Foraging Behavior of Surf Scoters (*Melanitta Perspicillata*) and White-Winged Scoters (*M. Fusca*) in Relation to Clam Density: Inferring Food Availability and Habitat Quality

Author(s): Tyler L. Lewis, Daniel Esler, W. Sean Boyd

FORAGING BEHAVIOR OF SURF SCOTERS (*MELANITTA PERSPICILLATA*) AND WHITE-WINGED SCOTERS (*M. FUSCA*) IN RELATION TO CLAM DENSITY: INFERRING FOOD AVAILABILITY AND HABITAT QUALITY

TYLER L. LEWIS,[1,4] DANIEL ESLER,[2,5] AND W. SEAN BOYD[3]

[1]*Centre for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada;*
[2]*Centre for Wildlife Ecology, Simon Fraser University, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada; and*
[3]*Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada*

ABSTRACT.—Birds are known to modify their foraging behavior in relation to food availability. Once understood, these relationships can be used to draw inferences about relative food availability and habitat quality. We measured foraging behavior of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) feeding on clams during winter in the Strait of Georgia, British Columbia, to evaluate the relative quality of the foraging landscape for wintering scoters. Because clam biomass does not increase appreciably during winter through growth or recruitment, scoters are faced with a depleting and potentially exhaustible food supply. Along with this temporal variation, clam densities vary widely by site. We considered the influence of variation in clam density on scoter foraging behavior, along with other factors known to affect foraging in other sea duck species, such as season, sex, age, and environmental attributes. Clam-capture success (clams captured per dive) and foraging effort (minutes underwater per hour) of Surf Scoters were not related to variation in clam density. Clam-capture success of White-winged Scoters was unrelated to clam density; however, their foraging effort was negatively related to clam density, though varying by only 4 min across the range of observed clam densities. For both species, foraging behavior was generally more strongly related to other factors, especially seasonal and age effects. These results suggest that (1) observed variation in clam density was relatively minor from the perspective of foraging scoters and (2) our study site constituted high-quality winter habitat in which scoters were not constrained by food availability. *Received 28 June 2006, accepted 30 March 2007.*

Key words: clam density, food availability, *Melanitta fusca*, *M. perspicillata*, scoter foraging behavior, sea duck, Surf Scoter, White-winged Scoter.

Comportamiento de Forrajeo de *Melanitta perspicillata* y *M. fusca* con Relación a la Densidad de Almejas: Inferencias sobre la Disponibilidad de Alimento y la Calidad del Hábitat

RESUMEN.—Las aves son conocidas por modificar su comportamiento de forrajeo en función de la disponibilidad de alimento. Una vez entendidas, estas relaciones pueden ser utilizadas para realizar inferencias sobre la disponibilidad relativa de alimento y la calidad del hábitat. Medimos el comportamiento de forrajeo de *Melanitta perspicillata* y *M. fusca*, dos especies que se alimentan de almejas en el estrecho de Georgia, British Columbia durante el invierno, para evaluar la calidad relativa del paisaje de forrajeo para estos anátidos marinos durante el invierno. Debido a que la biomasa de almejas aparentemente no aumenta mediante crecimiento ni reclutamiento durante el invierno, estas aves enfrentan una disminución y potencialmente un agotamiento de la disponibilidad de alimento. Además de esta variabilidad temporal, la densidad de almejas también varía considerablemente entre sitios. Consideramos la influencia de la variación en la densidad de almejas sobre el comportamiento de forrajeo de las dos especies estudiadas, además de otros factores conocidos por afectar el forrajeo de otras especies de anátidos marinos, como la época, el sexo, la edad y atributos ambientales. El éxito de captura de almejas (almejas capturadas por inmersión) y el esfuerzo de forrajeo (minutos de inmersión por hora) por parte de *M. perspicillata* no se relacionaron con la variación en la densidad de almejas. El éxito de captura de almejas por parte de *M. fusca* no se relacionó con la densidad de almejas, pero su esfuerzo de forrajeo estuvo relacionado negativamente con la densidad de almejas, a pesar de que éste varío en sólo 4 minutos en el rango de densidades de almejas observado. Para las dos especies, el comportamiento de forrajeo en general se correlacionó más fuertemente con otros factores, especialmente con efectos estacionales y de la edad. Estos resultados sugieren que (1) la variación observada en la densidad de almejas fue relativamente baja desde la perspectiva de forrajeo de las especies estudiadas y (2) nuestro sitio de estudio constituyó un hábitat de invierno de alta calidad en el cual *M. perspicillata* y *M. fusca* no se encontraron restringidos por disponibilidad de alimento.

[4]Present address: U.S. Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA.
[5]Address correspondence to this author. E-mail: desler@sfu.ca

ACQUISITION OF ENERGY and nutrition has direct effects on the reproductive success and survival of animals (Lemon 1991). Because of these fitness consequences, animals typically select food sources and employ foraging behaviors that optimize energy intake (Pyke 1984, Stephens and Krebs 1986). When faced with variation in food availability, animals tend to modify their foraging behavior. For example, when food becomes scarce, individuals often increase their overall foraging effort to maintain sufficient levels of energy intake (Hutto 1990, McKnight 1998, Cope 2003). Hence, foraging behavior often reflects food availability as perceived by the foraging animal, and an understanding of this relationship can be used to evaluate general habitat quality (Hutto 1990).

