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Author(s): Erika K. Lok, Molly Kirk, Daniel Esler, and W. Sean Boyd

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Movements of Pre-migratory Surf and White-winged Scoters in Response to Pacific Herring Spawn

ERIKA K. LOK¹, MOLLY KIRK², DANIEL ESLER³ AND W. SEAN BOYD⁴

¹Centre for Wildlife Ecology, Simon Fraser University,
8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada
Corresponding author; Internet: eklok@sfu.ca

²Centre for Wildlife Ecology, Simon Fraser University,
8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada
Internet: mollyk@alumni.sfu.ca

³Centre for Wildlife Ecology, Simon Fraser University,
5421 Robertson Road, Delta, British Columbia, V4K 3N2, Canada
Internet: desler@sfu.ca

⁴Canadian Wildlife Service, Pacific and Yukon Region,
5421 Robertson Road, Delta, British Columbia, V4K 3N2, Canada
Internet: sean.boyd@ec.gc.ca

Abstract.—We documented the movement and distribution patterns of wintering Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) in relation to herring spawn events in the Strait of Georgia, British Columbia. Radio-telemetry and surveys were conducted in Baynes Sound, an important wintering area where scoters feed primarily on clams. In early March, herring spawn events in areas adjacent to Baynes Sound provide a short-term pulse of abundant and easily accessible food, which could affect habitat use by wintering scoters from Baynes Sound. Radio-marked Surf Scoters and White-winged Scoters exhibited limited movements during winter, in contrast to the spring herring spawn season, when both scoter species moved greater distances to access herring eggs. Most individuals were located near spawning locations at least once during the spawning season, and the majority of telemetry locations were close to spawning sites, with Surf Scoters showing a higher association with spawn for both metrics. A marked decrease (66-98%) in the abundance of both scoter species in Baynes Sound was observed coincident with spawn initiation in adjacent sites. We conclude that scoters altered their movement and habitat use patterns in spring to take advantage of herring roe, an energy-rich food source. This dramatic change in behaviour suggests that herring spawn may be of particular importance to these species. Received 27 August 2007, Accepted 24 November 2007.

Key words.—*Clupea pallasii*, habitat use, herring spawn, movement, *Melanitta fusca*, *Melanitta perspicillata*, sea duck, Surf Scoter, White-winged Scoter.

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Many animals modify their habitat use to take advantage of seasonally available foods (Odum *et al.* 1995) that may enhance survival or reproduction, or fuel migration (Botton *et al.* 1994; Restani *et al.* 2000). In coastal ecosystems, mammals and birds are known to aggregate at seasonal resource pulses such as fish spawning events and consume both adult fish and eggs (Bishop and Green 2001; Marston *et al.* 2002; Sigler *et al.* 2004; Whomble *et al.* 2005). The annual spawning of Pacific Herring (*Clupea pallasii*) is a conspicuous example of a seasonal resource pulse for numerous avian predators. Although herring spawning locations are very localized (DFO 2007), herring eggs are abundant at spawn sites for several weeks during late win-

ter and early spring. Scoters and other sea ducks are known to feed heavily on this resource when it is available (Haegerle 1994; Vermeer *et al.* 1997; Sullivan *et al.* 2002; Rodway *et al.* 2003). The importance of herring spawn as a source of nutrients for migration and reproduction in sea ducks has been speculated (Rodway *et al.* 2003; Žydelis and Esler 2005), but this association has rarely been measured (Bond and Esler 2006).

To evaluate the importance of herring spawn to Pacific scoter populations, the distribution and movement patterns of individual Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) were documented during winter and spring. Although scoters are known to aggregate at

spawn sites, the influence of herring spawn on distributions and individual movements of local wintering scoters has never been quantified. We predicted that if herring spawn is an important source of nutrients for scoters in late winter, we would observe: (1) movements to spawn beyond the normal winter foraging range of individuals, (2) a high proportion of individuals using spawn, (3) a high use of spawn sites by marked individuals during the spawn period, and (4) changes in population distribution from winter to spawn seasons.

