



1992), while others extend foraging into nocturnal periods when food is scarce or day length is short (Lane and Hassall 1996, Systad and Bustnes 2001). Most sea duck species (tribe Mergini) are thought to be diurnal foragers (Nilsson 1970, Guillemette et al. 1992, McNeil et al. 1992), although few data exist to adequately address this assumption. This information gap limits thorough understanding of sea duck foraging ecology and energetics.

Many sea duck species winter at northern temperate to subarctic latitudes, where day length is short and ambient temperatures are low during mid-winter. This combination of winter conditions, which reduces diurnal foraging time and increases energy demands, may require that sea ducks forage at night to obtain necessary energy requirements. Previous studies have shown that some sea duck species compensate for short winter days by increasing the proportion of daylight hours spent feeding (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000) or by extending their feeding into low-light crepuscular periods (Nilsson 1970, Systad et al. 2000). However, recent data from high latitudes have demonstrated nocturnal feeding by some sea duck species during the shortest days of winter (Systad and Bustnes 2001). These nocturnal foraging sea ducks fed in shallow waters and employed non-dive feeding behaviors, such as surface-feeding and up-ending (Systad and Bustnes 2001). Owing to the high energetic cost of diving (de Leeuw 1996), the utilization of shallow water habitats and surface-feeding techniques may minimize energetic foraging costs that may be higher during nocturnal hours.

Surf Scoters (*Melanitta fusca*) and White-winged Scoters (*Melanitta perspicillata*) are believed to feed only diurnally (McNeil et al. 1992), although no studies have attempted to directly measure their nocturnal foraging during

nal bivalves (clams) in small sediment, intertidal areas (Canadian Wildlife Service [CWS], unpubl. data).

#### SCOTER CAPTURES

Surf and White-winged Scoters were captured during December 2002 and 2003 using modified floating mist nets (Kaiser et al. 1995). Mist nets were deployed predawn and positioned in foraging areas used by scoters. Captured scoters were removed from mist nets, placed into holding kennels, and transferred to shore for radio-transmitter implantation. Radio transmitters with external antennae were surgically implanted in the abdominal cavities of Surf Scoters (2002: 27 males, 15 females; 2003: 18 males, 9 females) and White-winged Scoters (2002: 21 males, 13 females; 2003: 28 males, 20 females). Abdominally implanted transmitters have been successfully used in other sea duck species without evidence of either short-term (Mulcahy and Esler 1999) or long-term (Esler et al. 2000) consequences. The transmitters (Holohil Systems, Ltd., Carp, Ontario) were cylindrical, weighed 17.5 g, transmitted at 45 pulses per minute, and contained mortality switches that doubled the pulse rate if the transmitter remained motionless for  $\geq 12$  hr. Surgeries to implant radio transmitters were performed by experienced veterinarians following procedures developed for other sea duck species (Mulcahy and Esler 1999). Scoters were held for at least one hour postsurgery and subsequently released at their capture sites.

#### RADIO TELEMETRY

We monitored the diving behavior and locations of radio-marked scoters during the winters of 2002–2003 (20 December–15 March) and 2003–2004 (1 November–1 March). Diving behavior data were gathered only during the winter of 2002–2003. Collection of location data in 2003 began in November, prior to that winter's transmitter deployment, due to the return of radio-marked scoters from the previous winter. We concluded monitoring each winter at the start of herring spawning, at which point scoters abandoned their typical winter habitats and food sources within Baynes Sound.

Dive behaviors of radio-marked scoters were monitored with hand-held 4-element Yagi antennas connected to Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receivers. The

radio signal disappeared when the bird dove and resumed when the bird resurfaced, allowing the observer to document both the occurrence and duration of foraging dives (Wanless and Harris 1991, Custer et al. 1996). To determine the appropriate observation duration, radio signals were monitored diurnally for  $\geq 1$  hr. Of all diurnal nondiving periods lasting  $\geq 5$  min ( $n = 1320$ ), only 4.5% were  $\geq 30$  min. Therefore, a 30-min observation time was used for monitoring, given the high likelihood of detecting dive foraging if it were to occur. The number of dives and length of each individual dive ( $\pm 1$  sec) were recorded during each 30-min observation block. Telemetry observations were conducted diurnally and nocturnally at multiple sites throughout Baynes Sound that offered both unobstructed water views and heightened elevation. Nautical twilight was used to define the boundary between night and day, as it assured almost complete darkness for nocturnally defined time periods. Start times of telemetry observation bouts were set so that a broad range of tide levels were frequently and evenly sampled within both diurnal and nocturnal periods. Furthermore, sampling bouts within nocturnal and diurnal observation periods were evenly spread across winter dates and the 24-hr cycle. Daytime visual observations of radio-marked scoters were used to confirm the loss of radio-signal during a dive.



