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CONTRASTS IN ENERGY STATUS AND MARINE FORAGING STRATEGIES OF WHITE-WINGED SCOTERS (*MELANITTA FUSCA*) AND SURF SCOTERS (*M. PERSPICILLATA*)

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Abstract.—White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*) are often assumed to rely on similar marine resources. To evaluate the accuracy of this assumption, we contrast seasonal distributions, foraging effort, and indicators of energy status (body mass and composition, plasma metabolites) in three major foraging sites in Puget Sound, Washington, for these rapidly declining sea duck congeners. For Surf Scoters, distributions and energy status indicated that a mussel-dominated site was relatively important in early winter, but that importance shifted during late winter and spring to seagrass sites that provided either herring spawn or epifaunal invertebrates. As winter progressed, movements among foraging sites and increased foraging effort by Surf Scoters were accompanied by greater variability in their energy status compared with White-winged Scoters; body mass declined over winter by >9% in about one-third of past studies for Surf Scoters, well above the range of losses observed in White-winged Scoters. For White-winged Scoters, lower variability in energy status, foraging effort, and distributions throughout winter suggests that they are better able to regulate energy balance regardless of changing foraging conditions. Greater resistance to seasonal environmental changes in White-winged Scoters may be related to their >50% larger body size, which confers lower mass-specific energy costs and access to a wider size range of bivalve prey. Perhaps because of their greater sensitivity to winter foraging conditions, Surf Scoters appear to rely on a broader range of foraging sites than White-winged Scoters. *Received 11 April 2010, accepted 9 January 2011.*

Key words: marine foraging ecology, *Melanitta fusca*, *M. perspicillata*, physiological condition, plasma metabolites, Surf Scoter, White-winged Scoter.

Contrastes del Estado Energético y de las Estrategias de Forrajeo Marino en *Melanitta fusca* y *M. perspicillata*

Resumen.—Con frecuencia se asume que las aves *Melanitta fusca* y *M. perspicillata* dependen de recursos similares. Para evaluar la certeza de esta suposición, contrastamos las distribuciones estacionales, el esfuerzo de forrajeo e indicadores del estado energético (masa y composición corporal, metabolitos plasmáticos) en tres de los principales sitios de alimentación en Puget Sound, Washington, para estas dos especies cogenéricas de patos cuyas poblaciones están disminuyendo rápidamente. Para *M. perspicillata*, la distribución y el estado energético indicaron que un sitio dominado por moluscos era relativamente importante al cominezo del invierno, pero que la importancia cambió hacia el final del invierno y la primavera hacia áreas con plantas acuáticas marinas que proveían de alevines de peces o epifauna de invertebrados. A medida que avanzaba el invierno, los movimientos entre las áreas de forrajeo y el aumento del esfuerzo de forrajeo por *M. perspicillata* fueron acompañados por una mayor variabilidad en su estado energético en comparación con *M. fusca*. La masa corporal bajó durante el invierno en más del 9% en cerca de un tercio de los estudios anteriores sobre *M. perspicillata*, mucho más que el rango de pérdidas observado para *M. fusca*. La menor variabilidad en el estado energético, el esfuerzo de forrajeo y la distribución durante el invierno para *M. fusca* sugiere que esta especie es más capaz de regular su balance energético independientemente de los cambios en las condiciones de forrajeo. La mayor resistencia ante variaciones ambientales estacionales de *M. fusca* puede estar relacionada con su tamaño corporal >50% mayor, lo que le confiere menores costos específicos de la masa y acceso a un mayor rango de presas bivalvas. Quizás por su mayor sensibilidad a las condiciones de forrajeo de invierno, *M. perspicillata* parece depender de una mayor variedad de sitios de forrajeo que *M. fusca*.

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Concurrent with declines in many species of nearshore marine birds, North American populations of White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*) have decreased by ~60% over the past 30 to 50 years (Hodges et al. 1996, Nysewander et al. 2005). The reasons for these declines are mostly unknown, but identifying and conserving adequate marine habitat used during the nonbreeding period is a high priority for both scoter species (Sea Duck Joint Venture 2008). These species have often been combined and treated identically in population and conservation assessments because they are difficult to distinguish in aerial surveys and their specific habitat needs are poorly known. Likewise, little information on differences in the marine foraging niches of these two species exists, and that which is available suggests that only standing stocks of bivalve prey need be considered when prioritizing critical foraging sites (Brown and Fredrickson 1997, Savard et al. 1998). However, recent findings suggest that the importance of non-bivalve foods has been underestimated (Anderson et al. 2008), and assessment of the complex of foraging habitats needed to meet the seasonal energy demands of each species is lacking.

At least two factors suggest that the assumption that foraging niches for White-winged and Surf Scoters are similar may be invalid. First, a reevaluation of diet indicated that, compared with White-winged Scoters, Surf Scoters eat smaller bivalves, have a lower and more variable fraction of bivalve prey in their diet, and consume a decreasing proportion of bivalves as winter progresses (Anderson et al. 2008). Second, because White-winged Scoters are >50% larger than Surf Scoters, the foraging strategies of these closely related species may also differ on the basis of size-dependent energetics. Among benthic-feeding waterbirds, larger species with lower mass-specific metabolic rates can have better access to larger, more predictable prey, as well as greater resistance to short-term variations in energy balance (Goudie and Ankney 1986, Richman and Lovvorn 2009). By contrast, smaller birds with higher mass-specific metabolism but lower total energy needs often show greater use of prey characterized by lower size, abundance, or predictability, and exhibit greater variations in energy balance (Persson 1985). Thus, one might predict that the smaller Surf Scoter (1,085 g) would display more labile energetics and foraging strategies, as well as greater reliance on a more diverse set of habitats, than the White-winged Scoter (1,714 g; mean December body masses for adult males).