METHODS

Study Area

The study was conducted in and around Baynes Sound, on the east coast of Vancouver Island (49.5°N, 124.8°W) (Fig. 1). Baynes Sound is a wide, protected channel and the intertidal habitat is composed primarily of low-grade deltas and soft-bottomed tidal flats. The winter diet of scoters consists almost exclusively of clams (Bourne 1984; Lewis *et al.* 2007a). Annual herring spawn activity in the region generally starts in the first or second week of March. Although herring spawn events occur at a few locations within the Baynes Sound study area, most spawn events occur just outside of Baynes Sound at sites on the east coast of Denman Island, Hornby Island, and along the east coast of Vancouver Island south of Baynes Sound (DFO 2007).

The Department of Fisheries and Oceans (DFO) calculates a cumulative spawn habitat index (SHI) that represents the combined long-term frequency and magnitude of herring spawn events along each kilometre

of coastline over time (DFO 2007). This measure of shoreline utilization by spawning herring is calculated as the product of the spawn shoreline length (m) and a spawn coefficient based on spawn width (m), egg layers, and percent cover, and is then pooled geographically. The total cumulative spawn habitat index for shoreline within the Baynes Sound study area is approximately a quarter of the spawn habitat index in the adjacent areas. Because herring spawn sites are generally located outside of the Baynes Sound wintering area and have a markedly higher frequency and magnitude of herring spawn activity, this study area provides a good system for documenting the movement responses of wintering scoters to herring spawn.

Radio-telemetry

Surf Scoters and White-winged Scoters were captured in late fall during 2001-2003 using a modified floating mist-net system (Kaiser *et al.* 1995). Birds were banded and weighed, sex was determined by plumage characteristics (Iverson *et al.* 2003), and age class was estimated by bursal probing (Mather and Esler 1999). The birds were fitted with subcutaneous transmitters or implanted with internal coelomic VHF radios with external antennae following standard procedures (Mulcahy and Esler 1999). These radio types perform well for scoters with low mortality effects and good signal strength, accuracy, and retention (Iverson *et al.* 2006). Transmitters had an expected transmission period of 18 months. Over the three study years, radio transmitters were deployed on 116 Surf Scoters (2001 N = 42, 2002 N = 47, 2003 N = 27) and 138 White-winged Scoters (2001 N = 56, 2002 N = 34, 2003 N = 48). Radio-marked scoters were tracked within Baynes Sound throughout the winter and spring. Each individual was located weekly or twice weekly when possible. At the beginning of herring spawn, the telemetry survey routes were expanded to include scoter concentrations along the east coast of Vancouver Island, Denman Island, and Hornby Island (Fig. 2).

Fixes were obtained by determining the compass range of the null of a signal using a null/peak combiner (Kuechle 2005). Radio-telemetry was conducted by observers in two separate vehicles, each mounted with four-element Yagi antennae and programmable scanning receivers (Advanced Telemetry Systems, Isanti, MN). Simultaneous bearings were taken by the two observers to obtain bi-angulated locations. Error testing of the telemetry system indicated that observer bearings had a standard deviation of $\pm 4.2^\circ$ from the true bearing and a mean 90% error polygon of 0.07 km^2 ($\pm 0.004 \text{ SE}$). Given the size of the study area, these errors are relatively small and yield locations with adequate accuracy for analyzing movement and habitat use.

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

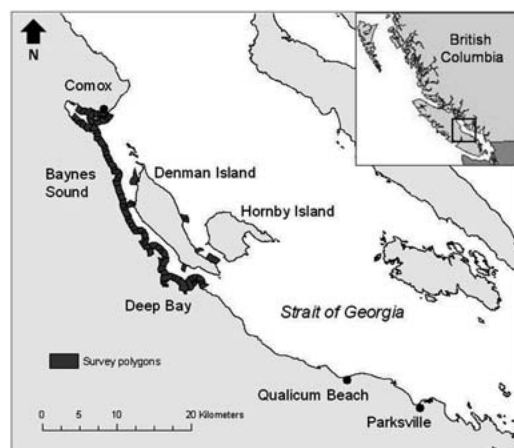


Figure 1. Baynes Sound study area and adjacent areas in the Strait of Georgia, British Columbia. Survey polygons are shaded to show the extent of the winter study area.

