

# Foraging effort of Surf Scoters (*Melanitta perspicillata*) wintering in a spatially and temporally variable prey landscape

Molly K. Kirk, Daniel Esler, and W. Sean Boyd

**Abstract:** We monitored foraging effort of radio-tagged Surf Scoters (*Melanitta perspicillata* (L., 1758)) in three different habitats: (1) shellfish farm structures with high densities of mussels and strong seasonal prey depletion, (2) soft-bottom clam beds with more stable but less available prey, and (3) rocky intertidal beds with moderate mussel densities and depletion rates. We predicted that foraging effort would vary uniquely by habitat, with effort increasing more where depletion was strongest. However, variation in both hourly and daily foraging efforts was best explained by date only. Effort per hour was lowest in early December (presumably owing to very high prey abundance), increased until mid-February as prey declined, and then decreased again in March (probably owing to increased daylight time for foraging). Foraging effort estimated over a full day increased steadily from December to March as prey were depleted. Temporal patterns of effort did not vary by habitat after accounting for seasonal effects. Instead of increasing foraging effort in habitats with strong depletion, Surf Scoters redistributed to habitats with lower degrees of prey reduction as the season progressed. We suggest that Surf Scoters respond to variation in prey by adjusting both foraging effort and habitat selection as the prey landscape changes.

**Résumé :** Nous avons suivi les efforts de recherche de nourriture de macreuses à front blanc (*Melanitta perspicillata* (L., 1758)) munies d'une étiquette radio dans trois habitats différents : (1) des structures d'élevage de coquillages avec de fortes densités de moules et une importante déprédation saisonnière, (2) des lits de palourdes à fond meuble avec des proies plus stables mais moins disponibles et (3) des fonds intertidaux rocheux avec des densités moyennes de moules et des taux de déprédation modérés. Nous avons prédit que les efforts de recherche de nourriture varieraient de façon particulière dans chaque habitat et que l'effort augmenterait plus là où la déprédation est la plus importante. Cependant, les variations horaires et journalières de l'effort de recherche de nourriture s'expliquent le mieux par la seule date. L'effort par heure est minimal en décembre (ce qui est sans doute dû à une très forte abondance de proies), il augmente jusqu'à la mi-février avec un déclin des proies et diminue encore en mars (probablement à cause de l'augmentation de la durée de l'éclaircissement pour la recherche de nourriture). L'effort de recherche de nourriture, estimé sur la journée complète, augmente régulièrement de décembre à mars alors que les proies s'épuisent. Les patrons temporels de l'effort ne varient pas en fonction de l'habitat, une fois qu'on a tenu compte des effets saisonniers. Au lieu d'augmenter leur effort de recherche de nourriture dans les habitats qui subissent un fort épuisement des proies, les macreuses à front blanc se répartissent, à mesure que la saison avance, dans les habitats où la réduction des proies est moins importante. Nous croyons que les macreuses à front blanc réagissent à la variation dans l'abondance des proies en ajustant à la fois leur effort de recherche de nourriture et leur sélection d'habitat aux changements dans le paysage des proies.

[Traduit par la Rédaction]

## Introduction

Availability of prey or variation in prey quality are known to influence the foraging component of the time-activity budgets of predators (Hutto 1990). For example, individuals that select prey items of lower gross energy content often must increase feeding time to maintain a positive energy balance (Paulus 1984, 1988; Turnbull and Baldassarre 1987). Density of prey also can be an important factor influencing foraging behaviours (Draulans 1982; Poulton et al. 2002). In particular, declines in prey abundance can elicit

an increase in foraging effort as birds compensate to maintain sufficient energy intake (Percival and Evans 1997; McKnight 1998; Cope 2003). When an increase in foraging effort is not possible because of physiological or behavioural constraints (Guillemette 1994; 1998), or prey intake rates fall below some threshold, predators would be expected to respond by abandoning their current patch in search of more profitable feeding areas (Pyke 1983; Stephens and Krebs 1986). Understanding how the landscape, including variation in availability and quality of prey, influences for-

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aging behaviours allows us to evaluate the value of different habitats (Hutto 1990).

Although variation in food supply is an important determinant of foraging behaviour, other environmental factors such as time of day, tide, weather, and season also influence time-activity budgets (Paulus 1988). For example, some waterfowl concentrate feeding effort into morning or evening bouts (Fisher and Griffin 2000; Cope 2003). Tidal height may influence diving birds by changing the depth of their benthic prey (Fisher and Griffin 2000; Holm and Burger 2002). Several sea duck species increase foraging effort at high tide because intertidal prey are available to obligate divers only when submerged (Goudie and Ankney 1986; Fisher and Griffin 2000). Adverse weather conditions such as elevated wind speeds can raise the energetic demands of waterbirds, resulting in increased feeding (Paulus 1984; Lovvorn 1994). A seasonal factor that influences birds wintering in northern regions is the change in the number of daylight hours (Systad et al. 2000). Sea ducks are generally diurnal foragers (Systad et al. 2000; Lewis et al. 2005; Rizzolo et al. 2005) and could be daylight-constrained during the shortest days of winter. To compensate for decreased day length in mid-winter, some species of waterfowl increase their foraging effort by spending a larger proportion of daylight hours feeding (Guillemette 1998; Fisher and Griffin 2000; Systad et al. 2000; Cope 2003).