Energetics and physiological states may vary with multiple confounding influences, so that habitat assessments based on these attributes should ideally rely on a suite of complementary indicators. Traditional measures of nutrient status such as body mass or composition enable comparisons of habitats in terms of their contributions to body reserves that are available to meet seasonal needs. However, for large birds these measures often change slowly over periods of weeks (Lovvorn 1994b) and, thus, may reflect reserve-depleting movements among sites, or environmental conditions encountered before arrival at the focal site. Levels of plasma metabolites reflect metabolic response to foraging conditions during the previous few hours to days (Jenni-Eiermann and Jenni 1994, Anteau and Afton 2008), enabling contrasts of sites in terms of the rates at which birds accumulate or deplete nutrients (Acevedo Seaman et al. 2006). Both body nutrient reserves and plasma metabolites can be endogenously regulated (Barboza and Jorde 2002, Williams et al. 2007), so variation in these measures may be at least partially independent of habitat conditions. Knowing seasonal patterns in foraging effort or bird distributions can help clarify whether changes in these measures of nutrient status are related to effects of local habitat or endogenous regulation. For instance, when local foods are inadequate, declines in lipid stores and in rates of lipid acquisition will likely be accompanied by increased feeding effort and departures of individuals from the focal site. Conversely, reduced feeding effort and stable distributions would suggest that such declines in nutrient status are endogenously regulated, as when benefits of body reserves are outweighed by costs of maintaining them (Macleod et al. 2005).

To explore ecological differences between these two scoter species, we contrasted their functional habitat needs by coupling analyses of their distributions, foraging rates, and energy status (body mass and composition, plasma metabolites) from winter to early spring in northern Puget Sound, Washington. We assessed the relative variability of these factors between species to clarify their sensitivity to winter foraging conditions and to identify the complement of foraging habitats needed to meet their seasonal requirements.

Methods

Study area and design.—We selected three bays in northern Puget Sound, according to two criteria. First, we selected bays that supported the largest numbers of the respective species; White-winged Scoters are far less abundant than Surf Scoters in Puget Sound, and sites used by White-winged Scoters are fewer and support smaller numbers of birds (Nysewander et al. 2005). Second, we selected bays that are characterized by relatively different benthic habitats, which suggested that they provide different feeding conditions for scoters. The three bays that we selected have benthic habitats that are generally representative of those available in northern Puget Sound. Penn Cove (48.2°N, 122.7°W) is largely unvegetated, and Bay Mussels (*Mytilus trossulus*) are common in the intertidal zone (Anderson 2009). Padilla Bay (48.5°N, 122.5°W) is mainly intertidal and contains one of the largest contiguous seagrass beds on the Pacific Coast of North America (Bulthuis 1995). Birch Bay (48.9°N, 122.8°W) has an extensive intertidal zone with abundant infaunal bivalves and has seagrass beds that become increasingly prevalent at lower intertidal to subtidal elevations. Compared with Padilla Bay, however, standing stocks of seagrass and associated epifaunal invertebrates (mainly shrimp, isopods, and snails) are lower in most areas of Birch Bay (Anderson 2009). We observed scoters diving throughout each bay, and maximum depths at mean low water were ~25 m in Penn Cove, ~2 m in Padilla Bay, and ~12 m in Birch Bay.

We related seasonal changes in scoter numbers in each bay to changes in their foraging effort and energy status; these measures were used as indicators of the relative ability of White-winged and Surf scoters to meet their energy demands in each bay. We measured foraging effort and energy status of scoters in each bay during two winter periods (data on foraging effort were not available for scoters in Padilla Bay, and energy status of White-winged Scoters was available only for Birch Bay—see below; Table 1). Measures of foraging effort considered for scoters included (1) water depth at which diving occurred, (2) the percentage of time spent underwater (i.e., diving), and (3) dive frequency.

Table 1. Sample timing and location for White-winged and Surf scoters in northern Puget Sound, Washington. Where conducted, focal animal surveys and collections of scoters occurred during an early (November–December) and late (January–March) period in each winter.

	Shore-based counts used for distributions			Focal animal surveys used for foraging rates		Collections[a] used for body mass and composition, plasma metabolites
	2003–2004	2004–2005	2005–2006	2003–2004	2004–2005	2005–2006
Penn Cove	Biweekly Nov–Sep	Biweekly Nov–Sep	Irregularly Dec–Sep	9–17 Nov 1–17 Feb	7–26 Nov 25 Jan–10 Feb	11–12 Dec 17 Mar
Padilla Bay		Biweekly Nov–Sep	Irregularly Dec–Sep			14 Dec 12–27 Mar
Birch Bay		Biweekly Nov–Sep	Irregularly Dec–Sep	6–21 Nov 5–20 Feb	5–30 Nov 22 Jan–8 Feb	12–13 Dec 18–19 Mar

[a] Surf Scoters were collected in all sites, but White-winged Scoters were collected only in Birch Bay.

We used two sets of measures that represent different time scales of foraging profitability to evaluate seasonal changes in energy status of scoters at each site. First, we considered scoter fresh body mass and body composition (total lipid, total protein), which typically reflect the profitability of foraging conditions over a period of weeks (Lovvorn 1994b). Second, we also assessed concentrations of metabolites in plasma, which are correlated with changes in nutrient status over the previous hours to a few days (Jenni-Eiermann and Jenni 1994). Plasma triglycerides increase during fat deposition, and β-hydroxybutyrate increases during catabolism of lipid (Anteau and Afton 2008). Analyses of body composition and plasma metabolites of White-winged Scoters from a single bay provided insufficient replication for evaluating the importance of food availability to their energy status. Thus, we supplemented our results with those of past studies that assessed changes in mean fresh body mass of White-winged and Surf scoters between two winter periods. In these past studies, scoters were captured or collected to assess contaminant exposure or changes in body condition, or to affix transmitters used to identify movements (see below for sources).