Waterfowl, like other birds, adjust their foraging behavior in response to variation in food abundance or quality. Many species increase their foraging effort, measured as the amount of time spent foraging, in response to declining food availability (Hill and Ellis 1984, Percival and Evans 1997). Similarly, waterfowl may adjust specific foraging behaviors, independent of time spent foraging, to cope with variation in food supplies. For example, when faced with declining food availability, dabbling ducks increased their surface feeding rate or swam faster while feeding to maintain adequate levels of food intake (McKnight 1998). For diving ducks, changes in foraging behaviors are often manifested through changes in dive behavior. During a foraging dive, variation in prey availability directly alters the amount of time that diving ducks spend searching and traveling underwater (Tome 1988). In areas with high prey availability, dive duration is often shorter because of the greater likelihood of encounting prey (Draulans 1982).

Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) forage exclusively by diving (Brown and Fredrickson 1997, Savard et al. 1998). During winter, diets of scoters are composed predominantly of bivalves (Vermeer 1981, Lewis et al. 2007). (Hereafter, when we use the term "scoters," we are referring to both species, unless stated otherwise.) Dive behavior of bivalve predators is strongly influenced by bivalve density (Richman and Lovvorn 2003), because most bivalve species are sessile and unable to actively escape predation. At low bivalve densities, scoters are predicted to increase their foraging effort, expressed as amount of time spent underwater, to compensate for the lower likelihood of encountering and capturing a bivalve. At some minimal bivalve density, scoters likely leave a foraging site rather than incur the energetic costs of further increases in foraging effort (Lovvorn and Gillingham 1996). Conversely, at high bivalve densities, scoters are predicted to decrease their foraging effort because of a higher likelihood of bivalve capture. Theoretically, foraging effort could decrease until search time is completely minimized, at which point foraging effort remains constant regardless of further increases in bivalve density. Therefore, an understanding of variation in scoter foraging effort and probability of bivalve capture will provide a strong indication of bivalve availability and general habitat quality.

Our study occurred in the Strait of Georgia, British Columbia, in areas composed of soft-bottom intertidal flats. Within the Strait of Georgia, wintering scoters are potentially exposed to high degrees of variation in the density of intertidal clams, their primary prey in soft-bottom habitats (Bourne 1984, Lewis et al. 2007). Temporal variation arises via the predation and mortality of clam populations that are not appreciably renewed by growth or recruitment during winter (Williams 1980, Bourne 1982), thus presenting wintering scoters with a dwindling and potentially exhaustible food supply. Similarly, scoters encounter considerable spatial variation in clam density, resulting from soft-bottom intertidal flats that differ widely in basic abiotic characteristics (Bourne 1982, Żydelis et al. 2006). To assess food availability and general habitat quality from the perspective of foraging scoters, we measured foraging effort and clam-capture success of wintering scoters and related these variables to spatial and temporal variation in clam density.

METHODS

Study area.—Our study area is located in the Strait of Georgia on the east coast of Vancouver Island, British Columbia, and encompasses the marine waters of Baynes Sound (49.5°N, 124.8°W). Baynes Sound is a 40-km coastal channel fringed with numerous shallow bays; the channel floor is largely composed of gravel and sand sediments (Dawe et al. 1998). The area produces significant amounts of both wild and cultured bivalves and is an important wintering area for waterfowl and other marine birds (Dawe et al. 1998). Surveys in Baynes Sound during the winters of 2002–2003 and 2003–2004 indicated a mean (± SE) of approximately 6,500 ± 250 scoters (Surf and White-winged scoters; W. S. Boyd unpubl. data).

Clam sampling.—Data were collected from six sample-plots (hereafter "plots") established throughout Baynes Sound in the winter of 2003–2004. Plots were chosen to represent a range of clam densities, as indicated by preliminary sampling, and were known to be used by scoters, thereby permitting quantification of foraging behaviors within the plots. To determine intertidal clam density, we sampled these plots twice, timed to coincide with scoter arrival in and departure from Baynes Sound: in the fall from 23 September to 17 October 2003, and in spring from 5 to 12 April 2004. Each plot measured 150 × 150 m and was contained within an intertidal area bounded by the 1.0-m and 3.5-m tidal heights, encompassing the tidal height range of the dominant intertidal clam species in Baynes Sound (Gillespie et al. 1999, 2001). Seventy-two quadrats, measuring 0.5 × 0.5 m, were sampled per plot in both fall and spring, which is consistent with the recommended sampling rate of 30 quadrats per hectare (Gillespie and Kronlund 1999), and no fall quadrat locations were resampled in the spring (detailed clam-sampling methods are described in Lewis et al. 2007). Each quadrat was excavated to a depth of 15 cm, below which clams were considered inaccessible to foraging scoters (Lovvorn 1989, Richman and Lovvorn 2003). All excavated substrate was passed through a 4-mm sieve. Retained clams were counted, and their shells were measured to 5-mm length classes. Sieve size was selected to retain the lengths of bivalves consumed by scoters; of entire bivalves found in the esophagi of collected scoters, as well as in the esophagi of similarly sized Canvasbacks (*Aythya valisineria*), Spectacled Eiders (*Somateria fischeri*), and Common Eiders (*S. mollissima*), few if any bivalves <4 mm in length were consumed (Bourne 1984, Lovvorn 1989, Nehls and Ketzenberg 2002, Lovvorn et al. 2003).