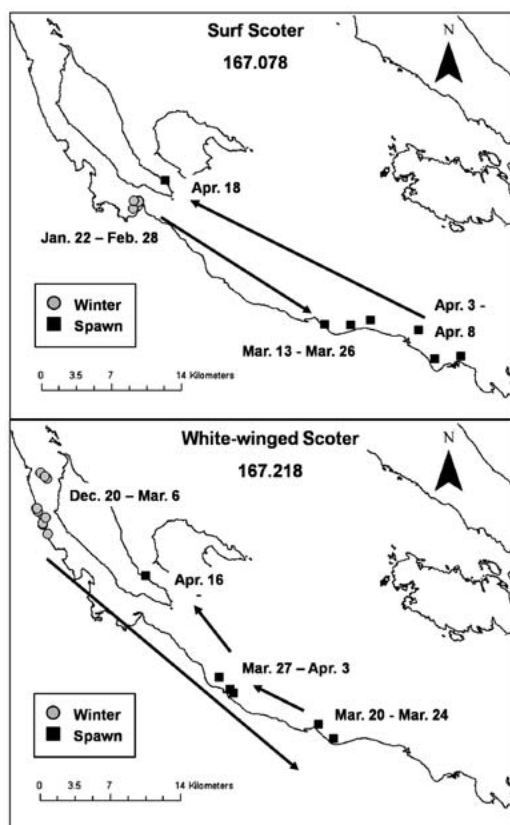


Figure 2. Examples of radio-telemetry locations and movements of representative Surf Scoter (top panel) and White-winged Scoter (bottom panel) individuals during winter and spring in the Strait of Georgia, British Columbia, December-April 2003. Herring spawn started on 13 March 2003. Note that telemetry surveys were not conducted outside of the Baynes Sound study area during winter.

out in ArcView 3.3 using the Animal Movement extension (AME) (Hooge and Eichenlaub 1997).

Scoter Distribution Surveys

Surveys were conducted in Baynes Sound to evaluate seasonal variation in scoter abundance and distribution patterns. The study area (from Comox to Deep Bay) was divided into survey polygons approximately 1.5 km in length that extended 800 m from shore (Fig. 1). Polygons were delineated according to habitat and anthropogenic characteristics of the environment. Counts were made using spotting scopes from one, two, or three observation points along the shore of each polygon. Surveys were conducted approximately biweekly from October to April during winters 2002-2003 and 2003-2004. Surveys were carried out only under good visibility conditions (i.e., surveys were suspended during fog, snow, heavy rain or winds exceeding ten knots). Surveys were not conducted at herring spawn sites outside Baynes Sound.

Data Analyses

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

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

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

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

The proportion of an individual's total number of locations during the spawn season that were within the vicinity of spawn using one km and two km buffers was determined to calculate an index of spawn use by individual scoters. Spawn use was calculated for all individuals with three or more locations within the spawn season (Surf Scoter $N = 32$, White-winged Scoter $N = 51$).

Constancy metrics were calculated for marked scoters wintering in Baynes Sound to estimate the likelihood of movement to alternate habitats during winter, in con-

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

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

RESULTS

Movement Response

Variation in interfix distance was strongly related to season; the season alone model received an AIC_c weight of 0.87 for both species (Table 1). There was little evidence that interfix distance varied by age or sex for either species. Both Surf Scoters and White-winged Scoters moved much longer distances between consecutive observations during spawn than during winter (Table 2). Spawn season mean interfix distances were nearly ten times greater than winter distances for Surf Scoters and more than three times

greater for White-winged Scoters. On a continuous time scale, both Surf Scoters and White-winged Scoters showed a marked increase in interfix distances at the initiation of spawn (Fig. 3), with several individuals from both species exhibiting increased movements just prior to spawn initiation. The difference between winter and spawn harmonic mean locations also differed by species, with Surf Scoters moving longer distances between seasons than White-winged Scoters (Table 2). On average Surf Scoters moved more than 17 km, and White-winged Scoters moved more than ten km away from winter foraging sites to spawn locations. Therefore, the interseasonal movements of scoters (winter to spawn) were up to ten times greater in distance than average winter movements.

