT satellite-transmitters following standard procedures (Mulcahy & Esler 1999). The implantation method has been shown to perform well for scoters (Iverson et al. 2006). Birds were released after a recovery period of at least 1 h. Individuals that did not leave winter areas, died, or experienced radio failure during migration were not included in analyses. Migration location data were obtained from 75 surf scoters fitted with PTT transmitters in 2003 to 2006 from the 4 wintering areas, SQ, SF, PS, and SG. Of these, 51 individuals (68%) migrated along the coasts of BC and SEAK; the remainder of the tracked birds migrated using other inland migratory routes. Detailed information on the migration patterns, routes, and chronology of these surf scoters was reported by De La Cruz et al. (2009).

Location data

The PTT transmitters were programmed with duty cycles to transmit location data for 6 to 8 h and turn off for 48 to 96 h. Transmitter signals were received by U.S. National Oceanic and Atmospheric Administration polar-orbiting weather satellites, and CLS America (Largo, Maryland) estimated the 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, in which at least 4 messages are received, CLS America rated accuracy as <150, <350, <1000, and >1000 m, respectively. Accuracy was not provided for LC A (3 messages received), LC B (2 messages) and LC Z (latitude and longitude often provided if >1 message received, but the information was considered invalid). Data for scoters from each wintering site were compiled at the USGS Western Ecological Research Center and filtered using an automated systematic plausibility test of direction, distance, and rate of movement between locations (Douglas 2006). The filtering program was set to ensure that the LC 1 to 3 locations were always retained (De La Cruz et al. 2009).

To select only coastal spring migration locations along the coastline of BC and SEAK, this dataset was then manually filtered. Surf scoters maintain small home ranges in the winter months (Kirk et al. 2008); a bird was classified as migrating when it had left wintering grounds and at least 2 consecutive locations were located at increasing latitudes. Location data usually included >1 useable location per bird in a transmission day, and a 'selected location' for each transmission day was determined 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 location classes. Although less conservative than filtering out locations with lower location quality classes or filtering completely randomly, 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.

Aerial surveys

We conducted aerial surveys to document the distribution and abundance of surf scoters both before and during the herring spawning and scoter migration period in 2006. Surveys were conducted along the shoreline in 3 regions of SEAK: Ketchikan, Juneau, and Haines (Fig. 1). All 3 regions were surveyed at least once prior to herring spawning initiation (1 to 2 April 2006). During the spawning and 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 between 09:00 h and 16:00 h in a Cessna 185 or Heliocourier with an experienced survey pilot and 1 observer on the passenger side. Surveys followed the shoreline at altitudes of 150 to 200 m and flight speeds of <200 km h^{-1}. Survey routes varied in shoreline length between regions (Ketchikan: 540 km, Juneau: 463 km, and Haines: 394 km), and the survey duration varied accordingly. Surf scoters typically forage close to the shoreline due to water depth and food availability (either bivalves or herring spawn), and previous observations indicated that scoters were typically within 500 m of the shore in the fjord habitat typical of SEAK. We used digital marine charts (NOAA 1:250 000) to record locations of all observed surf scoters within 500 m of the shoreline; groups were recorded as a single location with an estimate

of the group size. Groups of <100 were counted individually; larger groups were estimated by counting smaller groups of 10, 100, or 1000, depending on the size of the group. Surf scoter flocks exhibit synchronous diving behavior, which made the use of photographs for documenting flock size challenging. However, some photographs were used to confirm the flock size estimates.

Data analyses

Spawning progression and migration patterns

We used least-squares general linear models to evaluate the variation in latitude of herring spawning activity along the BC and SEAK coasts in relation to the year and the day of the year (SAS Institute 2003). 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 interannual variation in this relationship. We used an information theoretical approach to model selection (Burnham & Anderson 2002) and calculated Akaike's information criterion adjusted for small sample sizes (AIC_c) for each model within the candidate set. The candidate model set consisted of the following models: (1) Day-of-year, (2) Year, (3) Day-of-year + Year, (4) Day-of-year + (Day-of-year × Year), (5) Day-of-year + Year + (Day-of-year × 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 the overall model fit. Finally, we calculated model-averaged parameter estimates and unconditional standard errors based on Akaike weights for all of the candidate models (Burnham & Anderson 2002).