Surf Scoters (*Melanitta perspicillata* (L., 1758)) forage by diving in shallow coastal waters and either excavate clams from soft sediments or pry epibenthic mussels off rocks (Savard et al. 1998). Diving is energetically expensive (de Leeuw 1996). To compensate for the high energy demands of diving in a cold-water environment and the low energetic content of bivalves (with respect to the energetic demands of large waterfowl), sea ducks must consume large amounts of prey (Goudie and Ankney 1986; Guillemette 1994, 1998). A growing body of evidence indicates that wintering sea ducks, including Surf Scoters, can deplete food resources (Guillemette et al. 1996; Lacroix 2001; Kirk et al. 2007; Lewis et al. 2007). Because changes to prey availability are known to influence foraging behaviour (Percival and Evans 1997; Tuckwell and Nol 1997; McKnight 1998), we speculated that depletion of prey could directly affect subsequent foraging effort.

In Malaspina Inlet, British Columbia, we monitored foraging effort of Surf Scoters in three habitat types: (1) shellfish farms, (2) soft-bottom clam flats, and (3) rocky intertidal mussel beds. In a concurrent study, prey was intensively sampled in all three of these habitat types in the Malaspina Inlet (Kirk et al. 2007). Randomly selected quadrats of mussels and clams were sampled to measure density and size-class distribution. Prey sampling occurred in the fall (prior to Surf Scoter arrival) and again in the spring to estimate overwinter depletion. In this inlet, the abundance and quality of the primary prey resource (bay mussels, *Mytilus trossulus* Gould, 1850; hereinafter mussels) are enhanced by the presence of the shellfish farming structures, but these vary both spatially and temporally (Kirk et al. 2007). The structures provide a novel substrate for natural recruitment of wild mussels. Compared with mussels growing on natural intertidal substrates, mussels growing on shellfish farming structures grew at a higher density (Fig. 1), had weaker byssal thread attachments, thinner and less massive shells, and

lower shell-crushing resistance, but were similar in tissue mass and energy density (Kirk et al. 2007). These differences in abundance and morphology presumably reduce the energetic costs and increase foraging benefits, making farms higher quality habitats compared with intertidal areas. Although clam habitats are rare in Malaspina Inlet and clam densities are low relative to mussels (Fig. 1), the energy content of each clam is considerably higher than that of an average mussel (D. Esler, unpublished data), and clam flats are a viable foraging habitat for Surf Scoters (Lewis et al. 2007). Also, depletion of prey densities occurred over the course of winter (Fig. 1), particularly on shellfish aquaculture structures. Hence, this study area, with its quantified spatial and temporal variations in prey resources, allowed us to consider in detail the foraging responses of Surf Scoters.

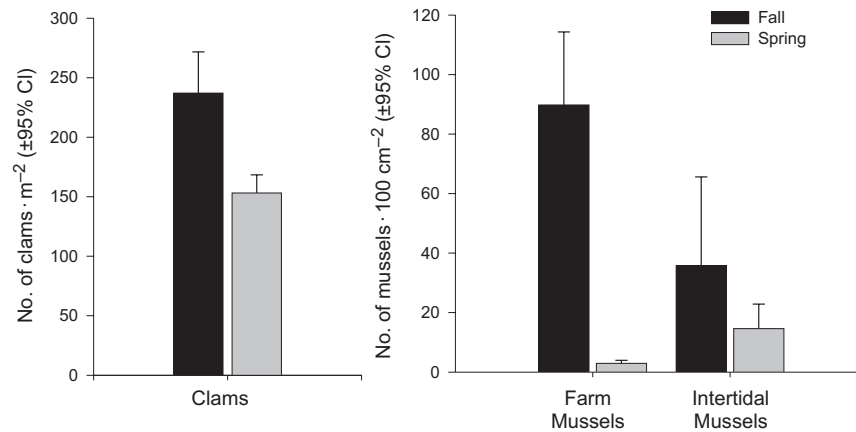
In this study, we considered how foraging effort of Surf Scoters varied in relation to differences in availability and temporal stability of prey in distinct habitats. Because of the high density and profitability of mussels on aquaculture structures, we predicted that Surf Scoters foraging on farms would exhibit reduced levels of effort compared with intertidal feeders, but that this would increase through winter because of prey depletion, while foraging effort in clam habitats would remain more constant throughout the season. We monitored foraging activities of Surf Scoters feeding in the three habitats in the Malaspina Inlet area throughout one winter and evaluated variation in both hourly and daily foraging efforts in relation to environmental features, attributes of individuals, and spatial and temporal variations in abundance and quality of prey.