Habitat Use

The majority of individuals (78-91%) of both species were located close to spawn at least once during the spawn period, although Surf Scoters showed a slightly higher proportional use of spawn than White-winged Scoters (Table 3). The proportion of individual locations within the vicinity of spawn differed by species; the mean individual spawn use by Surf Scoters (73 ± 5% of locations within one km, 82 ± 4% within two km) was higher than that of White-winged Scoters (53 ± 4% within 1 km, 60 ± 4% within 2 km).

Most individuals of both species were present in Baynes Sound every week (63% for both species), or not detected once (13% for both species) during winter (Table 4).

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

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

Table 2. Summary of movement metrics of Surf Scoters and White-winged Scoters in Baynes Sound, British Columbia. Means are reported \pm SE.

Movement metric		Surf Scoter		White-winged Scoter	
		Winter	Spawn	Winter	Spawn
Interfix distance (km)	Mean	1.2 ± 0.6	9.9 ± 0.8	1.8 ± 0.4	6.3 ± 0.5
	Range	0.2-12.6	1.2-31.2	0.2-18.1	0.5-36.7
	N	66	32	112	51
Interseason distance (km)	Mean	17.7 ± 1.9		10.4 ± 1.6	
	Range	0.3-33.8		0.3-42.3	
	N	28		48	

The mean constancy rates were high for both Surf Scoters ($90 \pm 2\%$) and White-winged Scoters ($92 \pm 2\%$). Only a small fraction of Surf Scoters (13%) and White-winged Scoters (12%) were undetected during the spawn period, and it is unknown whether they moved beyond the monitoring area or the radios failed.

Numerical Response

Survey totals of Surf Scoters and White-winged Scoters within Baynes Sound showed generally high winter abundance followed by a decrease in numbers in spring (Fig. 4). Herring spawn was first observed on 13 March 2003 and 6 March 2004 (DFO 2007). The abundance of Surf Scoters and White-winged Scoters within Baynes Sound decreased markedly between the surveys just prior to and just following the initiation of spawn; Surf Scoter abundance decreased by 66% in 2002 and by 86% in 2003, while White-winged Scoters decreased 78% in 2002 and 98% in 2003.

DISCUSSION

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

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

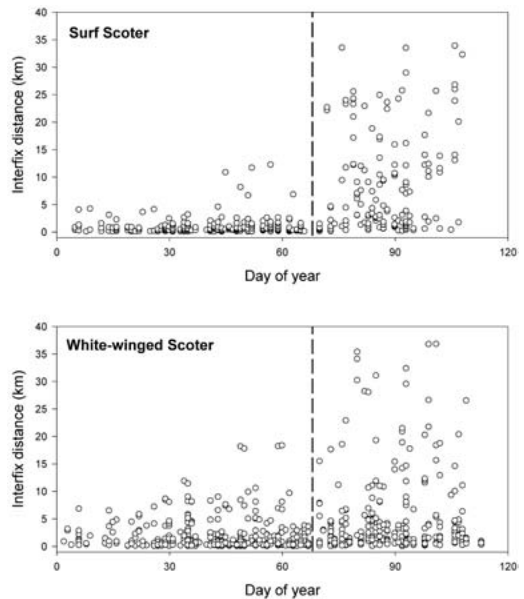


Figure 3. Interfix distances of all locations of Surf Scoters (28 individuals) and White-winged Scoters (48 individuals) from January through April in 2002-2004, in the Strait of Georgia, British Columbia. The vertical dashed lines indicate the mean date of spawn initiation (day of year = 70) for the study years.