For the silver wave hypothesis to be supported, we would expect a general correspondence between herring spawn availability and scoter locations, assuming that the basic premise that herring spawning progresses northward over time is correct. We compared the temporal and spatial patterns of herring spawn availability with those of PTT-fitted scoter locations. Estimates of the average spawning latitude for each date were calculated from model-averaged parameter estimates based on Akaike weights (Burnham & Anderson 2002) across the models in the candidate set describing the relationship of herring spawning date by latitude (see 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 sample; based on the silver wave hypothesis, we would expect a positive relationship, with a slope of ~1, indicating that the scoters are following the progression of herring spawn availability exactly.

We recognize that a positive relationship between scoter locations and herring spawning latitude could simply be a spurious result occurring because these phenomena are both northward-progressing during the spring but might not be directly related. To address this issue, we performed separate analyses to calculate residuals from regressions with day-of-year as the response variable and herring spawning latitude and scoter location latitude as explanatory variables; the residuals were calculated from year-specific regressions to account for any annual variation. We then regressed the residuals from these analyses against one another, with scoter locations matched with the closest spawning event for that year. A positive relationship between the residuals would indicate that herring spawning and scoter occurrences are spatially and temporally correlated beyond their similarity as northward-progressing phenomena.

Spawning event use metrics

The silver wave hypothesis predicts a general latitudinal correspondence between locations of migrating scoters and herring. However, 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. Based on the silver wave hypothesis, there should be close 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 spawning occurs at small, spatially discrete sites, and the silver wave hypothesis requires confirmation that these specific sites are used by migrating birds.

Satellite telemetry location data were imported into ArcGIS 9.1 (Environmental Systems Research Institute 2005) to create a map of surf scoter spring migration and herring spawning locations. Because spawning activity varied in both time and space, we filtered the location data both spatially and

temporally. We considered spawning event 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 scoter location to be at a spawning event if the scoter was within 22 km of the centroid of an active spawning management section. The 22 km radius is based on the 95th percentile of mean inter-fix distances (the distance between subsequent locations) for VHF radio-fitted surf scoters in late winter when herring spawn was available (Lok et al. 2008). Once we selected the data from scoters that spatially overlapped with the herring spawning event (i.e. within a 22 km radius buffer), we filtered the data temporally by comparing the date of the scoter location to the mean date of herring spawning within that management section. Locations were only considered as an active spawning event if the date was on, or within 21 d following, the mean spawning date, which we considered to be the most representative date of spawning within a management section (B. McCarter pers. comm). We chose a period of 21 d to account for the presence of eggs from 1.5 to 3 wk after deposition and the possibility of spawning events initiated after the mean spawning date within a management section.

The locations of scoters at active spawning events were used to calculate metrics of spawn use by scoters. The metrics included the number of scoters located at spawning events, the number of spawning events visited by an individual scoter, and the proportion of all scoter locations at herring spawning events.

Aerial survey data for SEAK were imported into ArcGIS 9.1 to create a map of surf scoter group locations, scoter abundance, and herring spawning distribution within each survey region (Ketchikan, Juneau, and Haines). We categorized surveys as before spawning and during spawning based on the timing of herring spawning 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 along the shoreline within the survey areas before and during spawning activity and weighted the locations of the studied scoter flocks by group size to calculate a mean distance from individual scoter locations to herring spawning events. 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 to create a buffer of 1 km around documented spawning locations to determine the number of scoters, and the proportion of all scoters, observed within 1 km of herring spawning events.

RESULTS

Spawning progression and migration patterns

Variation in the latitude of spawning activity was clearly related to the day of the year and year (Fig. 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), and the Day-of-year + Year model received slightly more than half of the support of the most strongly supported model (w_i = 0.32, R^2 = 0.61) (Table 1). Using data from all of the years combined, the regression equation describing herring spawn latitude as a function of the day of the year alone was herring spawn latitude = 41.73 (±0.67 standard error [SE]) + 0.12 (±0.01) × Day-of-year. In addition, this relationship varied somewhat inter-annually, with an inference of differences in both the intercepts and slopes among years supported by the data (Table 2).