## Materials and methods

We measured foraging effort of radio-tagged Surf Scoters in the Malaspina Inlet during the winter of 2004–2005. We defined hourly foraging effort as the amount of time spent underwater per hour and daily foraging effort as the estimated total time spent underwater per day. Variation in hourly foraging effort considers how a bird modifies behaviours within a single feeding bout. By also estimating daily foraging effort, we can examine the variation in total allocation per day to foraging in response to seasonal or habitat changes (Guillemette 1998). Malaspina Inlet (50.0°N, 124.7°W) is on the mainland coast of the Strait of Georgia in British Columbia. The study area is a series of narrow fjord-like inlets used extensively by the shellfish aquaculture industry. The primary shellfish farming activity is deep-water farming of oysters using floating structures. The intertidal area includes rock walls and shelves, reefs, and several soft-sediment beaches. In this study area, Surf Scoters foraged in three distinct habitats. The majority of prey consisted of mussels growing in epibiotic clusters on shellfish farming structures (hereinafter “farm” habitats). Mussels also occurred in natural beds on reefs and in rocky intertidal habitats. Lastly, there were several small soft-bottom tidal flats where Surf Scoters foraged on clams, including manila clams (*Venerupis philippinarum* (A. Adams and Reeve, 1850)), varnish clams (*Nuttallia obscurata* (Reeve, 1857)), and Pacific littleneck clams (*Protothaca staminea* (Conrad, 1837)).

In November 2004, Surf Scoters were trapped with a modified floating mist-net system (Kaiser et al. 1995). Each

**Fig. 1.** Prey densities in three habitats in the Malaspina Inlet, British Columbia, showing prey depletion from fall 2004 to spring 2005.



morning before dawn, floating sets of nets and decoys were placed at Surf Scoter foraging sites. As birds were captured, they were placed in kennels and transported to a banding station where they 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). Either subcutaneous or internal abdominal VHF radios with external antennae were then implanted in Surf Scoters ( $n = 74$ ), following standard procedures (Mulcahy and Esler 1999). These radio types have been shown to perform well for Surf Scoters, with low mortality rates and good signal strength and accuracy for telemetry (Iverson et al. 2006). All capture, banding, and radio-implantation procedures were approved by the Animal Care Review Committee at Simon Fraser University.

The radio signal of VHF transmitters disappears when the bird submerges and resumes upon resurfacing (Custer et al. 1996), allowing quantification of time spent foraging by diving birds. Following methods of Lewis et al. (2005, 2008), radio-tagged Surf Scoters were monitored for 1 h periods at selected foraging locations covering all three habitat types (clam flats, farms, and intertidal mussel beds) over the season. The 1 h observation periods spanned available daylight hours throughout the season, ranging from 0800 to 1700. A hand-held four-element Yagi antenna was positioned for optimal signal strength from a land-based observation point and connected to a radio receiver (Advanced Telemetry Systems, Isanti, Minnesota). During the 1 h observation period, each dive length was recorded as minutes underwater measured to the nearest second using a standard stopwatch. Individuals were monitored a maximum of once per day. At the end of the observation period, the total minutes underwater per hour were summed. For each individual 1 h observation, daily foraging time, or total minutes underwater per day, was also estimated. Because Surf Scoters are generally diurnal foragers (Lewis et al. 2005), daily time foraging is calculated as the product of minutes underwater per hour and number of daylight hours (from Environment Canada meteorological data for Powell River, British Columbia). The number of daylight hours ranged from 8.1 h in mid-December to 12.4 h in late March. Habitat type was determined by projecting the biangulated telemetry locations in an ArcView<sup>®</sup> GIS map of the study area including a habitat layer (digitized from digital nautical charts and geo-referenced

field notes). The projected telemetry locations had a mean 90% error polygon of 0.02 km<sup>2</sup> (SE 0.008) and habitat type was confirmed by visually noting the flock location at the time of observation. Time of day, tidal height (from the Canadian Hydrographic Service tidal predictions for Lund, British Columbia), and wind speed (Beaufort scale) were recorded at the beginning of each 1 h observation period. From 09 December 2004 to 24 March 2005, 160 h of Surf Scoter foraging were monitored on 51 individuals in all three habitats in the Malaspina Inlet ( $n = 89, 23,$  and 48 h on farms, clam beds, and mussel beds, respectively).