Scoter counts.—We conducted counts of scoters in each bay from shore with a 20–60× spotting scope (Table 1). We report counts for each species as total number and as a percentage of peak number from October through May to better clarify overwinter changes in distributions. Scoters aggregate to consume spawn of Pacific Herring (*Clupea pallasii*), so we present dates of spawn availability for comparison with changes in scoter numbers in Birch Bay (significant spawning activity did not occur in Penn Cove or Padilla Bay). We estimated the timing of spawn availability as in Anderson et al. (2009).

Scoter foraging behavior.—We quantified foraging behavior of scoters in Penn Cove and Birch Bay using focal-animal sampling (Lehner 1996). In Padilla Bay, foraging observations were not possible because scoters were located too far from shore to ensure accurate sampling by observations made with a 20–60× spotting scope. We conducted observations during two winter periods (Table 1) and partitioned observation time about equally among sites and seasons during 2003–2004 (140 h total observation time) and 2004–2005 (180 h total observation time). Observations were distributed evenly within the period starting 30 min before sunrise and ending 30 min after sunset. We randomly sampled scoters by rotating the spotting scope across the range of visible birds, stopping the scope at intervals of ~15° and selecting the individual closest to the center of the horizontal field of view (Lovvorn 1989); this technique avoids bias in selecting scoters in relation to their distance from the observer, and, thus, our samples should approximately represent the distribution of scoters in relation to water depth. Because sex and age classes cannot be distinguished reliably during winter on the basis of plumage (Iverson et al. 2003), we grouped focal individuals into two categories: (1) after-hatch-year males, and (2) females + hatch-year males.

We observed focal individuals for 5 min, during which we dictated into a tape recorder whether the bird was underwater at 20-s intervals, its total number of dives, and its distance to waterline at the shore. Within sites, distance to waterline was used as a metric of water depth at which diving occurred. Compared with water depth, estimating distance to waterline for individual scoters was less prone to error, and the two measures were strongly related in each bay according to nautical charts and our boat-based observations using a depth sounder. We estimated distance to waterline using frequent comparisons with distances measured using a laser rangefinder; distance classes were <50, 50–100, 100–200, and >200 m. For each focal individual, we recorded several additional factors that could affect foraging behavior: duration of civil twilight (day length may limit feeding time available to scoters, which feed mainly during the day; Lewis et al. 2005), diurnal period (before 1000, 1000–1400, or after 1400 hours), tide level (to the nearest 0.3 m), sea state (Beaufort 0–1, 2–3, >3), and hourly mean temperature for the preceding calendar day (which can alter body condition and foraging effort; Goudie and Ankney 1986).

Scoter collections, body composition, and plasma metabolites.—We collected scoters with shotguns from small boats during two winter periods in 2005–2006 (Table 1). During December in Padilla Bay, the number of Surf Scoters collected was lower than for other seasons and sites because scoters are difficult to approach by boat when they occur at low densities. Similarly, in Penn Cove and Padilla Bay, White-winged Scoters were not collected because their relatively low densities made collection of adequate samples infeasible. To avoid partitioning our limited sample size among multiple sex and age classes, we collected only after-hatch-year males; for White-winged Scoters in Birch Bay and Surf Scoters in all three bays, this was the main cohort present during most of December through March, and we did not observe sex- or age-related segregation in foraging areas within each site (E. M. Anderson unpubl. data).

We sampled blood within 30 min of collection, and completed other parts of dissections within 4 h of collection. A sterile 12-gauge needle was used to transfer up to 5 mL of heart blood to a heparinized vial for analyses of plasma metabolites. We verified age class and sex using a combination of bursal depth and plumage (Iverson et al. 2003). Fresh body mass (±5 g) and length (±1 mm) of the culmen, wing chord, and tarsus of each scoter were measured. We removed and measured fresh mass (±1 g) of the esophagus, gizzard, liver, and both kidneys for use in related studies. We separated blood plasma and cells by centrifugation within 12 h of collections and stored all tissues at –20°C until analyzed.

The length of time between when a bird was flushed and when it died was <15 min. Plasma triglycerides and β-hydroxybutyrate did not vary with the length of this interval in White-winged Scoters or in Long-tailed Ducks (*Clangula hyemalis*) collected in another study (all $r^2 < 0.09$, $P > 0.10$; D. Esler, Simon Fraser University, unpubl. data). As in clinical pathology studies of human disease, we assumed that levels of these metabolites would change little within 12 h of death (e.g., Takeichi et al. 1999).

Body composition (total protein, lipid, water, and ash) of ingesta-free dry carcass mass including plumage was analyzed by the methods of Afton and Ankney (1991) by the Long Point Waterfowl and Wetlands Research Fund Avian Energetics Lab, Port Rowan, Ontario. As in Lovvorn et al. (2003), we (1) adjusted composition estimates for tissues that were removed during dissections and (2) assessed whether total protein or lipid were influenced by structural body size as estimated by the first principal component of culmen, wing chord, and tarsus lengths. Body size was not correlated with total protein or lipid for either species (all $r^2 < 0.20$, $P > 0.50$), so we did not correct these nutrients for body size. We analyzed plasma metabolites as in Anderson and Lovvorn (2008). For some scoters, the amount of plasma available was not adequate to analyze one or both metabolites.

Statistical analyses.—We conducted statistical analyses using JMP, version 5.0.1 (SAS Institute, Cary, North Carolina). For each species in each site, we evaluated the effect of season on (1) the distribution of scoters in terms of distance to waterline using ordinal logistic regression and (2) foraging behavior (percent time underwater, dives h^{-1}) using analysis of covariance (ANCOVA). In each of these analyses, additional factors included year and cohort (after-hatch-year males, females + hatch-year males), and covariates included diurnal period, tide level, sea state, and (for analyses of foraging behavior only) distance to waterline and mean temperature during the previous day. Within each distance to waterline category, water depth was much greater in Penn Cove than in Birch Bay. Thus, our evaluations did not include between-site contrasts of scoter distributions in relation to distance from waterline or between-site contrasts of their foraging rates, which were substantially affected by water depth (see below).

