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VARIATION IN PHYSIOLOGY AND ENERGY MANAGEMENT OF WINTERING WHITE-WINGED SCOTERS IN RELATION TO LOCAL HABITAT CONDITIONS

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Abstract. Along the Pacific coast of North America, White-winged Scoters (*Melanitta fusca*) winter in sites that vary widely in habitat conditions. This habitat variation likely alters the relative costs and benefits of using specific sites in terms of factors such as foraging conditions, degree of predation danger, and thermoregulatory costs. To assess how White-winged Scoters adjust their physiology and energy management in response to variation in habitat conditions, we contrasted overwinter dynamics in several physiological indicators across five sites in British Columbia and Washington. We tested the relative support for various hypotheses that considered exposure to wind and waves, water depth, predation danger, diet composition, and collection period as possible underlying causes of variation in physiological indicators. Total body mass and lipid mass were highest at an exposed offshore site, which may reflect an adaptive response to buffer against unpredictable foraging conditions and increased thermoregulatory costs. At nearshore sites where exposure was lower, scoters maintained lower lipid masses throughout the winter. Total lipid mass declined through the winter in all sites, a result consistent with findings for many waterfowl species. However, levels of plasma metabolites (triglycerides, β-hydroxybutyrate) varied little by site, suggesting that, irrespective of body composition, birds at all sites maintained physiological homeostasis. Digestive morphology was strongly related to diet, with smaller gizzards and longer intestines associated with a greater fraction of soft-bodied foods in the diet. Our results suggest that the physiology and energy management of wintering White-winged Scoters is related to local habitat conditions.

Key words: *body condition, digestive morphology, energy management,* Melanitta fusca*, physiology, plasma metabolites, White-winged Scoter, wintering habitat.*

Variación en Fisiología y Manejo de Energía de Individuos Invernantes de *Melanitta fusca* con Relación a las Condiciones Locales de Hábitat

Resumen. A lo largo de la costa pacífica de América del Norte, *Melanitta fusca* inverna en sitios que varían enormemente en las condiciones de hábitat. Esta variación de hábitat probablemente altera los costos y beneficios relativos del uso de sitios específicos en términos de factores como condiciones de forrajeo, grado de peligro de depredación y costos termo-regulatorios. Para evaluar como *M. fusca* ajusta su fisiología y manejo de la energía en respuesta a la variación en las condiciones de hábitat, comparamos las dinámicas de varios indicadores fisiológicos a lo largo del invierno en cinco sitios en la Columbia Británica y Washington. Evaluamos el apoyo relativo a varias hipótesis que consideraron exposición a los vientos y olas, profundidad del agua, peligro de depredación, composición de la dieta y período de colecta como posibles causas subyacentes de variación en los indicadores fisiológicos. La masa corporal total y la masa de lípidos fueron las más altas en un sitio expuesto mar adentro, lo cual puede reflejar una respuesta adaptativa para amortiguar condiciones de forrajeo impredecibles y aumentar los costos de termo regulación. En los sitios cercanos a la costa donde la exposición fue más baja, *M. fusca* mantuvo masas de lípidos más bajas a lo largo del invierno. La masa total de lípidos disminuyó a lo largo del invierno en todos los sitios, lo que es consistente con los hallazgos para muchas especies de aves acuáticas. Sin embargo, los niveles de metabolitos en plasma (triglicéridos, β-hidroxibutírico) variaron poco entre sitios, sugiriendo que, independientemente de la composición corporal, las aves mantuvieron en todos los sitios la homeostasis fisiológica. La morfología digestiva estuvo fuertemente relacionada a la dieta, con mollejas más pequeñas e intestinos más largos asociados con una fracción mayor de alimentos de cuerpo blando en la dieta. Nuestros resultados sugieren que la fisiología y el manejo de la energía de los individuos invernantes de *M. fusca* están relacionados con las condiciones locales de hábitat.

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INTRODUCTION

Throughout the annual cycle, birds must respond physiologically to an array of environmental factors, including food availability, climate, and predator density (Lima 1986, Hamilton 2000). As habitat conditions vary, they can have direct and indirect effects on an individual's physiological status and energy management, through either adjustments in strategy or through imposed constraints. A habitat's average conditions, as well as its degree of predictability, can affect birds' physiology and energy-management responses (Cuthill et al. 2000).

To increase chances of surviving the winter and emerging in optimal condition for subsequent stages of the annual cycle, wintering birds must balance costs and benefits of nutrient acquisition and storage (Lima 1986, Witter and Cuthill 1993). The relative costs and benefits of acquiring and maintaining energy reserves vary with the season and habitat conditions that affect foraging conditions. For example, a bird can use lipid reserves to buffer itself against food shortages or to meet the costs of increased thermoregulatory demands during harsh weather (Smith and Metcalfe 1997, Cuthill et al. 2000, Rogers and Reed 2003). However, maintaining large lipid reserves may require increased foraging effort and decrease mobility (Lima 1986, Bednekoff and Krebs 1995, Cuthill et al. 2000). Birds are generally presumed to balance these trade-offs by managing energy to maximize winter survival and provide reserves sufficient for current and subsequent stages of their annual cycle. Such responses vary depending on the suite of local habitat conditions.