We compared the latitude of the PTT-fitted surf scoter locations to the predicted latitude of spawning activity for the same day of year for all of the study years combined. The predicted spawning latitude explained some of the variation in the surf scoter latitudes (R^2 = 0.21). The relationship between the predicted spawning latitude and surf scoter latitude was
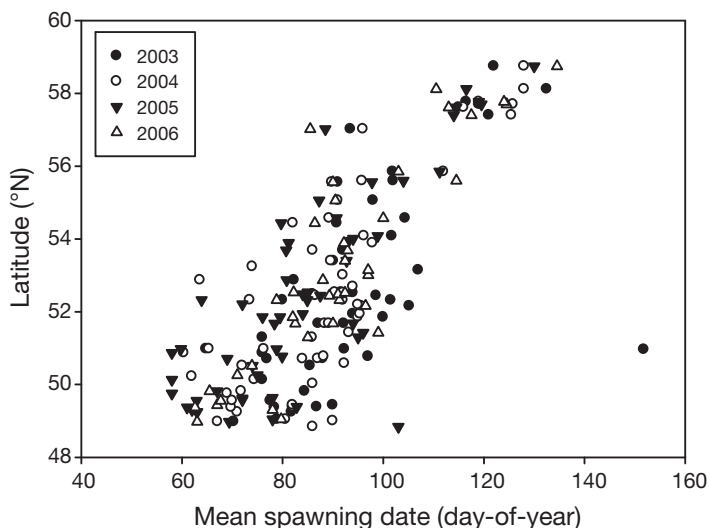

Fig. 2. *Clupea pallasi*. Latitude and mean spawning date for all management sections with documented Pacific herring spawning activity along the British Columbia and southeast Alaska coasts from 2003 to 2006. Day-of-year is scaled so 1 January = 1

Table 1. Summary of AIC results from general linear models assessing variation in latitude of Pacific herring *Clupea pallasi* spawning activity along the coasts of British Columbia and southeast Alaska from 2003 to 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. For day-of-year, 1 January = 1

Model	Parameters (K)	AIC_c	ΔAIC_c	w_i	R^2
Day-of-year + Day-of-year × Year	6	228.18	0.00	0.55	0.61
Day-of-year + Year	6	229.26	1.08	0.32	0.61
Day-of-year	3	232.11	3.93	0.08	0.59
Day-of-year + Year + Day-of-year × Year	9	232.87	4.69	0.05	0.61
Null	2	406.05	177.87	0.00	na
Year	5	410.31	182.12	0.00	0.01

Table 2. Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SEU) of weighted parameter estimates calculated from all candidate models of the latitude of Pacific herring *Clupea pallasi* spawning activity along the coasts of British Columbia and southeast Alaska from 2003 to 2006. Day-of-year is scaled so 1 January = 1. Categorical variable year 2006 is set as the reference value in all candidate models

Parameter	Summed w_i	Weighted parameter estimate	SEU
Intercept	1	41.43	0.77
Day-of-year	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
Day-of-year × 2003	0.60	−0.01	0.00
Day-of-year × 2004	0.60	0.00	0.00
Day-of-year × 2005	0.60	0.00	0.00

positive, as expected, but the slope was <1.0 (surf scoter latitude = 19.11 (±2.65) + 0.64 (±0.05) × predicted spawn latitude). This finding indicated that surf scoters showed a delayed progression up the coast in comparison to herring spawning activity.

We also found that the residuals from the relationships between the day of the year and scoter locations were positively correlated with the residuals from a day-of-year and herring-spawning latitude relationship, although there was a high degree of variation in the relationship ($R^2 = 0.02$). However, the relationship between the residuals was strongly supported ($w_i = 0.99$) relative to a null model, indicating that spatiotemporal relationships between scoter locations and spawning events existed well beyond the shared general but variable phenology of northward progression.