#### Data analyses

We evaluated variation in foraging effort using a mixed model repeated measures analysis because the data included multiple observations (ranging from 1 to 12) on single individuals. We tested two response variables as measures of foraging effort: (1) hourly foraging effort or total minutes underwater for each 1 h observation period and (2) daily time foraging or minutes underwater per day. For each response variable, a candidate model set was generated to include the following explanatory variables: habitat type (classed as farm, intertidal clam, or intertidal mussel), date, individual (Surf Scoter sex and age class), and environmental variables (Table 1). The date variable was defined as the number of days from 09 December 2004 and included a quadratic date function (day<sup>2</sup>), which allowed foraging effort to vary nonlinearly over time (Guillemette 1998; Fisher and Griffin 2000; Systad et al. 2000). Some variables were always considered in combination to limit the candidate model set size. The environmental variables (envir) that we used (time of day, tidal height (m), and wind speed (Beaufort scale converted to km·h<sup>-1</sup>)) were always considered together. The individual parameters of age (juvenile or adult) and sex (male or female) of each Surf Scoter subject were included or excluded in models as a group, described as the individual variable. A habitat × date interaction term was also added to a subset of models, because of the a priori prediction that foraging effort could vary differently by date in distinct habitat types. Each candidate set included 17 models with different combinations of explanatory variables singly and additively, with and without the habitat × date interaction term, as well as a null or equal means model (Table 1).

**Table 1.** General linear model selection results assessing variation in hourly (min underwater-h<sup>-1</sup>) and daily (estimated min underwater-d<sup>-1</sup>) foraging efforts of radio-tagged Surf Scoters (*Melanitta perspicillata*) in the Malaspina Inlet, British Columbia.

Response variable	Model	No. of parameters	$\Delta AIC_c$	AIC <sub>c</sub> weight
Hourly foraging effort	Date <sup>a</sup>	5	0.00	0.45
	Habitat + date	7	1.84	0.18
	Habitat + date + indiv <sup>b</sup>	9	2.54	0.13
	Date + envir <sup>c</sup>	8	4.26	0.05
	Date + habitat × date	9	4.62	0.05
	Habitat	5	4.89	0.04
	Indiv + habitat × date	11	5.69	0.03
	Date + indiv + envir	10	5.91	0.02
	Habitat + date + indiv + envir	12	7.08	0.01
	Habitat + date + habitat × date	11	7.70	0.01
	Indiv	5	8.14	0.01
	Date + envir + habitat × date	12	8.37	0.01
	Habitat + date + indiv + habitat × date	13	8.85	0.01
	Habitat + envir	8	9.84	0.00
	Date + indiv + envir + habitat × date	14	10.22	0.00
	Habitat + date + envir + habitat × date	14	11.79	0.00
	Null	2	15.82	0.00
Daily foraging effort	Date	5	0.00	0.40
	Habitat + date + indiv	9	1.50	0.19
	Habitat + date	7	1.70	0.17
	Date + habitat × date	9	3.70	0.06
	Indiv + habitat × date	11	3.90	0.06
	Date + envir	8	4.60	0.04
	Date + indiv + envir	10	5.20	0.03
	Habitat + date + indiv + envir	12	6.50	0.02
	Date + envir + habitat × date	12	7.70	0.01
	Habitat + date + habitat × date	11	7.80	0.01
	Habitat + date + indiv + habitat × date	13	8.10	0.01
	Date + indiv + envir + habitat × date	14	8.80	0.00
	Habitat + date + envir + habitat × date	14	12.20	0.00
	Habitat	5	13.80	0.00
	Habitat + envir	8	18.00	0.00
	Indiv	5	21.60	0.00
	Null	2	35.80	0.00

**Note:** The number of parameters includes +1 for an intercept and +1 for a model variance estimated. Covariance structures for repeated measures include +1 parameter for all models except the null model. Models listed in order of  $\Delta AIC_c$ , where  $\Delta AIC_c$  is Akaike's information criterion adjusted for small sample sizes.

<sup>a</sup>Date = day + day<sup>2</sup>, where day 1 = 09 December 2004.

<sup>b</sup>Indiv = sex (male or female) + age (adult or hatch-year).

<sup>c</sup>Envir = tide (m) + wind speed (km·h<sup>-1</sup>) + time of day.