We discontinued some foraging observations before 5 min had elapsed because the focal scoter could not be reliably located after a dive (i.e., "lost in dive"). For analyses of foraging rates, we compared methods that excluded scoters lost in dive versus those that used either low or high estimates of foraging rates that we interpolated for each scoter lost in dive (Anderson 2009). Means of percent time underwater and dives per hour and seasonal changes in these foraging parameters did not differ among these methods. Thus, we excluded scoters lost in dive from all estimates and from statistical analyses of these foraging parameters.

For White-winged and Surf scoters separately, we used ANCOVA to contrast individual measures of energy status (total fresh mass, total protein, total lipid, triglycerides, β-hydroxybutyrate) between collection periods. For each model, we included collection site and season * site as additional factors and conducted post hoc tests on least-squares means using Tukey's HSD method of adjusting for multiple comparisons. As in Williams et al. (2007), we included scoter body mass and collection time as covariates in models for each plasma metabolite, and we backward-eliminated these terms when they did not contribute significantly to the model. Sex, age class (after-hatch-year), and handling time were the same for all birds in these analyses. For data from this and past studies, we used repeated-measures analysis of variance (ANOVA) to contrast White-winged and Surf scoters in terms of changes in mean fresh body mass over an interval between two winter periods (October–January, January–March). Covariates in this model included the interval start date and interval length. We transformed all percentage and metabolite data using ln(variable + 1), which reduced but did not eliminate all deviations from the assumptions of normality (Shapiro-Wilks test) and variance equality (Levene's test). However, general linear models are typically robust to such deviations (Sheskin 2007). We report all means ± SE for back-transformed data, and set all significance levels at $\alpha = 0.05$.

RESULTS

Scoter counts.—Numbers of both scoter species in Penn Cove peaked between November and January (except during 2005–2006; see below), and then declined through spring (Fig. 1): maximum numbers of Surf Scoters in Penn Cove were 5,000–8,000, but White-winged Scoters rarely exceeded 500. In Padilla Bay, numbers of Surf Scoters peaked at or above 8,000 during spring staging in late April to early May, and again during wing molt in late August to early September. In Birch Bay, half or more of the approximately 1,000–2,000 scoters observed from early winter through March were White-winged Scoters. However, during late March to May in Birch Bay, White-winged Scoters declined while Surf Scoters increased to about 2,500–3,500. This seasonal increase in Surf Scoter numbers in Birch Bay coincided with availability of herring spawn in each year, and most Surf Scoters during this period were observed feeding in concentrated flocks over areas of spawn deposition. We did not conduct formal counts in Padilla and Birch bays during 2003–2004 and conducted relatively few counts in all sites during 2005–2006. However, our regular informal observations indicated that seasonal patterns of change in scoter numbers within each site were similar during all three years, except in Penn Cove, where numbers of both species were lower from about September through March during 2005–2006 than in the two preceding years.

Scoter foraging behavior.—Year, cohort, and all covariates (except for distance to waterline in analyses of percent time underwater and dives h^{-1}) varied in their significance among analyses, but in no case did they appreciably alter the effect of season on each of the three measures of foraging effort. Thus, results are reported for models that include only terms for season and (for analyses of percent time underwater and dives h^{-1}) distance to waterline and season * distance to waterline. Distance to waterline increased from November to January–February for each species at all sites, except for White-winged Scoters in Penn Cove, for which an increased distance over winter was not significant (Fig. 2A).

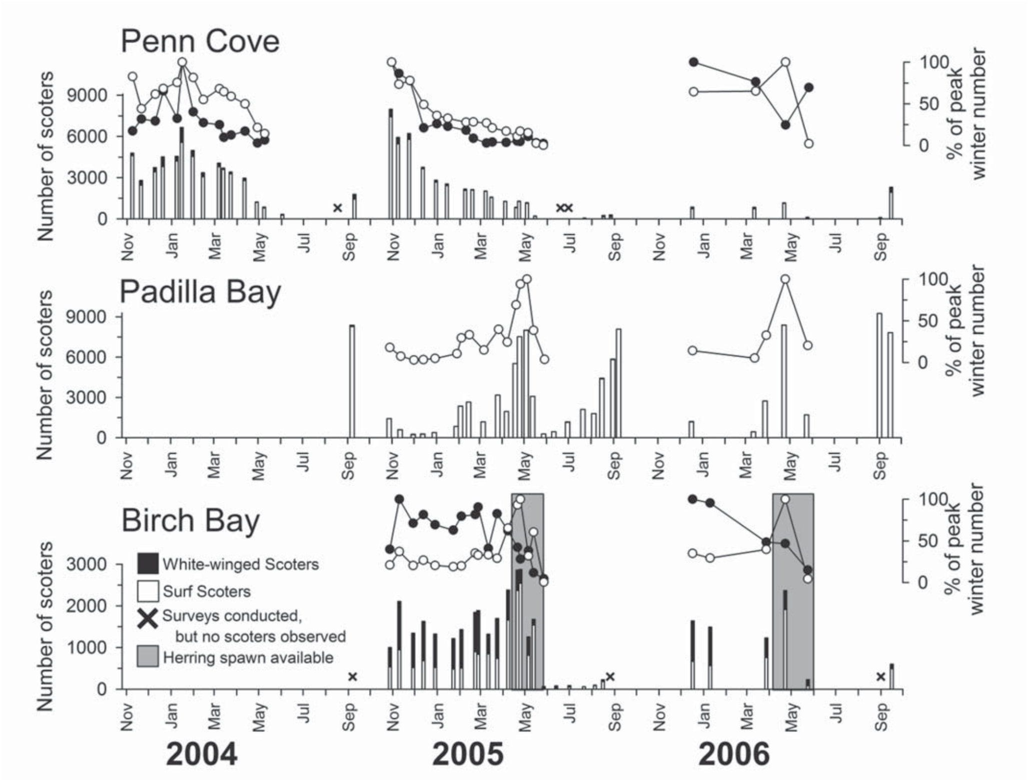

FIG. 1. Counts of White-winged and Surf scoters for three sites in northern Puget Sound, Washington, during 2003–2006. Counts are reported as total numbers (bars) and as a percentage of peak abundance observed during October through May (circles).