Spawning event use metrics

The patterns of PTT-fitted surf scoter spring migration generally paralleled those of northward-progressing herring spawn availability and varied from year to year (Fig. 3). However, the majority of tracked surf scoters were located at spawning events at least once. Of 51 individuals located within BC and SEAK, 31 (60%) were located at a spawning event at least once during spring migration. Those 31 individuals were located at spawning events for an average of 33 ± 4% of their total locations and visited 2.1 ± 0.6 spawning events during coastal spring migration through BC and SEAK. Including all of the tracked scoters (n = 51), 24% of all of the sampled scoter locations were detected at spawning events during spring migration.

The use of all 3 survey regions was relatively low prior to the spring migration period and very high during the spawning/migration period, with >100 000 scoters observed in the Haines region during surveys in May (Table 3). The mean distance to spawning events also varied among the survey areas, with scoters in the Ketchikan and Juneau regions showing marked decreases in distance to spawning events between pre-spawning and spawning surveys, while scoters in the Haines region showed little change in distance to spawning events (Table 3). The use of spawning events varied markedly among the survey areas (Table 3). When the amount of coastline with available spawn was considered relative to scoter densities, the number of scoters per length of coastline with spawning herring was highest in the Haines region, where there was little coastline with spawning herring and high numbers of scoters (Table 4).

DISCUSSION

We found moderate support for the silver wave hypothesis, suggesting that during spring migration, surf scoters take advantage of the availability of herring spawn as an abundant food resource. Data consistent with the silver wave hypothesis include our finding that herring spawning activity is initiated later in the spring at higher latitudes, creating a northward progression of food availability for scoters. The northward progression of herring spawning
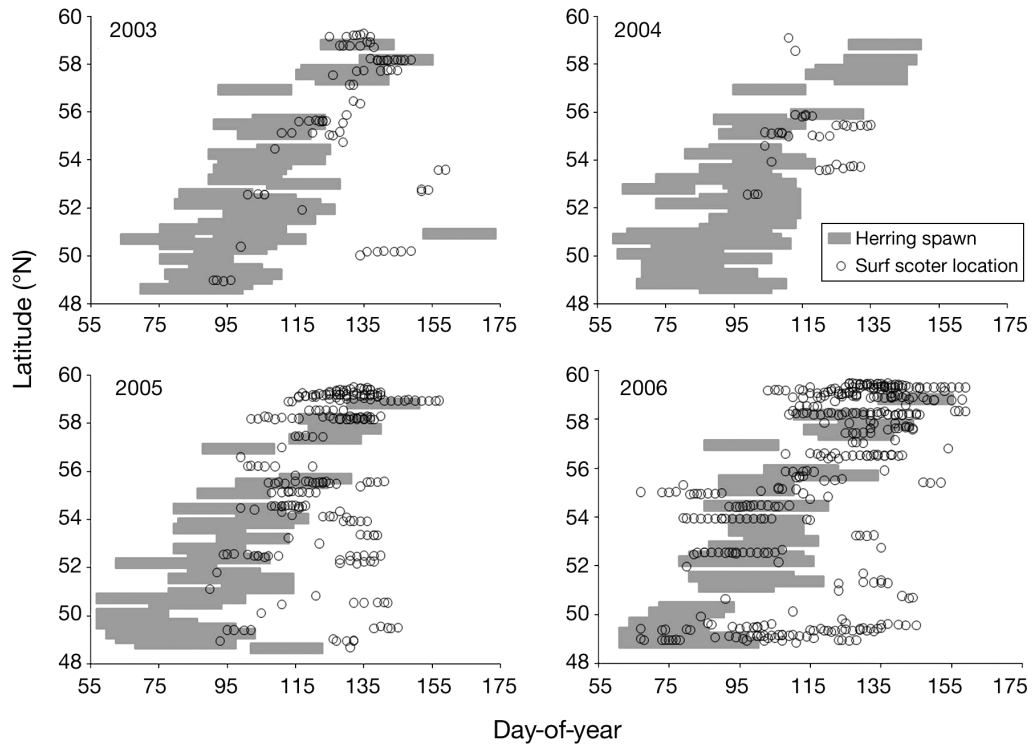
Fig. 3. *Melanitta perspicillata.* Comparison of herring spawn availability and locations of PTT-fitted surf scoters along the coasts of British Columbia and southeast Alaska from 2003 to 2006. Herring spawn availability (shaded area) was determined based on spawning times and estimates of the time before eggs hatch (mean spawn date + 21 d). Day-of-year is scaled so 1 January = 1