TABLE 1. Minutes diving per 30-min observation block and distance to shore (m) of Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2002–2004. Data are summarized for day and night periods, and scoter species. Values are presented as means  $\pm$  SE and numbers in parentheses indicate sample sizes.

	Surf Scoter		White-winged Scoter	
	Minutes diving per 30 min	Distance to shore (m)	Minutes diving per 30 min	Distance to shore (m)
Day	7.2 $\pm$ 0.3 (271)	231.1 $\pm$ 8.4 (481)	6.9 $\pm$ 0.2 (316)	254.4 $\pm$ 9.6 (649)
Night	0.1 $\pm$ 0.1 (61)	703.8 $\pm$ 44.0 (46)	0.2 $\pm$ 0.1 (77)	911.6 $\pm$ 54.1 (58)

tive model in the set. Thus,  $\Delta\text{AIC} = 0$  for the model of best fit. All models with a  $\Delta\text{AIC} \leq 2$  were considered to have substantial support and received consideration in making data inferences (Burnham and Anderson 2002). AIC weights ( $w_i$ ), which indicate the relative likelihood of a model given the data and set of candidate models, also were calculated to provide a relative weight of evidence for each model (Burnham and Anderson 2002). To determine the relative importance of each explanatory variable within a candidate model set, AIC weights were summed for all candidate models containing the explanatory variable under consideration, providing a parameter likelihood value. Also, weighted parameter estimates and unconditional standard errors were calculated for the explanatory variables in each analysis, based on AIC weights for all candidate models, to account for model uncertainty (Burnham and Anderson 2002).

General linear mixed models were used to account for repeated measures on radio-marked individuals and to include subject as a random effect (Littell et al. 2000). Mixed models structure the correlation of residuals both within and among individuals by incorporating covariance parameters in the models. The covariance structures we considered for each response variable included the spatial power law, both with and without a random between-subject effect, to model decreasing correlation with increasing time between repeated observations and compound symmetry to model constant correlation among repeated observations. The best-fitting covariance structure for each response variable was chosen using AIC model selection criteria (Littell et al. 2000). For the response variables of distance to shore and water depth, compound symmetry was selected as the best fitting covariance structure. For total time underwater per

30 min, the spatial power law structure with a random between-subject effect was chosen as the best-fitting covariance structure. The selected covariance structure for each response variable was included in all fixed effects candidate model combinations.

## RESULTS

### DIVE FORAGING

Of 587 diurnal 30-min observation blocks for both Surf Scoters and White-winged Scoters combined, 98% of observation blocks contained radio-signal loss indicative of diving. In contrast, only 2% of 138 nocturnal observation blocks contained diving. Results were similar for both species, as Surf Scoters dove in 97% of diurnal observations ( $n = 271$ ) and 3% of nocturnal observations ( $n = 61$ ), and White-winged Scoters dove during 98% of diurnal observations ( $n = 316$ ) and 1% of nocturnal observations ( $n = 77$ ).

Both scoter species spent more time diving during the day than at night (Table 1). Results indicated that the model containing only night/day as an explanatory variable best explained variation in minutes diving per 30 min (Table 2). Two additional model combinations also received substantial support ( $\Delta\text{AIC} \leq 2$ ), each of which included night/day (Table 2). All models without night/day received no empirical support from the data ( $\Delta\text{AIC} > 265$ ,  $w_i = 0$ ). Further, only night/day had a large parameter likelihood value and 95% confidence intervals (weighted parameter estimate  $\pm 1.96 \times \text{SE}$ ) that did not overlap zero (Table 3). Hence, species and sex offered little value for explaining variation in the amount of time spent diving.