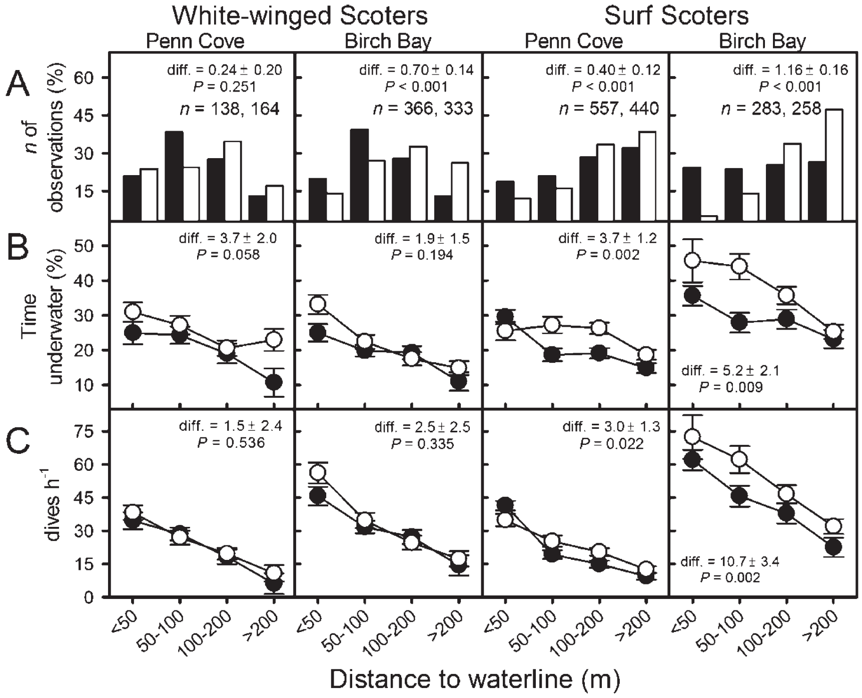

FIG. 2. Foraging observations of White-winged and Surf scoters for two sites in northern Puget Sound, Washington, during November (black bars and circles) and January–February (white bars and circles) of 2003–2004 and 2004–2005 combined. (A) Seasonal percentage of observations for each species by distance-to-waterline classes (a metric of diving depth). Mean seasonal values (± SE) by distance-to-waterline classes for (B) percent time underwater and (C) dives h^{-1}. Test results are for the effect of season on each variable, controlling for distance to waterline in B and C. In A, sample sizes (*n*) are provided for November and January–February, respectively; in B and C, sample sizes were slightly smaller (see text).

Table 2. Seasonal body mass and composition (including plumage), and concentrations of plasma metabolites (mean ± SE) for after-hatch-year male White-winged and Surf scoters collected in northern Puget Sound, Washington, during 2005–2006. For Surf Scoters, season*site effects were significant for fresh body mass and concentrations of the two plasma metabolites (Table 3); for these measures, means associated with different superscript letters differed significantly (Tukey's HSD test, $P < 0.05$).

				Body composition						Plasma metabolites (mmol L^{-1})			
	Season	*n*	Fresh body mass (g)	Protein (g)	Percent protein in fresh mass	Lipid (g)	Percent lipid in fresh mass	Water (g)	Ash (g)	*n*	Triglyceride	*n*	β-hydroxybutyrate
White-winged Scoters													
Birch Bay	December	9	1,890 ± 34	420 ± 9	22 ± 0.3	190 ± 21	10.0 ± 1.0	1,200 ± 32	80 ± 4	6	1.11 ± 0.09	4	0.47 ± 0.09
	March	8	1,796 ± 36	399 ± 7	22 ± 0.3	137 ± 12	7.6 ± 0.6	1,179 ± 25	81 ± 3	6	1.10 ± 0.07	4	0.42 ± 0.09
Surf Scoters													
Penn Cove	December	9	$1,177 \pm 18^{a}$	259 ± 10	22 ± 0.8	112 ± 16	9.4 ± 1.2	748 ± 22	57 ± 5	8	1.80 ± 0.19^{a}	5	0.31 ± 0.07^{a}
	March	10	$1,021 \pm 20^{b}$	234 ± 4	23 ± 0.2	63 ± 9	6.1 ± 0.8	673 ± 13	50 ± 1	8	0.89 ± 0.06^{b}	5	0.63 ± 0.09^{b}
Padilla Bay	December	3	$1,087 \pm 39^{a,b}$	234 ± 3	22 ± 0.5	111 ± 29	9.4 ± 2.4	691 ± 12	51 ± 1	3	$1.40 \pm 0.30^{a,b}$	3	$0.52 \pm 0.03^{a,b}$
	March	10	$1,025 \pm 25^{b}$	234 ± 6	23 ± 0.2	58 ± 8	5.6 ± 0.7	680 ± 19	53 ± 1	8	$1.14 \pm 0.09^{a,b}$	4	$0.43 \pm 0.04^{a,b}$
Birch Bay	December	9	$1,112 \pm 24^{a,b}$	255 ± 4	23 ± 0.2	102 ± 12	9.2 ± 1.0	700 ± 18	54 ± 2	7	$1.23 \pm 0.18^{a,b}$	4	$0.58 \pm 0.06^{a,b}$
	March	10	$1,078 \pm 21^{b}$	246 ± 4	23 ± 0.3	73 ± 7	6.7 ± 0.6	706 ± 16	53 ± 2	7	1.07 ± 0.13^{b}	5	$0.51 \pm 0.08^{a,b}$