Some of the Baynes Sound intertidal area is used by the shellfish aquaculture industry for commercial production of Manila

Clams (*Venerupis philippinarum*). In some locations, large nets are placed atop portions of intertidal flats to protect cultured clam stocks from predation. Four of our six plots contained nets within their boundaries; for these four plots, we measured the total area that was covered by net. Because scoters are effectively excluded from preying on clams underneath these nets, our calculations of overall clam density for each plot account for only the net-free portions of the plot. During clam sampling, when randomly selected quadrat locations overlapped nets, we estimated the portion of the quadrat covered by net and sampled only net-free portions of the quadrat.

Foraging effort.—To estimate foraging effort, defined as the amount of time spent underwater, dive behavior of scoters was monitored via radiotelemetry during winter 2003–2004. Scoters were captured and affixed with radiotransmitters during December of 2002 and 2003, following the procedures described in Lewis et al. (2005). Because radiotransmitter batteries lasted 18 months and some radiotagged scoters returned to Baynes Sound for consecutive winters, we were able to monitor some individuals captured in December 2002 during winter 2003–2004. The total number of radiotagged scoters present in Baynes Sound during winter 2003–2004 included 42 Surf Scoters (28 males, 14 females) and 56 White-winged Scoters (34 males, 22 females).

Because radio signals disappeared when radiotagged scoters dove and resumed when they resurfaced, we documented both the number and duration of dives (Custer et al. 1996). Diving was monitored from 12 November to 16 March, concluding in March with the start of Pacific Herring (*Clupea pallasii*) spawning, at which point scoters abandoned their typical habitats and food sources in Baynes Sound. Diving was monitored only during diurnal hours because of the rarity of nocturnal foraging by scoters in our study site (Lewis et al. 2005). We used 1-h observation blocks to record the number of dives and length of each individual dive (±1 s). On the basis of preliminary sampling, observation blocks of 1-h duration were chosen because of their high likelihood (>99%) of detecting diving. Radio signals were rarely lost during diving observations (<1% of observations), and only complete 1-h observations were included in analyses. We used a maximum of one randomly selected diving observation per individual per day in analyses.

To ensure a spatial and temporal connection between diving observations of radiotagged scoters and clam density of plots, we determined locations of radiotagged scoters via biangulation. Biangulated scoter locations and telemetry accuracy (mean [± SE] 90% error polygon = 3.0 ± 0.2 ha) were determined following methods described in Lewis et al. (2005). We used ARCVIEW, version 3.2 (ESRI, Redlands, California; ESRI 2004), geographic information system (GIS) software to project scoter point locations and plots on a digital 1:20000 TRIM base-map of the British Columbia coast (British Columbia Ministry of Sustainable Resource Management, Victoria). A buffer was created around each plot, radiating 750 m from the center point of each plot, which exceeded the size of average location error. For each diving observation, inclusion in our foraging-effort analyses required the following temporal and spatial criteria: (1) an individual's point location was collected on the same day as that individual's diving observation, and (2) the point location was located within a 750-m plot buffer. We assume that foraging behaviors of scoters located within the buffer can be relevantly related to clam density within the plot.

Clam-capture success.—Clam-capture success, defined as the proportion of dives in which a clam was captured, was monitored once per week at each plot from 1 November 2003 to 5 March 2004, unless the plot was unoccupied by scoters during observation attempts. When feeding on bivalves, particularly larger size classes, scoters bring captured bivalves to the surface for manipulation and ingestion (Ydenberg 1988). The area within the plot, which was delineated with buoys on the offshore corners, was continually scanned for surfacing scoters. As a scoter surfaced after a foraging dive, the presence or absence of a clam in the bill was recorded, and then the observer recommenced scanning until the next surfacing scoter was observed. Only scoters for which the surfacing event was distinctly observed were selected for observation, minimizing potential bias caused by scoters that stayed longer at the surface to manipulate captured bivalves or differential handling times among bivalve species. Unmarked scoters (i.e., not radiotagged) were used for these observations, preventing the observer from distinguishing between individuals. Although scoters could move freely into and out of the plots, most scoters present in the plot were likely sampled because (1) the entire plot was used for observations; (2) the duration of observations (mean = 59 min) was long enough that each scoter surfaced numerous times; and (3) scoters typically occurred in the plots only for feeding, moving slightly offshore from plots for resting (T. L. Lewis pers. obs.).

Observations of clam-capture success were restricted to the core daylight hours of 0800–1600, because scoters rarely foraged at night (Lewis et al. 2005) and sufficient light was required to observe clam capture. Sampling effort per plot was approximately evenly distributed throughout these hours. From mid-October to late February in our study site, the lowest daily low tide occurs exclusively at night. Therefore, diurnal observations were all conducted with a substantially flooded plot. Only observation sessions with a minimum of five individuals present in the plot (mean: 29.7 scoters, range: 5–120 scoters) and 30 recorded surfacing events (mean: 113.0 surfacing events, range: 30–410 surfacing events) per scoter species were included in analyses. Clam-capture success was summarized for each observation period for each scoter species as the proportion of total dives that were successful. Thus, observation periods served as our unit of measurement for data analyses.