### WATER DEPTH

In general, both scoter species were located within intertidal areas during diurnal hours and

TABLE 2. General linear mixed models evaluating variation in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002–2004. Night/day is a categorical variable with two levels (night and day). For all models, the number of parameters ( $k$ ) includes  $+1k$  for an intercept and  $+1k$  for variance estimate. Covariance structures for repeated measures and random between-subject effect include  $+2k$  for all models of minutes diving per 30-min observation block and  $+1k$  for all models of water depth and distance to shore. Only models with  $w_i > 0.01$  and the null model are presented. Candidate models are listed in order of  $\Delta AIC$ .

Response variable	Model	$k$	Log-likelihood	$\Delta AIC$	AIC weight ( $w_i$ )
Minutes diving per 30 min	night/day	5	-1907.06	0.00	0.46
	night/day + species	6	-1906.88	1.26	0.25
	night/day + sex	6	-1907.11	1.74	0.19
	night/day + species + sex	7	-1906.74	3.03	0.10
	null	2	-2095.10	369.71	0.00
Water depth (m)	night/day	4	-4627.61	0.00	0.41
	night/day + species	5	-4627.17	1.14	0.23
	night/day + sex	5	-4627.19	1.19	0.23
	night/day + species + sex	6	-4626.74	2.31	0.13
	null	2	-4784.30	309.40	0.00
Distance to shore (m)	night/day + species	5	-8277.47	0.00	0.63
	night/day + species + sex	6	-8277.45	1.96	0.24
	night/day	4	-8280.34	6.39	0.10
	night/day + sex	5	-8280.31	16.97	0.03
	null	2	-8536.70	512.43	0.00

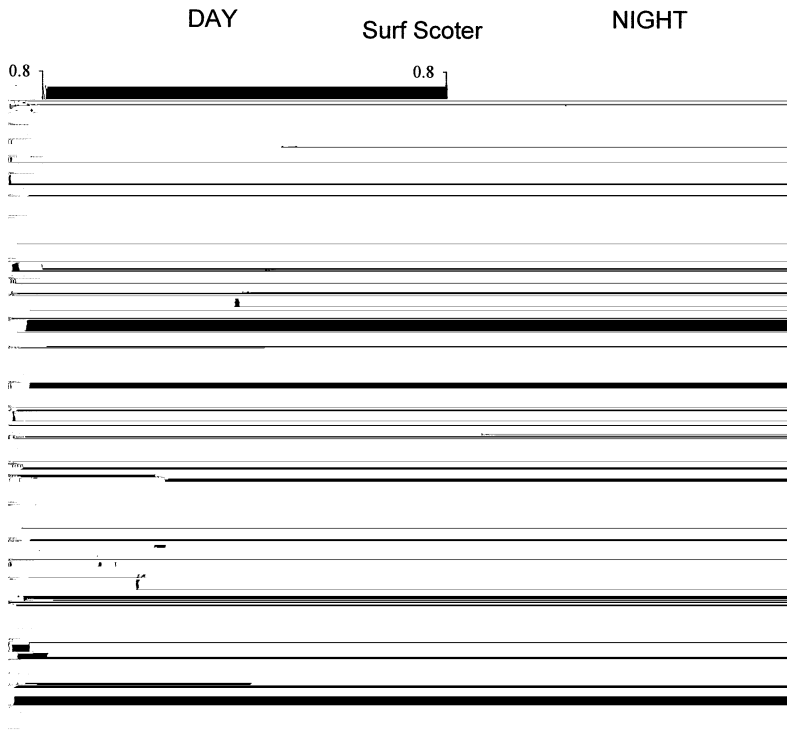
in subtidal areas during nocturnal hours (Fig. 1). The model that best explained variation in water depth at scoter locations contained only night/day as an explanatory variable (Table 2). The model containing night/day and species, as well as the global model, also received substantial support ( $\Delta AIC \leq 2$ ), although their AIC weights

were low ( $w_i = 0.23$ ) relative to the top model ( $w_i = 0.41$ ). Model combinations not including night/day as an explanatory variable