Table 3. Fraction of radio-marked Surf Scoters and White-winged Scoters located close to herring spawn sites in the Strait of Georgia, British Columbia.

Fraction of individuals (%)	Surf Scoter			White-winged Scoter		
	Total	Male	Female	Total	Male	Female
N	57	41	16	87	50	37
Within one km of spawn	88	85	94	78	74	84
Within two km of spawn	91	88	100	81	78	84

herring spawn was the best-supported explanation for both scoter species.

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

Surf Scoters showed a stronger proportional response to spawn than White-winged Scoters, with a greater fraction of the marked population located near spawn, and individuals located proportionally more often close

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

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

Table 4. Fractions of radio-marked Surf Scoters (N = 60) and White-winged Scoters (N = 100) located during the winter in Baynes Sound, British Columbia. Winter was defined as the time from capture (December) to the date of herring spawn initiation each spring (March).

Fraction of individuals (%)	Surf Scoter	White-winged Scoter
Present every week	63	63
Not detected one week	13	13
Not detected ≥ two weeks	24	24

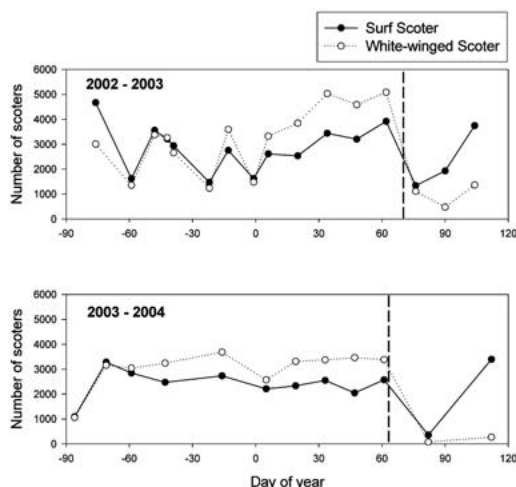


Figure 4. Abundance of Surf Scoters and White-winged Scoters in Baynes Sound for surveys from October to April in 2002-2003 and 2003-2004. The vertical dashed line indicates the date of spawn initiation each year.

Harlequin Ducks and Steller's Eiders (*Polysticta stelleri*) modify their movements and food habits to use herring spawn (Rodway *et al.* 2003; Žydelis and Esler 2005). Although the aggregation of scoters at Pacific herring spawn sites is well documented (Haeghele 1994; Vermeer *et al.* 1997; Bishop and Green 2001; Sullivan *et al.* 2002), this is the only study that has quantified movement responses of individual scoters using radio-telemetry. Vermeer *et al.* (1997) speculated that the fraction of a population using herring spawn sites may indicate the dependence of that population on spawn for acquiring energy. Species that deplete winter foods, such as Surf Scoters (Lacroix 2001; Kirk *et al.* 2007) may be more likely to rely on herring spawn for building energy reserves in late winter and early spring (Bond and Esler 2006), and those species that aggregate at herring spawn may depend on this resource for breeding in less resource rich areas (Žydelis and Esler 2005). The high fraction of both Surf Scoters and White-winged Scoters located close to herring spawn sites and the greater distances moved during this time period suggest that herring spawn may be an important food resource for scoters in late winter. Compared to White-winged Scoters, Surf Scoters exhibited higher use and

greater movement distances, indicating that herring spawn may be more important for this species.

Late winter and spring migration habitat conditions are known to have important implications for waterfowl productivity. Energy intake and body mass often increase during the pre-breeding season, as an energy management strategy to help meet high costs of reproduction and migration (Alisauskas and Ankney 1992). The effects of habitat conditions and nutrient reserve levels during the pre-breeding season carry over to subsequent stages of the annual cycle, and can influence variation in survival and reproductive success (Webster *et al.* 2002; Anteau and Afton 2004; Reed *et al.* 2004).

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

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