Table 3. *Melanitta perspicillata.* Summary of spawning event use metrics for surf scoters observed during aerial surveys in 3 regions in southeast Alaska from April to May 2006. Pre-spawning surveys in all regions were conducted from 1 to 2 April 2006. Spawning surveys were conducted on 20 April and 24 April 2006 in Ketchikan, 8 May 2006 in Juneau, and 9 May and 15 May 2006 in Haines. (–) No data available

Metric	Survey area	Pre-spawning surveys		Spawning surveys	
		Survey 1	Survey 2	Survey 1	Survey 2
Number of scoters observed	Ketchikan	729	–	77 860	24 530
	Juneau	2442	–	51 160	–
	Haines	452	120 690	–	141 600
Scoters within 1 km of spawning (%)	Ketchikan	28	–	98	90
	Juneau	3	–	49	–
	Haines	0	3	–	15
Mean distance to spawning event (km)	Ketchikan	7.3	–	0.4	0.9
	Juneau	21.9	–	9.5	–
	Haines	52.9	42.0	–	55.5

activity was strongly related to the day of the 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 showed that the reliability and timing of herring spawning events are quite variable from year to year at small geographic scales, but the events

become increasingly predictable at broader geographic scales (Willson & Womble 2006). Because herring eggs are available to predators for up to 3 wk after the initiation of spawning (Haegele & Schweigert 1985, Hay 1985), the eggs are available at multiple locations, creating generally continuous availability of spawn along the coast during spring. This means that variation in herring spawning timing

Table 4. *Melanitta perspicillata*. Percentage of surveyed shoreline with spawing activity and densities (scoters km^{-1}) of surf scoters observed along shoreline survey routes in 3 regions in southeast Alaska from April to May 2006. Pre-spawn surveys in all regions were conducted from 1 to 2 April 2006. Spawning surveys were conducted on 20 April and 24 April 2006 in Ketchikan, 8 May 2006 in Juneau, and 9 May and 15 May 2006 in Haines

	Ketchikan	Juneau	Haines
% of surveyed shoreline with spawning activity	7.3	5.8	1.8
Scoter density			
Pre-spawning survey	1.3	5.3	1.1
Spawning survey	144.1	306.0	359.0
Spawning survey density at spawning events	1937.9	938.7	2904.5

and distribution may not constrain habitat use by highly mobile predators, such as scoters (Willson & Womble 2006). Pre-migratory surf scoters show increased movements in response to herring spawn at a local scale (Lok et al. 2008) 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 closely. 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 spawning events, and not all of the locations of each individual were at spawning events. Our metrics of the association between scoters and spawn may be minimum estimates because not all spawning events along the entire coast can be documented with complete certainty, and there are often smaller subsequent spawning events after the mean spawning date for a management section that may go undetected (Haegele & Schweigert 1985). However, there was considerable use of spawning events during migration; 60% of the tracked surf scoters used herring spawning events at some point during migration, despite the very small proportion of coastline used by spawning herring. In particular, the aerial survey data showed that when spawn was available, it was used heavily, as evidenced by the high densities of scoters at the small number of available herring spawn sites in the Haines region. This finding lends support to the silver wave hypothesis but suggests that herring spawn availability is not the only important factor driving scoter migration strategies and habitat use.