Estimates of clam-capture success depend on the assumption that captured clams are consumed largely at the surface. Typically, diving ducks swallow large bivalves at the surface and small bivalves underwater (de Leeuw and van Eerden 1992). Large bivalves require extended handling times to properly orient the bivalve for swallowing and are handled at the surface to avoid extra costs of diving (Ydenberg 1988, de Leeuw and van Eerden 1992). Lewis et al. (2007) found that our Baynes Sound plots were dominated by large clams (74% were >25 mm) and that overwinter declines in clam abundance, as caused by scoter predation, were concentrated in the larger size classes, primarily 25–45 mm. Accordingly, Lewis et al. (2007) concluded that most of the clam consumption by scoters occurred at the water's surface. We are therefore comfortable with the assumption that our surface observations provide a reliable measure of clam-capture success. Furthermore, because length distributions of clams were similar across plots, clam-capture success provides a comparable index across plots and clam densities, even if some portion of consumption occurred underwater.

Table 1. Linear regression equations describing overwinter changes in clam density (clams per square meter) for each of six sample-plots in coastal British Columbia, 2003–2004. Regression equations are based on clam density measurements determined from fall and spring clam sampling for Manila (*Venerupis philippinarum*), Varnish (*Nuttallia obscurata*), and Pacific Littleneck (*Protothaca staminea*) clams combined. Date is scaled so that 1 November 2003 = 1.

Sample-plot	Regression equation
1	Clam density = 155.38 − 0.49*date
2	Clam density = 173.30 + 0.06*date
3	Clam density = 178.29 − 0.39*date
4	Clam density = 158.32 − 0.13*date
5	Clam density = 112.35 − 0.27*date
6	Clam density = 159.78 − 0.10*date

Statistical analyses.—We examined factors affecting foraging effort and clam-capture success of scoters. Our primary interest was the relationship between these foraging behaviors and clam density. Clam density was measured twice per plot, once in the fall and once in the spring. Thus, to obtain a clam-density estimate for the specific date of each observation of foraging effort and clam-capture success, daily clam-density values for each plot were estimated from linear regression equations based on the fall and spring clam density measurements (Table 1). Although the shape of changes in clam densities is unknown, we believe that linear relationships provide a reasonable estimate of daily clam-density values because overwinter changes in clam numbers were mostly driven by scoter predation (Lewis et al. 2007) and scoter numbers in Baynes Sound were stable during winter (D. Esler unpubl. data). Measurements of clam density are a composite density of Manila Clam, Varnish Clam (*Nuttallia obscurata*), and Pacific Littleneck Clam (*Protothaca staminea*), which constitute most (>80%) of the scoter diet within our study site (Lewis et al. 2007).

To quantify foraging effort, we summarized all diving observations into minutes underwater per hour (min underwater h^{-1}). In total, 137 and 168 diving observations were used in foraging-effort analyses for Surf and White-winged scoters, respectively. Using minutes underwater per hour as our response variable, we fit a candidate set of general linear mixed models (Littell et al. 2000) using PROC MIXED in SAS (SAS Institute, Cary, North Carolina). We used general linear mixed models to account for repeated measures of radiotagged individuals and to include subject as a random effect (Littell et al. 2000). We considered the following explanatory variables to examine variation in foraging effort: clam density, tidal height, time of day, wind speed, scoter age and sex, and date. We used a quadratic relationship (date + $date^2$) for date (DATE), with all values of date adjusted in relation to 1 November 2003 = 1, to account for well-established patterns of foraging effort that vary nonlinearly over the winter in sea ducks (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000). To restrict the size of our candidate model set, while still accounting for individual and environmental effects known to affect waterfowl foraging effort (Brodsky and Weatherhead 1985, Goudie 1999, Systad et al. 2000), certain explanatory variables were always considered in combination. Scoter age (hatch-year [HY] or adult) and scoter

sex were always considered in combination and are together referred to as "individual effects" (INDIV). Time of day, wind speed (estimated from Beaufort sea state), and tidal height also were always considered in combination and are together referred to as "environmental effects" (ENVIR). Daylight was not included as an ENVIR variable because of its high correlation ($r^2 = 0.98$) with date; no other explanatory variables were strongly correlated. Using DATE, INDIV, ENVIR, and clam density (CLAM) as units for model construction, we constructed separate and identical *a priori* candidate model sets for Surf and White-winged scoters that consisted of the following 16 models: all single-variable models, all combinations of additive models, and a null model with only an intercept. Models with interaction terms were not used to restrict the number of candidate models and because there were no strong *a priori* biological explanations for putative interactions.

We used an information-theoretic approach to guide model selection (Burnham and Anderson 2002). Akaike's Information Criterion adjusted for small sample size (AIC_c) was calculated for each model in the candidate set. We used ΔAIC_c and AIC_c weights (w_i) to infer the relative support of each model. To determine the relative importance of each explanatory variable within a candidate model set, we summed w_i for all candidate models containing the explanatory variable under consideration, providing a parameter-likelihood value. Parameters that are well supported will have parameter-likelihood values close to one. Also, model-averaged parameter estimates and unconditional standard errors were calculated for each explanatory variable.