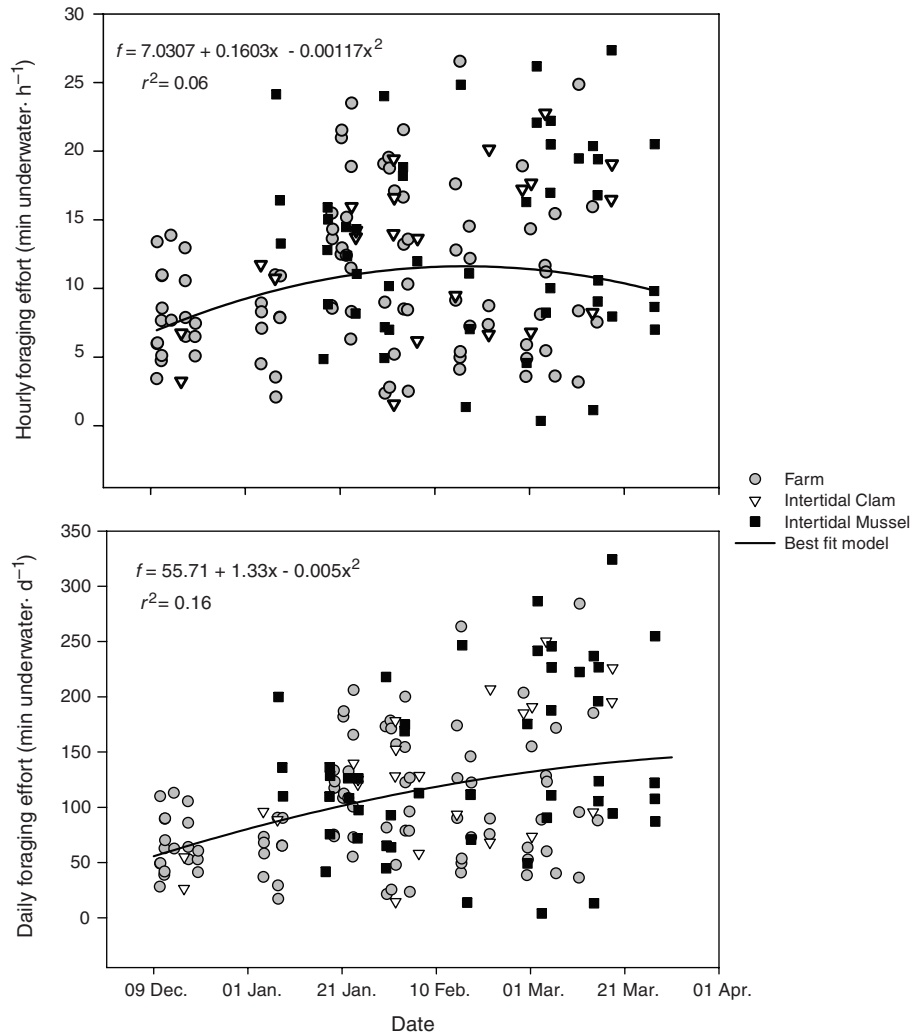
We used general linear mixed models generated from PROC MIXED in SAS<sup>®</sup> version 9.1 (SAS Institute Inc. 2003), with a repeated-measures term to account for multiple observations on individual Surf Scoters. The use of mixed models allowed us to include subject as a random effect, thereby accounting for within-subject correlation (Littell et al. 2000). The structure of this correlation was incorporated as a covariance parameter in each model. Several covariance structures were considered by applying them to the global model (not including interaction terms) and AIC model selection criteria were used to select the best fitting structure. Compound symmetry covariance was deemed most appropriate to apply in the analysis. With a compound symmetry structure, the correlation between subjects is con-

stant regardless of the distance in time between pairs of observations (Littell et al. 2000).

An information-theoretic approach was used to evaluate fit of the candidate set of models (Burnham and Anderson 2002). Akaike's information criterion adjusted for small sample sizes (AIC<sub>c</sub>) was generated for each candidate model. The candidate set was ranked by  $\Delta AIC_c$ , the difference between the AIC<sub>c</sub> of the best fitting model and each model in the set. AIC<sub>c</sub> weights were used to deduce the relative support for each model. Also, parameter likelihood values were generated by summing the AIC<sub>c</sub> weights for all candidate models containing the parameter under consideration. These parameter likelihoods allow us to assess the relative importance of each variable within the model set; a



**Fig. 2.** Variation in hourly (top panel) and daily (bottom panel) foraging efforts for Surf Scoters in the Malaspina Inlet, British Columbia, from 09 December 2004 to 24 March 2005. Curves were generated from parameter estimates of the top-ranked models.



value close to one indicates a well-supported or important variable. Weighted parameter estimates with 95% confidence intervals (CIs) also were produced for each explanatory variable (Burnham and Anderson 2002); they provide another measure of the importance of individual parameters for explaining variation in the response variable.