TABLE 3. Parameter likelihoods and weighted parameter estimates  $\pm$  unconditional SE from general linear mixed models evaluating variance in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002–2004. Explanatory variables are listed in order of parameter likelihood values. Parameter likelihoods are the summed AIC weights ( $w_i$ ) for all candidate models containing the explanatory variable under consideration.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate $\pm$ SE
Minutes diving per 30 min	Intercept		0.11 $\pm$ 0.40
	Night/day <sup>a</sup>	1.00	6.77 $\pm$ 0.37
	Species <sup>b</sup>	0.35	0.14 $\pm$ 0.18
	Sex <sup>c</sup>	0.29	-0.07 $\pm$ 0.15
Water depth (m)	Intercept		26.07 $\pm$ 1.25
	Night/day <sup>a</sup>	1.00	-21.39 $\pm$ 1.18
	Species <sup>b</sup>	0.36	0.34 $\pm$ 0.42
	Sex <sup>c</sup>	0.36	0.34 $\pm$ 0.43
Distance to shore (m)	Intercept		854.01 $\pm$ 27.15
	Night/day <sup>a</sup>	1.00	-584.07 $\pm$ 20.65
	Species <sup>b</sup>	0.87	-47.54 $\pm$ 20.65
	Sex <sup>c</sup>	0.27	1.49 $\pm$ 6.29

<sup>a</sup> Night/day is a categorical variable (day or night) with night as the reference value.  
<sup>b</sup> Species is a categorical variable (Surf Scoter or White-winged Scoter) with White-winged Scoter as the reference value.  
<sup>c</sup> Sex is a categorical variable (male or female) with male as the reference value.



explained by day or night period, with little effect associated with species or sex.

Both species of scoters were located farther offshore and in deeper waters during nocturnal hours, generally removed from the intertidal foraging areas used during the day. The concomitant relationship between distance from shore and water depth was expected, given that these variables are highly positively correlated. Mean distances to shore for Surf Scoters and White-winged Scoters were 231 m and 254 m during







- PERCIVAL, S. M., AND P. R. EVANS. 1997. Brent Geese *Branta bernicla* and *Zostera*; factors affecting the exploitation of a seasonally declining food resource. *Ibis* 139:121–128.
- PYKE, G. H. 1984. Optimal foraging: a critical review. *Annual Review of Ecology and Systematics* 15: 523–575.
- RAVELING, D. G., W. E. CREWS, AND W. D. KLIMSTRA. 1972. Activity patterns of Canada Geese during winter. *Wilson Bulletin* 84:278–295.
- RIZZOLO, D. J., D. ESLER, D. D. ROBY, AND R. L. JARVIS. 2005. Do Harlequin Ducks forage at night near the northern extent of their wintering range? *Condor* 107:173–177.
- SAS INSTITUTE INC. 1999. SAS/STAT Software, Version 8.0. SAS Institute, Cary, NC.
- SAVARD, J.-P., L. D. BORDAGE, AND A. REED. 1998. Surf Scoter (*Melanitta perspicillata*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 363. The Birds of North America, Inc., Philadelphia, PA.
- SCHMUTZ, J. A., AND G. C. WHITE. 1990. Error in telemetry studies: effects of animal movement on triangulation. *Journal of Wildlife Management* 54: 506–510.
- SYSTAD, G. H., AND J. O. BUSTNES. 2001. Coping with darkness and low temperatures: foraging strategies in Steller's Eiders, *Polysticta stelleri*, wintering at high latitudes. *Canadian Journal of Zoology* 79: 402–406.
- SYSTAD, G. H., J. O. BUSTNES, AND K. E. ERIKSTAD. 2000. Behavioral responses to decreasing day length in wintering sea ducks. *Auk* 117:33–40.
- TUCKWELL, J., AND E. NOL. 1997. Foraging behaviour of American Oystercatchers in response to declining prey densities. *Canadian Journal of Zoology* 75:170–181.
- VERMEER, K., AND N. BOURNE. 1984. The White-winged Scoter diet in British Columbia waters: resource partitioning with other scoters, p. 30–38. In D. N. Nettleship, G. A. Sanger, and P. F. Spring [EDS.], *Marine birds: their feeding ecology and commercial fisheries relationships*. Canadian Wildlife Service Special Publication, Ottawa, Ontario, Canada.
- WANLESS, S., AND M. P. HARRIS. 1991. Diving patterns of full-grown and juvenile Rock Shags. *Condor* 93:44–48.
- WHITE, J. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, CA.