For White-winged Scoters, percent time underwater and number of dives per hour did not change between November and January–February at either site (Fig. 2B, C; for all models, $P < 0.012$ for distance to waterline and $P > 0.34$ for season * distance to waterline). For Surf Scoters between these same periods, percent time underwater and dives per hour increased in both sites (Fig. 2B, C; $P < 0.001$ for distance to waterline in all models). For Surf Scoters in Penn Cove, the overwinter increase in dives per hour occurred mainly at greater water depths ($P = 0.024$ for season * distance to waterline, and $P < 0.05$ in Tukey's HSD tests for seasonal contrasts in dives per hour only for Surf Scoters >50 m from waterline; $P > 0.09$ for season * distance to waterline in all other models of Surf Scoter foraging rates). For most Surf Scoters in Penn Cove and Birch Bay (i.e., those >50 m from the waterline), the proportional increase between periods for percent time underwater and dives per hour ranged from 10–58% and 23–42%, respectively (ranges encompass combinations of site * distance to waterline).

Scoter energy status.—White-winged Scoters collected in Birch Bay between December 2005 and March 2006 exhibited a 28% decline in total body lipid, but no change in levels of the two plasma metabolites (Tables 2 and 3). The relatively small sample size for White-winged Scoters may have limited our power to detect changes in their fresh body mass and total protein, which showed marginally nonsignificant declines. The combined sample of Surf Scoters from all three sites showed significant declines between December and March in fresh body mass (−8%), total protein (−6%), total lipid (−40%), and concentrations of plasma triglycerides (−32%). However, seasonal changes in body mass and plasma metabolites for Surf Scoters were not uniform among sites: season * site interactions and post hoc analyses indicate that in Penn Cove, but not in Padilla or Birch bays, body mass and plasma triglycerides declined, whereas β-hydroxybutyrate increased (Tables 2 and 3). The percentage of fresh body mass that consisted of protein was similar for both scoter species across collection sites and seasons (Table 2). The percentage of fresh body mass that consisted of lipid declined from December to March for both species; declines for Surf Scoters varied among sites but were generally greater than declines for White-winged Scoters in Birch Bay.

Excluding one past study in which Surf Scoter diets were artificially supplemented with grain, there was no difference between scoter species in terms of changes in mean fresh body mass between two winter periods ($P = 0.769$ for period * species in repeated-measures ANOVA; $P > 0.797$ for interval start date and for interval length; Fig. 3). However, body mass declined by >9% in about one-third of past studies for Surf Scoters, well above the range of losses observed for White-winged Scoters. Although the major body-mass increase of Surf Scoters feeding on spilled grain is unnatural, it suggests that this species can gain appreciable mass in late winter if food is not limiting.

DISCUSSION

White-winged and Surf scoters have often been combined in population and conservation assessments, yet our study indicates that these species differ in the variability of their seasonal energetics and breadth of habitat needs. For Surf Scoters, seasonal changes in abundance, body composition, and plasma metabolites indicated

TABLE 3. ANCOVA results for the effect of collection season (December or March) on body mass and composition, and on concentrations of plasma metabolites, for after-hatch-year male White-winged and Surf scoters collected in northern Puget Sound, Washington, during 2005–2006. For Surf Scoters, each model includes collection site (Penn Cove, Padilla Bay, Birch Bay) and season * site as additional independent variables (White-winged Scoters were collected only in Birch Bay). For Surf Scoters, test results are for individual effects in full models.

	White-winged Scoters		Surf Scoters			
	Season[a]		Season		Site	Season * site[b]
	diff. ± SE	*P*	diff. ± SE	*P*	*P*	*P*
Body mass and composition (g)						
Fresh body mass	−94 ± 50	0.079	−95 ± 20	<0.001	0.258	0.023
Total protein	−21 ± 11	0.082	−16 ± 5	0.047	0.083	0.184
Total lipid	−53 ± 25	0.049	−43 ± 9	<0.001	0.967	0.568
Plasma metabolites (mmol L^{-1})[c]						
Triglyceride	−0.002 ± 0.06	0.968	−0.18 ± 0.06	0.001	0.440	0.024
β-hydroxybutyrate	−0.04 ± 0.09	0.691	0.05 ± 0.05	0.418	0.493	0.012

[a] Season is a categorical variable (December or March), with December as the reference value.

[b] For measures with significant season*site effects, see Table 2 for results of post hoc analyses.

[c] For models of plasma metabolites, effects of body mass and collection time of day were not significant.

that a mussel-dominated site (Penn Cove) was relatively important in early winter, but that importance shifted during late winter and spring to seagrass sites that provided either herring spawn (Birch Bay) or epifaunal invertebrates (Padilla Bay). Our results and those of past studies indicate that shifts in foraging sites during this period are common in Surf Scoters and may be driven by difficulty in meeting their seasonal energy demands (see below). Conversely, in White-winged Scoters, lower variability in energy status, foraging effort, and distributions suggest more constant energy balance regardless of changing prey abundance.

Scoter counts and foraging behavior.—Foraging effort increases over winter in Surf Scoters more than in White-winged Scoters (Goudie 1999, Lewis et al. 2008, present study). In Penn Cove and Birch Bay, this pattern likely resulted from seasonal changes in the availability of bivalve foods. In terms of ash-free dry mass, foods available to scoters in intertidal areas of both sites consisted mainly of bivalves (Anderson 2009). Scoters often deplete bivalves (Kirk et al. 2007, Lewis et al. 2008), and depletion probably occurs at greater water depths as winter progresses because the profitability of foods for diving ducks generally declines with increasing water depth (Lovvorn 1994a). This pattern of depletion would explain the overwinter increase in typical dive depths in Penn Cove and Birch Bay for both scoter species (Fig. 2A). However, compared with White-winged Scoters, Surf Scoters fed at consistently greater depths and also increased their foraging rates over winter (Figs. 2B, C), probably because they are restricted to smaller bivalves, compared with the broader size range consumed by White-winged Scoters (Anderson et al. 2008).