## Results

Throughout winter, Surf Scoters spent a mean of  $11.7 \text{ min}\cdot\text{h}^{-1}$ , or 19.5% of their time, underwater in a foraging dive. In our mixed model analysis of minutes underwater per hour, the model including only the date variables was the most parsimonious for explaining variation in hourly foraging time ( $\text{AIC}_c$  weight = 0.45; Table 1). Hourly time spent diving was lowest in early December ( $7.8 \text{ min}\cdot\text{h}^{-1}$  or 13%), increased to  $12.6 \text{ min}\cdot\text{h}^{-1}$  or 21% by mid-February, and declined again slightly by late March ( $10.8 \text{ min}\cdot\text{h}^{-1}$  or 18%) ( $r^2 = 0.06$ ; Fig. 2). The habitat + date model ( $\text{AIC}_c$  weight = 0.18) received some support (Table 1), which suggested that some variation in hourly dive investment was due to habitat type. However, because the habitat  $\times$  date interaction models were not supported ( $\text{AIC}_c$

weights < 0.05), the temporal pattern of minutes underwater per hour was similar in all habitats. The habitat + date + indiv model was the third most parsimonious ( $\text{AIC}_c$  weight = 0.13), although it received less than one-third of the support of the date model. All other models, including the null and global models, were very poorly supported.

The parameter likelihood values also supported the date variables (day and day<sup>2</sup>) as the best explanatory variables for minutes underwater per hour (Table 2). Their weighted parameter estimates confirmed that hourly dive effort tended to increase until mid-winter (day = 0.15, 95% CI = 0.06) then decreased slightly (day<sup>2</sup> =  $-0.001$ , 95% CI = 0.0005). The habitat variables, with parameter likelihood values of 0.38, were second to the date variables in their explanatory value (Table 2), although this was not a strong level of support. Mean dive time per hour was slightly lower on farms ( $10.5 \text{ min}\cdot\text{h}^{-1}$  or 17.5%) than at intertidal clam beds ( $12.7 \text{ min}\cdot\text{h}^{-1}$  or 21.2%) and intertidal mussel reefs ( $13.4 \text{ min}\cdot\text{h}^{-1}$  or 22.3%). Similarly, model-averaged parameter estimates revealed that Surf Scoters foraging in farm habitats spent less time underwater per hour compared with those foraging in intertidal mussel and clam beds (Table 2), although the 95% CIs broadly overlapped zero. Therefore,

**Table 2.** Parameter likelihood values and weighted parameter estimates with 95% confidence intervals (CIs) from the general linear mixed models evaluating variation in hourly and daily foraging efforts of Surf Scoters in three habitats (farm, clam, and intertidal mussel) in Malaspina Inlet, British Columbia.

Parameter	Hourly foraging (min underwater-h <sup>-1</sup> )			Daily foraging (min underwater-d <sup>-1</sup> )		
	Parameter likelihood value	Weighted parameter estimate	Unconditional 95% CI	Parameter likelihood value	Weighted parameter estimate	Unconditional 95% CI
Intercept	1.00	6.77	5.93	1.00	48.30	57.37
Sex						
Female	0.21	0.37	0.74	0.30	5.74	10.39
Male	0.21	0.00	0.00	0.30	0.00	0.00
Age						
Adult	0.21	0.32	0.70	0.30	5.80	10.68
Hatch-year	0.21	0.00	0.00	0.30	0.00	0.00
Date						
Day	0.92	0.15	0.12	0.94	1.27	1.18
Day <sup>2</sup>	0.92	-0.0011	0.0005	0.94	-0.005	0.01
Habitat						
Farm habitat	0.38	-0.84	1.47	0.39	-7.83	14.36
Intertidal clam habitat	0.38	-0.35	1.44	0.39	-2.59	14.99
Intertidal mussel habitat	0.38	0.00	0.00	0.39	0.00	0.00
Envir						
Tide	0.11	0.15	0.33	0.10	1.33	3.05
Wind	0.11	0.00	0.00	0.10	-0.02	0.05
Time	0.11	0.00	0.00	0.10	0.00	0.00
Habitat × date						
Farm × day	0.10	0.01	0.03	0.15	0.10	0.38
Farm × day <sup>2</sup>	0.10	0.00	0.00	0.15	0.00	0.02
Clam × day	0.10	0.01	0.03	0.15	0.03	0.44
Clam × day <sup>2</sup>	0.10	0.00	0.00	0.15	0.02	0.01
Mussel × day	0.10	0.01	0.01	0.15	0.11	0.22
Mussel × day <sup>2</sup>	0.10	0.00	0.00	0.15	0.00	0.00

**Note:** Parameter likelihoods closest to 1.0 have the greatest relative support. Parameter estimates for date are scaled so that 09 December 2004 is equal to 1.

despite these trends in habitat variation, this result was not strongly supported. None of the other variables received support for explaining variation in minutes underwater per hour, with all parameter likelihoods  $\leq 0.21$  and 95% CIs broadly overlapping zero (Table 2).