To evaluate variation in clam-capture success, we fitted a candidate set of generalized linear models using PROC GENMOD in SAS, with separate and identical model sets for Surf and White-winged scoters. A total of 57 and 70 observation periods were used for Surf and White-winged scoters, representing 5,972 and 8,381 surfacing events, respectively. We used generalized linear models based on logistic regressions to account for the binary measurement of clam-capture success (clam or no clam). To construct *a priori* candidate model sets, we included explanatory variables that explained the probability of clam capture by scoters, which differed from those considered for foraging effort. Specifically, we examined the following explanatory variables: clam density (CLAM), tide, and sex. Because scoters in Baynes Sound forage predominantly in the intertidal zone by diving, tide was included to account for differences in water depth and the amount of submerged intertidal habitat. Sex was measured as the proportion of surfacing events per observation that involved males. Age was not included, because only HY Surf Scoter males can be differentiated by plumage (Iverson et al. 2003), and they accounted for <0.5% of total observations. Candidate model sets consisted of all single-variable models, all combinations of additive models, and a null model with only an intercept, for a total of eight models. Models with interaction terms were not used because there were no strong *a priori* biological explanations for putative interactions.

Scoters moved very little during the winter season (Kirk 2007); thus, our clam-capture success observations may have included repeated observations of individual scoters. However, because observations were not of radiotagged individuals, we could not account for bird identity as a random factor to control for repeated measurements. Therefore, we based our data inference on $QAIC_c$ and $QAIC_c$ weights (Burnham and Anderson 2002), which account

for overdispersion (ĉ) of variance, including that potentially caused by repeated measurement of individuals. All QAIC$_c$ and QAIC$_c$ weights were based on estimates of ĉ calculated from the global model. Model-averaged estimates of clam-capture success were backtransformed from the logit scale to estimates of probability. All other data-inference methods follow those described for foraging effort.

RESULTS

On 1 November, the first day we monitored scoter foraging behaviors, clam densities within our plots ranged between 112 and 178 clams m^{-2} (Table 1). Clam density decreased over the winter at five of six plots, with decreases ranging from 8% to 42% (Lewis et al. 2007). At one plot, we estimated an increase in clam density of 4%. For the duration of winter 2003–2004, total variation in spatial and temporal clam density ranged between 82 and 180 clams m^{-2} (Table 1). Average standard error of clam density estimates for all six plots during both seasons was 18% of the mean. This relatively low standard error, along with plots that spanned the entire intertidal height range of Manila and Varnish clams, indicates that our sampling protocol sufficiently accounted for the spatial distribution of intertidal clams (Lewis et al. 2007).

Foraging effort.—Averaged over the entire winter, Surf Scoters spent ~12 min underwater h^{-1} (20% of their time). The best-fitting model to explain variation in minutes underwater per hour contained only DATE as an explanatory variable (Table 2). The model containing DATE and INDIV received moderate support, though its w_i was half that of the top model (Table 2). DATE was the only well-supported explanatory variable and the only explanatory variable with a parameter likelihood >0.33 (Table 3). On the basis of model-averaged parameter estimates for DATE, minutes underwater per hour decreased from approximately 12 November to 1 January, and then increased from approximately 1 January to 15 March (Fig. 1A). CLAM had a model-averaged parameter estimate of essentially zero, which indicates no change in minutes underwater per hour across the range of clam densities in our plots (Fig. 1B).

TABLE 2. General linear mixed models evaluating variation in foraging effort (minutes underwater per hour) of radiotagged Surf and White-winged scoters during winter in coastal British Columbia, 2003–2004. For all models, the number of parameters (k) includes +1k for an intercept and +1k for variance estimate. Covariance structures for repeated measures include +1k for all models except the null model. All models with substantial support (AIC$_c$ ≤ 2) and the null model are presented, listed in order of ΔAIC$_c$. Explanatory variable abbreviations: CLAM = clam density, DATE = quadratic date, and INDIV = individual effects (age, sex).

Species	Model	k	ΔAIC$_c$	w_i
Surf Scoter	DATE	5	0.00	0.38
	INDIV + DATE	7	1.41	0.19
	Null	2	56.42	0.00
White-winged Scoter	CLAM + INDIV + DATE	8	0.00	0.47
	CLAM + INDIV	6	0.60	0.35
	Null	2	16.41	0.00

TABLE 3. Parameter likelihoods and weighted-parameter estimates ± unconditional standard error (SE) from general linear mixed models evaluating variance in foraging effort (minutes underwater per hour) of radiotagged Surf and White-winged scoters during winter in coastal British Columbia, 2003–2004. Explanatory variables with the greatest relative support have parameter likelihoods close to 1.0. Explanatory variable abbreviations: CLAM = clam density, ENVIR = environmental effects, INDIV = individual effects, and DATE = quadratic date.