Compared with Surf Scoters, the more stable distributions and less variable foraging rates of White-winged Scoters suggest that they are better able to regulate their energy status independently of environmental conditions. Numbers of both species in Penn Cove decreased over winter in 2003–2004 and 2004–2005, yet lower variability in foraging rates for White-winged Scoters suggests that declines in foraging conditions there were less severe than for Surf Scoters. Both counts and telemetry studies throughout Puget Sound indicate that Surf Scoters move more extensively to meet their foraging needs; although White-winged Scoter numbers vary over winter in some sites, seasonal movements of Surf Scoters are typically of greater distance and are often associated with clear changes in food availability (E. M. Anderson unpubl. survey data; J. R. Evenson, Washington Department of Fish and Wildlife [WDFW], unpubl. telemetry data).

Scoter energy status.—Although the smaller number of White-winged Scoters that we collected likely limited the statistical power of some analyses, overwinter dynamics in energy status appear to be more variable for Surf Scoters. Our measures of Surf Scoter energy status indicated an overwinter shift in importance of our Puget Sound sites that is consistent with our counts and foraging observations. Similar comparison among these sites was not possible for White-winged Scoters that we collected only in Birch Bay, but overwinter body mass assessed in past studies was more variable among sites in Surf Scoters. Body mass declined by >9% in about one third of past studies for Surf Scoters, well above the range of losses observed in White-winged Scoters and the losses commonly reported in other wintering waterfowl (Lovvorn 1994b, Barboza and Jorde 2002). Only Surf Scoters showed declines in plasma triglycerides over winter. Compared with body composition, plasma metabolites reflect rates of nutrient acquisition and, thus, are more reliable indicators of changes in energy status when movements among sites are likely (Williams et al. 2007). Surf Scoter numbers in Penn Cove were lower in 2005–2006 than in the two previous winters, which suggests that our estimates of their energy status were obtained during a year with relatively poor foraging conditions at this site. However, overwinter decreases in Surf Scoter numbers while foraging effort increased suggest that their energy status declines in Penn Cove even in years when foraging profitability is likely greater (2003–2004, 2004–2005).

Body size, energetics, and diversity of habitat needs.—To clarify the needs of White-winged and Surf scoters in marine habitat, we used our own data and information from the literature to contrast their nutritional requirements, prey size constraints, and seasonal