The spatial and temporal availability of resources influences stopover site use and migration timing (Ottich & Dierschke 2003, van der Graaf et al. 2006). For highly mobile scoters, the generally continuous availability of herring spawn and abundant alternative foraging habitat likely gives them flexibility to modify their migration timing and habitat use. Surf scoters might use a combination of stopover sites that provide varying habitat resources (Lok et al. 2011). The location data suggest that although some surf scoters do appear to generally follow a silver wave of herring spawn availability, they are likely making use of alternative food sources at sites during migration as well. It is likely that herring spawn is an important resource at a site while it is present, but other resources are used once the eggs are no longer available. 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 SEAK indicates that the distribution of blue mussels is more continuous along shorelines closer to the mainland coast (ShoreZone Program 2006), which could provide predictable food resources for scoters (Lok et al. 2011).

Very high numbers of surf scoters were observed in Lynn Canal (Fig. 1), despite the lack of herring spawn in the area during the study years. Lynn Canal is the most northeastern marine waterbody in SEAK, creating a natural break and stopover area for migrating birds. This area provides scoters with the last access to marine resources along their coastal migration route before they turn inland to breed (Lok et al. 2011). Not all spring migration habitats serve the same resource function (Mehlman et al. 2005), and Lynn Canal may be distinct as a final migration staging area before inland migration. However, it is also important to note that herring numbers in Lynn Canal have declined markedly in the last 4 decades, and herring spawn availability in this area has been reduced to a small fraction of the former distribution (Willson & Womble 2006), when it occurs at all. It is possible that this region is heavily used because it was traditionally used as a staging site when herring stocks were more robust.

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 & Himmelman 1996, Hunt et al. 1998, Litzow et al. 2002, Žydelis et al. 2006) and to adjust their foraging efforts and locations in response to ephemeral or novel prey (Marston et al. 2002,

Christie & Reimchen 2005, Lacroix et al. 2005, Lewis et al. 2007b, Lok et al. 2008, Anderson et al. 2009). However, to our knowledge, the present study is the first documentation of spatiotemporal relationships between migrating marine birds and the ephemeral and spatially fluctuating 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 spawning events to forage either on congregated adult fish or the spawn (Haegele 1993, Vermeer et al. 1997, Bishop & Green 2001, Sullivan et al. 2002). Herring eggs are an easily accessible, high-energy, lipid-rich food item (Paul & Paul 1999) and have been shown to be used to build energy reserves prior to and during spring migration and reproduction (Bishop & Green 2001, Bond & Esler 2006, Willson & Womble 2006, Anderson et al. 2009). Vermeer et al. (1997) speculated that the fraction of a population using herring spawning events could indicate the dependence of that population on herring spawn for acquiring energy. Species that deplete winter foods, such as surf scoters (Kirk et al. 2007, Lewis et al. 2007a), might rely heavily on herring spawn for acquiring energy reserves in late winter and early spring (Bond & Esler 2006), and species that aggregate at herring spawning events may depend on this resource for breeding in less resource-rich areas (Žydelis & Esler 2005). Anderson et al. (2009) found that in late winter and spring, surf scoters reached their greatest body mass during late April to mid-May while migrating through SEAK. Although plasma triglyceride data from this period suggested that mass gain was not entirely related to spawn consumption, surf scoters aggregated to consume spawn whenever it was available.

The availability and quality of resources during spring migration may have implications for success during subsequent stages of the annual cycle (Ankney & MacInnes 1978, Alisauskas & Ankney 1992, Warnock & Bishop 1998, Smith & Moore 2003, Morrison & Hobson 2004). Several researchers have described cross-seasonal effects of spring habitats on reproductive performance by migratory waterfowl (Anteau & Afton 2004, Reed et al. 2004, Schmutz et al. 2006), and because these events provide the energy and nutrients required for reproduction, it follows that population dynamics might be influenced by habitat conditions during spring migration. Although it is not clear whether herring spawn directly influences population dynamics, spawning events are clearly preferred foraging sites for surf scoters (Anderson et al. 2009).

Variation in non-breeding habitat, such as areas supporting herring spawn, may have important conservation implications. Herring spawning events are heavily used by many marine bird and mammal species (Haegele 1993, Sullivan et al. 2002, Willson & Womble 2006). However, traditional spawning events in many areas have declined in numbers and shifted in distribution, and species are increasingly restricted to fewer spawning sites (Stick 2005, Willson & 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 the management and conservation of scoter populations and many other marine species that use herring spawn.

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