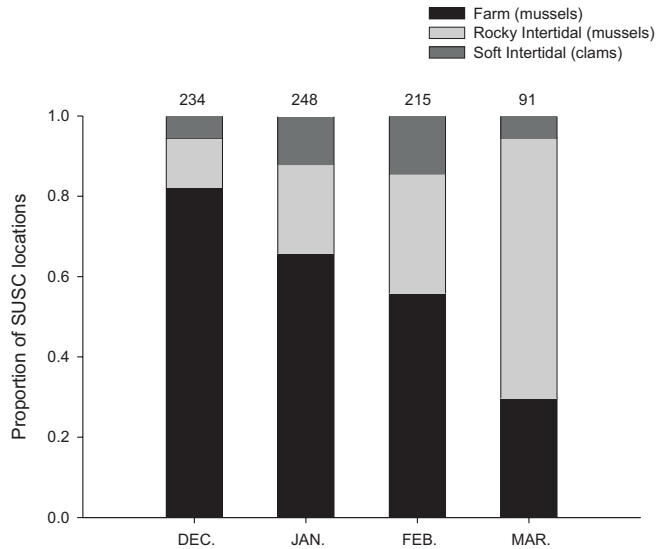
For daily time foraging, or minutes underwater per day, the date model again received the strongest support for explaining variation in foraging time ( $AIC_c$  weight = 0.40; Table 1). Daily investment in foraging increased with date, from a mean of 64 min (SE 5) in December to 154 min (SE 14) in March (Fig. 2). The second- and third-ranked models (Table 1) indicated that some variation in daily foraging was due to habitat type ( $AIC_c$  weight = 0.19 and 0.17, respectively). Generally, daily time underwater was lower at farms than in intertidal habitats. However, like in the hourly dive time results, habitat-specific temporal variation in daily foraging effort (i.e., the habitat × date interaction) was not well supported.

Model-averaged parameter estimates confirmed that, of the variables considered in the daily foraging time analysis, the date variable offered the most explanatory value (parameter likelihood value = 0.94). Daily investment in diving increased with day (day = 1.27, 95% CI = 1.18; Fig. 2). The day<sup>2</sup> parameter estimate was small but negative, indicating a nonlinear relationship between daily diving and date

(Table 2). However, this result was poorly supported, as the 95% CIs for the day<sup>2</sup> parameter overlapped zero. Again, the habitat variables appeared to explain some variation (parameter likelihood value = 0.39), but these 95% CIs also suggested a nonsignificant level of support. The individual variables of sex and age came out slightly stronger in the daily foraging analysis than in the hourly diving results (parameter likelihood values = 0.30). However, overall, date was the only variable with sufficiently strong support to explain variation in daily foraging times.

Given the lack of evidence for any strong effects of habitat or habitat interactions with date on foraging effort, we examined data that would indicate whether Surf Scoters were moving in response to heavy depletion in farm habitats, instead of increasing their foraging effort. We found that, based on the locations of radio-tagged individuals, Surf Scoters increased their use of intertidal habitats as the season progressed (Fig. 3). This indicated that when mussel exhaustion was evident on the farms (mid-February), Surf Scoters switched to using intertidal habitats where depletion was less pronounced (Fig. 1). Also, based on survey data, Surf Scoter numbers peaked in early December and declined thereafter (Fig. 4), suggesting that some individuals abandoned the study area and moved to other areas, perhaps as a response to prey depletion. Aerial telemetry surveys con-

**Fig. 3.** Proportions of radio-tagged Surf Scoter (SUSC) locations in three foraging habitats in Malaspina Inlet, British Columbia, summarized by month from December 2004 to March 2005. The number above each bar indicates sample size (i.e., the number of telemetry locations) for each month.



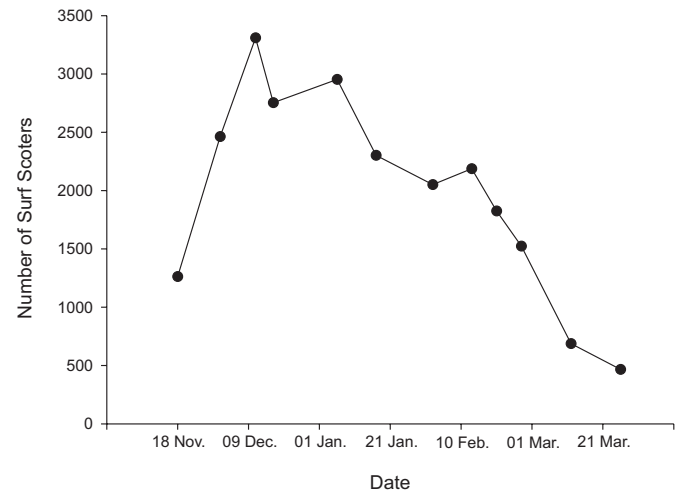
ducted in late February established that several of our radio-tagged Surf Scoters had moved to occupy foraging locations outside the study area.