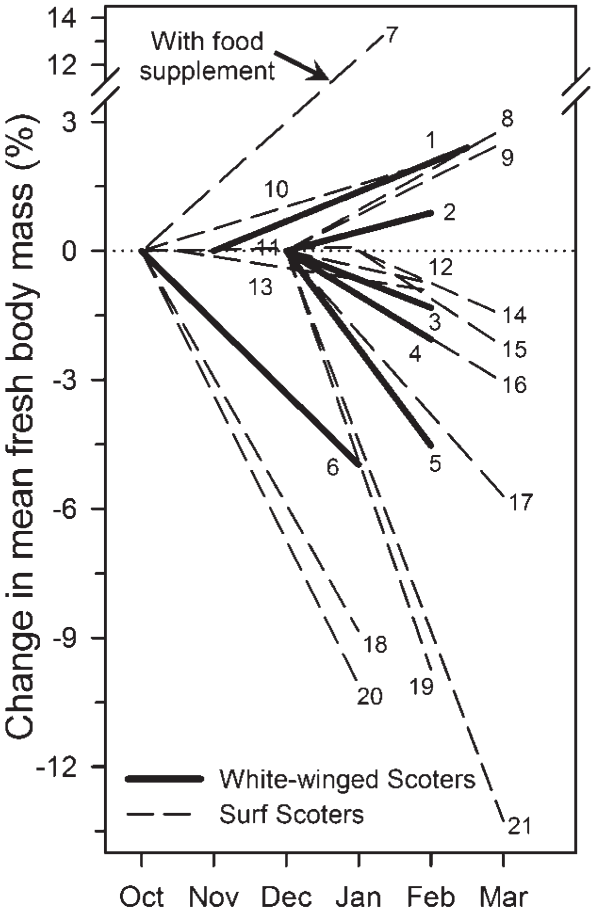

Fig. 3. Overwinter changes in mean fresh body mass for after-hatch-year male White-winged and Surf scoters from multiple locations on the Pacific coast. White-winged Scoters: (1) southern Puget Sound, Washington (WA), 20–21 November 2003 (*n* = 7) and 24 February–12 March 2004 (*n* = 11; J. R. Evenson, WDFW, unpubl. data); (2) Baynes Sound, British Columbia (BC), 1–9 December 2003 (*n* = 38) and 23–27 February 2004 (*n* = 23; Anderson et al. 2009); (3) Chatham Sound, BC, 11 December 2009 (*n* = 13) and 22–24 February 2010 (*n* = 10; D. Esler, Simon Fraser University, unpubl. data); (4) Baynes Sound, 10–16 December 2002 (*n* = 18) and 24–27 February 2003 (*n* = 22; Anderson et al. 2009); (5) Hecate Strait, BC, 8–9 December 2009 (*n* = 20) and 20–21 February 2010 (*n* = 18; D. Esler unpubl. data); (6) Birch Bay (present study). Surf Scoters: (7) Elliott Bay, WA, 26–31 October 1984 (*n* = 5) and 18–23 January 1985 (*n* = 10; Henny et al. 1991); (8) Howe Sound, BC, 3 December 1998 (*n* = 7) and 1 March 1999 (*n* = 5; J. E. Elliott, Pacific Wildlife Research Centre, Environment Canada, unpubl. data); (9) Baynes Sound, 15 December 1998 (*n* = 6) and 2 March 1999 (*n* = 9; J. E. Elliott unpubl. data); (10) Bellingham Bay, WA, 29–30 October 1996 (*n* = 18) and 24–25 February 1997 (*n* = 14; M. Mahaffy, Western Washington Fish and Wildlife Office, U.S. Fish and Wildlife Service, unpubl. data); (11) Commencement Bay, WA, 26–31 October 1984 (*n* = 6) and 18–23 January 1985 (*n* = 10; Henny et al. 1991); (12) Baynes Sound, 1–9 December 2003 (*n* = 34) and 23–27 February 2004 (*n* = 19; Anderson et al. 2009); (13) Commencement Bay, 30 October–1 November 1995 (*n* = 20) and 26–27 February 1996 (*n* = 20; Mahaffy et al. 1997); (14) southern San Francisco Bay, California, January (*n* = 20) and March 1985 (*n* = 20; exact dates not reported, Ohlendorf et al. 1991); (15) northern San Francisco Bay, January (*n* = 19) and March 1985 (*n* = 20; exact dates not reported, Ohlendorf et al. 1991); (16) Birch Bay (present study); (17) Padilla Bay (present study); (18) Alsea Bay, Oregon, 26–31 October 1984 (*n* = 5) and 18–23 January 1985 (*n* = 8; Henny et al. 1991); (19) Baynes Sound, 10–16 December 2002 (*n* = 29) and 25–27 February 2003 (*n* = 15; Anderson et al. 2009); (20) Hood Canal, WA, 28 October 1997 (*n* = 15) and 23–26 February 1998 (*n* = 15; M. Mahaffy unpubl. data); (21) Penn Cove (present study).

changes in body mass and diet (Table 4). White-winged Scoters during December are >50% heavier; accordingly, the estimated mass-specific field metabolic rate (kJ g^{-1} day^{-1}) of each sex is >11% lower for White-winged Scoters than for Surf Scoters. Surf Scoters consume smaller bivalves and, as winter progresses, display more variable changes in body mass along with increased foraging effort (Table 4). Finally, shifts in diet and foraging locations during late winter and spring have been reported mainly in Surf Scoters.

The smaller body size of Surf Scoters may contribute to their reliance on a greater diversity of marine foods and foraging habitats. Per unit of body mass, smaller species have higher metabolic rates, have greater costs of thermoregulation and locomotion, and store less energy (Turner 1988, Lovvorn et al. 1991, McNab 2009). These aspects of smaller size can be a disadvantage in challenging environments—cold temperatures or declines in food availability may require greater increases in foraging effort to maintain adequate body reserves (Goudie and Ankney 1986). As smaller bivalves that are preferred by both scoter species are depleted, the ability to consume progressively larger sizes appears to make reliance on bivalves a seasonally stable foraging strategy only for the larger White-winged Scoter (Anderson et al. 2008). Conversely, for Surf Scoters, proportionally higher maintenance costs and depletion of smaller bivalves to which they are limited may drive their greater overwinter variability in energy status. We suggest that in response to their more variable energy status, which can decline appreciably in some winters (Fig. 3), Surf Scoters increase their foraging effort and often change foraging sites to take advantage of seasonally available foods (Table 4). The greater foraging flexibility of Surf Scoters may be beneficial in years and seasons when bivalve foods on which White-winged Scoters often rely become scarce (Beukema and Dekker 2006, Anderson et al. 2008). However, in most years, Surf Scoters appear to require a broader range of foraging opportunities to meet their energy needs.

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TABLE 4. Contrast of White-winged and Surf scoters in terms of nutritional requirements, prey size constraints, and seasonal changes in body mass and diet. Where available, means ± SE are provided with their ranges (in parentheses).

	White-winged Scoter	Surf Scoter	Source
Body mass (g)			Puget Sound, Washington, and British Columbia (sources include those cited in Fig. 3 for which masses of individual birds were available)
Female, December	1,393 ± 14 (1,178–1,580), *n* = 41	925 ± 10 (800–1,050), *n* = 42	
Male, December	1,714 ± 20 (1,404–2,250), *n* = 104	1,085 ± 7 (927–1,300), *n* = 114	
Field metabolic rate (kJ g^{-1} day^{-1})			Equation for seabirds in Nagy (1987)
Female, December	0.94 (0.91–0.99)	1.06 (1.02–1.11)	
Male, December	0.88 (0.82–0.94)	1.01 (0.96–1.06)	
Prey size constraints (mm)			Anderson et al. 2008
Mean length of bivalve ingested across *n* studies	28 ± 4 (21–34), *n* = 3	14 ± 2 (6–20), *n* = 7	
Maximum length of bivalve ingested across *n* studies	56 ± 5 (42–77), *n* = 7	38 ± 2 (25–48), *n* = 8	
Body mass during winter	Less variable compared to Surf Scoters	Variable with declines often greater than in White-winged Scoters	See Fig. 3
Foraging effort during winter	Less change than in Surf Scoters	Typically increases	Puget Sound, Washington (present study; Fig. 2), Queen Charlotte Islands, British Columbia (Goudie 1999), Strait of Georgia, British Columbia (Lewis et al. 2008)
Shifts in diet during late winter and spring			
Herring spawn	Late-season food	Late-season food; more important to body reserves than for White-winged Scoters	Anderson et al. 2009
Seagrass epifauna	Not found	Late-season food	Anderson et al. 2008, Anderson 2009
Reproducing polychaetes	No reports	Late-season food	Lacroix et al. 2005
Invertebrates made available by gray whales	Used by very few individuals compared with Surf Scoters	Late-season food	Anderson and Lovvorn 2008
Solen sicarius bivalves	Not found	Late-season food	Anderson et al. 2008

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