Explanatory variable	Surf Scoter		White-winged Scoter	
	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Intercept		11.781 ± 5.577		17.590 ± 4.116
CLAM	0.25	−0.000 ± 0.010	0.89	−0.041 ± 0.017
ENVIR	0.24		0.05	
Tide		0.243 ± 0.258		0.021 ± 0.036
Time of day		0.053 ± 0.066		0.006 ± 0.011
Wind		0.026 ± 0.028		−0.000 ± 0.004
INDIV	0.33		0.94	
Age[a]		1.136 ± 1.333		3.842 ± 1.441
Sex[b]		1.154 ± 1.062		−1.538 ± 0.931
DATE[c]	0.98		0.58	
Date		−0.146 ± 0.056		−0.067 ± 0.047
Date^2		0.001 ± 0.000		0.000 ± 0.000

[a] Age is a categorical variable (hatch-year or adult) with hatch-year as the reference value.
[b] Sex is a categorical variable (female or male) with male as the reference value.
[c] Parameter estimates for DATE are scaled so that 1 November 2003 = 1.

Averaged over the winter, White-winged Scoters spent ~13 min underwater h^{-1} (22% of their time). Two models were well supported, each of which contained CLAM and INDIV as explanatory variables (Table 2). INDIV had the largest parameter-likelihood value, because adults spent more time underwater than HY birds (Table 3). CLAM also had a large parameter-likelihood value and was negatively related to minutes underwater per hour (Table 3). On the basis of model-averaged estimates, White-winged Scoters foraging at the highest observed clam density of 180 clams m^{-2} dove for ~4 min less per hour than individuals at the lowest density of 82 clams m^{-2} (Fig. 1B). DATE was not well supported, and minutes underwater per hour varied relatively little in relation to date (Fig. 1A). Similarly, ENVIR variables received almost no support.

Clam-capture success.—The best-supported model for describing variation in clam-capture success of Surf Scoters was our null model, which fit an intercept only (Table 4). Six of eight models had Δ QAIC$_c$ ≤ 4, indicating that the best-fitting model did not receive substantial support over lower-ranking models. All of the explanatory variables had parameter likelihood values <0.34, which offered little power for explaining variation in clam-capture success. On the basis of model-averaged parameter estimates, clam-capture success changed <1% over the range of clam densities documented within our study site (Fig. 1C), and nontransformed, unconditional 95% confidence intervals (95% CI) for CLAM were larger in magnitude than the actual parameter estimate.

The best-supported model for describing variation in clam-capture success of White-winged Scoters contained CLAM as an
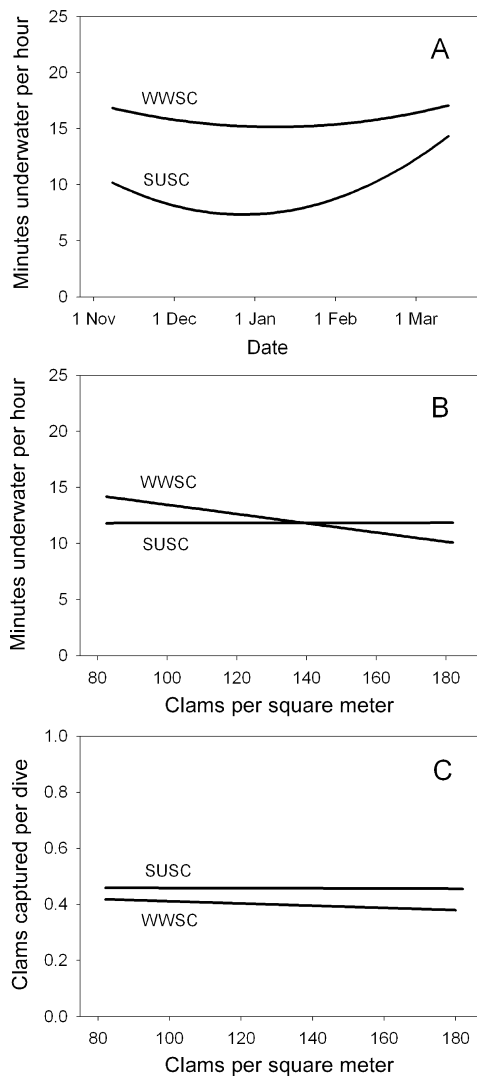
TABLE 4. Generalized linear models evaluating variation in clam-capture success (clams captured per dive) of Surf and White-winged scoters during winter in coastal British Columbia, 2003–2004. For all models, the number of parameters (k) includes +1k for an intercept, +1k for a variance estimate, and +1k for a variance inflation factor. All models with substantial support ($\Delta QAIC_c \leq 2$) are presented, listed in order of $\Delta QAIC_c$. Explanatory variable abbreviation: CLAM = clam density.

Species	Model	k	$\Delta QAIC_c$	w_i
Surf Scoter	Null	3	0.00	0.37
	Sex	4	1.42	0.18
White-winged Scoter	CLAM	4	0.00	0.34
	Null	3	1.16	0.19
	CLAM + Tide	5	1.83	0.14

is small, essentially indicating no relation between clam density and clam-capture success. Further, nontransformed, unconditional 95% confidence intervals for CLAM were larger in magnitude than the actual parameter estimate.

DISCUSSION

Inferring food availability and habitat quality.—Clam stocks in Baynes Sound, which are not appreciably renewed via growth or recruitment during winter (Williams 1980, Bourne 1982) and declined in density at five of six samples sites, nonetheless remained sufficiently abundant so that scoter foraging was largely unaffected. Neither foraging effort nor clam-capture success of Surf Scoters was related to variation in clam density. White-winged Scoter foraging effort was negatively related to clam density, yet their clam-capture success was unrelated. Any considerable change in clam density would be expected to cause concomitant changes in clam-capture success, which is a direct measurement of a scoter's ability to obtain food. As a whole, our results suggest that overwinter variation in clam density in Baynes Sound was relatively negligible from the perspective of scoters.