## Discussion

We found that Surf Scoters wintering in Malaspina Inlet exhibited seasonal variation in diving behaviours. Both the hourly investment in diving and daily foraging effort of Surf Scoters changed with date (Fig. 2). Contrary to our predictions, foraging times were only slightly, but not significantly, lower in farm habitats compared with clam and intertidal mussel habitats, and seasonal changes in foraging effort did not differ by habitat. Although other factors can influence the time-activity budgets of wintering waterfowl (weather events, tidal fluctuations), in this study we found little support for age, sex, or environmental attributes as having important effects on foraging effort of Surf Scoters.

When faced with daylight constraints, many waterfowl species will increase their relative investment in foraging during the shortest days of winter (Guillemette 1998; Fisher and Griffin 2000; Systad et al. 2000; Cope 2003). Because Surf Scoters rarely forage nocturnally (Lewis et al. 2005), they must meet their energetic costs during daylight hours. Surf Scoters in Malaspina Inlet, however, showed the lowest hourly foraging times during the shortest days. This was likely due to the highly abundant prey that existed early in the winter, when mean mussel density on shellfish farming structures was 9600 mussels·m<sup>-2</sup> (Kirk et al. 2007). Telemetry locations of radio-tagged Surf Scoters indicated that the majority of birds were foraging in farm habitats in December (Fig. 3). As the season progressed and prey densities declined, dive time per hour increased. The highest hourly investment in foraging was in mid-February when days were already considerably longer (10.3 h of daylight compared with 8.2 h in early December). Therefore, the increase

**Fig. 4.** Numbers of Surf Scoters in the Malaspina Inlet, British Columbia, study area throughout the range of dates that foraging effort was monitored. Each point indicates an individual survey.



in effort per hour observed here was almost certainly a result of prey depletion. By early February, farm habitats were heavily depleted of mussels (M. Kirk, personal observation). Surf Scoters remaining in these habitats presumably would require longer search times for scarcer prey. Also, many birds switched to intertidal habitats (Fig. 3), where both search and capture costs were most likely higher (Kirk et al. 2007). The slight decline in hourly foraging time in early spring is probably a result of increased daylight hours (mean of 11.5 h of daylight in March), allowing birds to feed through more of the day to meet energetic requirements. The trend in daily foraging time indicated that Surf Scoters worked harder as the season progressed. This, again, was likely due to declining prey in preferred habitats and the use of less profitable habitats. Mussel depletion, particularly in farm habitats, was very strong within the study area (Fig. 1). As mussels became more scarce and daylight hours longer, Surf Scoters were diving for more minutes per day likely because prey was harder to find.

Contrary to our a priori predictions, temporal patterns of foraging effort (hourly or daily) did not vary by habitat. Given the pronounced changes in prey availability in mussel habitats, and especially in farms, we predicted that foraging effort of Surf Scoters there would intensify as the season progressed, more so than in clam habitats where depletion was less dramatic. Early in the season, overall effort was slightly reduced in farms where mussels were more plentiful at shallow depths with weak byssal threads and low shell-crushing resistance (Kirk et al. 2007). However, despite the rapid depletion of these mussels, our data indicate that there was no difference in temporal trends in foraging effort between habitats. Surf Scoters were more likely to move to alternate habitats as the season progressed rather than increase effort levels (Fig. 3). A concurrent study of Surf Scoter movement behaviours showed that individual scoters in the study area had high levels of movement and foraged at many feeding sites throughout the season (Kirk et al. 2008). This suggests that Surf Scoters are not able to adjust foraging effort significantly because of digestive or physiological constraints, but may have more behavioural flexibility in

habitat choice and movements. Alternatively, Surf Scoters may balance foraging effort with habitat selection to optimally meet their energetic requirements. Also, as hourly and daily foraging efforts increased in mid-winter (February), many Surf Scoters departed the study area to forage elsewhere (Fig. 4). These movements are too early in the year to be migratory (S. Wainwright De La Cruz, unpublished data). As the demands of feeding in an area with declining prey increased, clearly many birds sought alternative feeding areas.

Our study confirms that Surf Scoters adjust both foraging effort and habitat selection during the winter season. When faced with declining prey, Surf Scoters can increase foraging efforts to work harder or, alternatively, move to habitats with increased prey abundance. We found no evidence of habitat- or prey-specific foraging behaviours. Surf Scoters appear to respond to prey depletion in specific habitats by adjusting both levels of foraging effort and habitat or prey selection.

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