Averaged over the entire winter, Surf and White-winged scoters spent approximately 20% and 22% of their time underwater in our study site, respectively. Goudie (1999) reported values of between 30% and 35% of time spent underwater for Surf and White-winged scoters during winter in the Queen Charlotte Islands, British Columbia. Although Goudie (1999) did not quantify foraging effort with radiotelemetry, the large discrepancy between our foraging effort values and those of Goudie (1999) suggests that the lower foraging effort of scoters in Baynes Sound is a real phenomenon, not a product of different sampling methodologies. In the event of food limitations, scoters would be expected to increase their foraging effort toward maximal values to compensate for the decreased probability of food encounter and capture. The values reported by Goudie (1999) indicate that both scoter species can increase their overall foraging effort well beyond the values we observed, which further suggests that clam availability was relatively high for scoters in Baynes Sound. Also, scoters in Baynes Sound did not switch winter prey sources or move long distances to new foraging sites (Kirk 2007), as has been documented for other marine birds that experience food limitations (Guillemette et al. 1996, Lovvorn and Gillingham 1996, Suryan et al. 2000).

FIG. 1. Model-averaged estimates of (A) foraging effort (minutes underwater per hour) by date, (B) foraging effort (minutes underwater pher hour) by clam density, and (C) clam-capture success (clams captured per dive) by clam density for radiotagged Surf Scoters (SUSC) and White-winged Scoters (WWSC) wintering in coastal British Columbia, 2003–2004. Model-averaged estimates are restricted to either (A) the range of dates for which foraging effort was sampled or (B, C) the range of clam densities observed within our sample-plots.

explanatory variable (Table 4). However, seven of eight models had $\Delta QAIC_c \leq 4$, including the null model, which indicates a high degree of model uncertainty and general lack of explanatory power for all models. Of the explanatory variables, CLAM received marginal support (parameter likelihood = 0.64), whereas sex and tide had parameter likelihood values <0.30. On the basis of model-averaged parameter estimates, clam-capture success at the highest clam density was ~4% lower than at the lowest clam density (Fig. 1C). This result is the opposite of our prediction of higher clam-capture success at higher-clam densities. A difference of only 4% at the extreme clam-density values of our study site, however,

Relating foraging behaviors to clam density.—For diving ducks feeding on benthic prey, the rate of prey intake often follows a type II functional response (Lovvorn and Gillingham 1996, Richman and Lovvorn 2003), whereby intake rate increases with increasing prey density up to an asymptote, after which intake rate becomes limited by handling time and cannot increase further. Accordingly, our observed lack of correlation between clam density and clam-capture success of both scoter species, as well as foraging effort of Surf Scoters, could result from clam-density values in the asymptote range of a type II functional response curve (Poulton et al. 2002). Clam densities, however, were more likely in the increasing portion of the functional response curve, as indicated by clam-capture-success values that ranged from 30% to 50%. This inability of scoters to consistently capture clams suggests that scoters were not limited strictly by handling time, but rather by a combination of both search and handling times. Richman and Lovvorn (2003) documented increasing intake rates of captive White-winged Scoters for densities $\leq$1,600 clams m^{-2} for small clams, and $\leq$400 clams m^{-2} for large clams. The average densities of our plots did not exceed 180 clams m^{-2}, and only two individual quadrats from our plots (out of >700 quadrats sampled) had densities >1,000 clams m^{-2}.

Assuming that clam densities were in the increasing portion of a type II functional response curve, the general lack of correlation between clam density and scoter foraging behaviors suggests that the range of clam-density variation in Baynes Sound (82–180 clams m^{-2}) was relatively insignificant from the perspective of scoters. This range of clam-density variation was apparently large enough to affect only the foraging effort of White-winged Scoters. At the highest clam densities, White-winged Scoters spent ~16.8% of their time underwater, versus 23.6% at the lowest densities. Although we expected changes in foraging effort to be accompanied by changes in clam-capture success, the <7% range of variation in time spent underwater by White-winged Scoters may have been too small to detect parallel changes in clam-capture success. Also, dive duration of White-winged Scoters was not related to clam density (Lewis 2005), which indicates that they did not increase the length of their dives at low clam densities to maintain a heightened clam-capture success.

In addition to density, quality and size structure of prey populations may also affect foraging behavior of predators. For diving ducks, which often select certain sizes of bivalves (de Leeuw and van Eerden 1992, Hamilton et al. 1999), the relative foraging value of a bivalve population varies strongly by size (age) structure (Richman and Lovvorn 2003). Similarly, numerous aspects of bivalve quality that are likely important to diving ducks—including energy density, shell-to-flesh ratio, burial depth, shell impact resistance, and digestibility—may vary both by size and species (Zwarts and Wanink 1993, Richman and Lovvorn 2003). For example, large clams often have considerably lower shell-to-flesh ratios (Gillespie et al. 1999), which increases the energetic content of the clam (Zwarts and Wanink 1993), yet require more time for handling, increasing the energetic costs of foraging. Winter diets of both Surf and White-winged scoters in Baynes Sound are dominated by two clam species, Manila and Varnish clams (Lewis et al. 2007). Although not quantified in our study, the value to foraging scoters of similarly sized Manila and Varnish clams may differ, because Varnish Clams generally have thinner shells and less flesh

and reside deeper in the sediment (Gillespie et al. 1999, 2001). Size-class distributions in Baynes Sound, however, were relatively similar for Manila and Varnish clams, as well as among plots (Lewis et al. 2007), minimizing the effects of size class on variation in scoter foraging behavior.

Species, age, and season effects.—The relationship between foraging effort and variation in clam density differed by scoter species, with only White-winged Scoters demonstrating a detectable relationship. Foraging effort should reflect not only the quality of the foraging environment but also daily energetic requirements. Of four sea duck species, Goudie and Ankney (1986) found that the smaller species spent more time feeding and consumed prey of higher energy density to compensate for their greater energetic demands per unit body mass. These smaller sea ducks, however, consumed predominantly small prey, such as amphipods and isopods, whereas the larger sea duck species consumed prey of greater biomass, such as mussels and urchins. When consuming foods of similar size and energetic value, individuals of larger species must consume more biomass per day than smaller species (Goudie and Ankney 1986) and would be expected to spend more time feeding. White-winged Scoters (males 1,500 g; females 1,200 g) are larger than Surf Scoters (males 1,000 g; females 900 g), and the diets of both species in Baynes Sound are similar (Lewis et al. 2007). Although White-winged Scoters consume, on average, slightly larger clams, size-class preferences are not pronounced (Bourne 1984). On the basis of such similar diets, larger-bodied White-winged Scoters should consume more food and spend more time feeding. Consequently, the greater energetic and time demands on White-winged Scoters may make them more sensitive than Surf Scoters to variation in clam density, resulting in their slightly negative correlation between foraging effort and clam density.

In addition to species differences, age-related differences in foraging effort were also evident in White-winged Scoters. Adult White-winged Scoters spent more time underwater than HY individuals. This was unexpected, given that HY birds are often less-adept foragers, because of their inexperience, and typically exert greater foraging effort and lower foraging efficiency (Heise and Moore 2003). Adult White-winged Scoters, however, typically weigh more than juveniles and, thus, may have to spend more time foraging to sustain their greater body mass. Also, HY White-winged Scoters do not breed during the subsequent summer (Kehoe et al. 1989) and may have less need to acquire fat stores, via increased foraging efforts, for subsequent migration and reproduction. Age-related differences were not detected in Surf Scoters, though we sampled only two HY individuals.

With respect to date, the amount of time spent underwater by Surf Scoters decreased by 4% from mid-November to mid-winter, and then increased by 10% to mid-March. This pattern is the opposite that observed in Surf Scoters wintering at the Queen Charlotte Islands (53°N), as well as in other sea duck species wintering at northern latitudes, in which time spent feeding increased during mid-winter (Guillemette 1998, Goudie 1999, Fischer and Griffin 2000, Systad et al. 2000). Because many sea duck species are not believed to forage nocturnally (Nilsson 1970, McNeil et al. 1992), an increased foraging effort during mid-winter likely compensates for the decreased amount of feeding time. During the shortest days of winter at 70°N, Common Eiders and Long-tailed

Ducks (*Clangula hyemalis*) spent at least twice as much time underwater per hour as they did in spring (Systad et al. 2000). Similarly, Harlequin Ducks (*Histrionicus histrionicus*) wintering at 52°N spent a greater proportion of time underwater during mid-winter than during early or late winter (Fischer and Griffin 2000). Surf Scoters in Baynes Sound (49°N) rarely foraged at night (Lewis et al. 2005). Thus, the observed minimization of foraging effort during mid-winter suggests that Surf Scoters in Baynes Sound were not constrained by day length, sufficiently meeting their energetic requirements during the short days of mid-winter.

As compared with Surf Scoters, the amount of time spent underwater by White-winged Scoters was largely unrelated to date. Because of the negative correlation between foraging effort and clam density, White-winged Scoters may have been restricted in their ability to decrease time spent underwater during mid-winter, when day length is shortest. White-winged Scoters, however, did not increase their foraging effort during mid-winter, as has been reported in studies of other sea ducks (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000). White-winged Scoters in Baynes Sound, like Surf Scoters, were apparently not constrained by day length.

Our collective results indicate that Baynes Sound constituted high-quality foraging habitat for wintering scoters, given their lack of strong behavioral responses to clam density variation and relatively low overall foraging effort. The recent invasion of the Varnish Clam to Baynes Sound, within the last 15 years, has likely increased clam densities significantly above historical levels (Gillespie et al. 1999, 2001), enhancing overall habitat quality for wintering scoters. Also, recent activities of the shellfish aquaculture industry in Baynes Sound may have further increased clam densities, mainly via the spread and spawning of seeded Manila Clams. For these reasons, Baynes Sound likely provides important, high-quality habitat for wintering scoters, as further evidenced by the large numbers of scoters (~6,500 scoters) wintering in the area and the strong distributional relationship between scoters and clams (Žydelis et al. 2006, D. Esler unpubl. data).

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