Measures of body mass and composition have been used to make inferences about difference in foraging conditions among sites (Hepp et al. 1986, Gauthier et al. 1992, Anderson and Lovvorn 2011). However, in light of the potential costs and benefits of storing reserves described above, lower masses of body and lipids do not necessarily indicate poorer condition of an individual or lower quality of a habitat. Instead, birds presumably optimize body mass and nutrient reserves to reflect trade-offs associated with local conditions (Lima 1986, Krams et al. 2010, Zimmer et al. 2011). Recent studies have used plasma metabolites as an additional tool for measuring metabolic response to foraging conditions (Seaman et al. 2006, Anteau and Afton 2008). Unlike static measures of nutritional status such as lipid mass, plasma metabolites reflect rates of energy acquisition or depletion (Jenni-Eiermann and Jenni 1994). Specifically, plasma concentrations of triglyceride (TRIG) and β-hydroxybutyrate (BOHB) reflect the rates of lipid accumulation and lipid catabolism, respectively (Anteau and Afton 2008).

Digestive morphology also can be used as an indicator of variability in foraging conditions. Birds modify their digestive morphology in response to seasonal energy requirements, as well as the quantity and types of food they ingest (Piersma and van Gils 2011). Gizzard size and mass vary considerably in relation to prey type and size. Birds feeding on larger, hard-shelled prey items require larger gizzards to process food than do those feeding on smaller or soft-bodied prey (Goudie and Ryan 1991, van Gils et al. 2005). Variation in gut size and length can be interpreted in many ways. In response to unpredictable food availability, birds may increase food intake, which requires a larger or longer gut to maintain digestive efficiency (Piersma 2002, Piersma and van Gils 2011). Increased length or mass of the small intestine also facilitates nutrient assimilation in areas with lower food quality or availability, even where intake rates remain unchanged. In either case, maintaining a larger gut incurs higher energetic costs. Birds presumably adjust gut size to balance potential costs and benefits associated with digestive capacity, and these trade-offs may vary with the stage of the annual cycle or local habitat conditions (Piersma and van Gils 2011).

Birds endogenously regulate their body composition, plasma metabolites, and digestive morphology throughout the annual cycle (Barboza and Jorde 2002, Williams et al. 2007). For example, in many species of waterfowl, body mass declines steadily through winter until preparation for migration and reproduction in spring (Hepp et al. 1986, Perry et al. 1986, Barboza and Jorde 2002). Declines in body mass over winter have been observed in both wild and captive waterfowl for which food was not limiting, suggesting some degree of endogenous control. Declines in body mass and lipid mass during winter are presumably adaptive, reflecting energy-management responses to maximize survival. Variation from site to site in this seasonal pattern and in body mass itself may result from differences in local habitat conditions (Mason et al. 2007).

Measures of physiology and morphology in birds can vary as a result of multiple confounding factors, which can be difficult to distinguish from one another. Contrasting these measures across habitats may help clarify whether variation in energy management and physiology is largely a result of local conditions, endogenous regulation, or both. Further, considering variation in multiple indicators within one stage of the annual cycle provides a broader perspective on relationships between habitat characteristics and physiology than does any single indicator on its own.

The White-winged Scoter (*Melanitta fusca*) is a sea duck that spends the majority of the year in marine environments across a broad range of northern latitudes. Although the British Columbia (BC) coastline represents a significant portion of its winter range along the Pacific coast of North America, there are few areas in BC where it concentrates during the winter (Savard 1979). This may be due in part to its preference for habitats with soft bottoms and large stocks of bivalves, which are relatively uncommon in BC. Even within these habitats, however, areas used by wintering White-winged Scoters vary in factors such as prey availability, exposure to wind and waves, water depth, and predation danger. Widespread declines in the populations of some sea ducks, including the White-winged Scoter, have prompted efforts to identify functional values of seasonal habitats (e.g., Žydelis et al. 2006, Lewis et al. 2008, Anderson and Lovvorn 2011).

We measured overwinter dynamics in body mass and composition, digestive morphology, and plasma metabolite concentrations of White-winged Scoters from five sites along the coast of BC and Washington (Fig. 1) that varied markedly in habitat conditions. We evaluated whether different conditions at these sites were related to variation in physiology and energy status, and we contrasted specific hypotheses about the roles of prey type and diversity, exposure, water depth, and predation danger in observed variation. Rather than considering responses to shorter-term environmental variation, we primarily addressed physiological responses to average habitat conditions over a period of months. We predicted that at sites where conditions for foraging are less predictable, birds body mass and lipid levels should be higher, under the expectation that larger fat reserves should buffer a bird against periods of low food availability or poor foraging conditions (Cuthill et al. 2000, Rogers and Reed 2003). We expected that increased exposure to harsh weather should result in thermoregulatory costs, rates of food intake and fat catabolism, and levels of plasma TRIG and BOHB being higher offshore than near shore. We predicted that greater predation danger near shore should increase the scoters' vigilance behavior, which may lead to lower rates of food intake and so to lower body mass, lipid mass, and plasma TRIG levels. We expected that consumption of soft-bodied rather than shelled foods should reduce the amount of strength needed to crush whole prey, resulting in lower gizzard masses. Finally, we predicted that intestine mass and length should vary in response to diet composition.

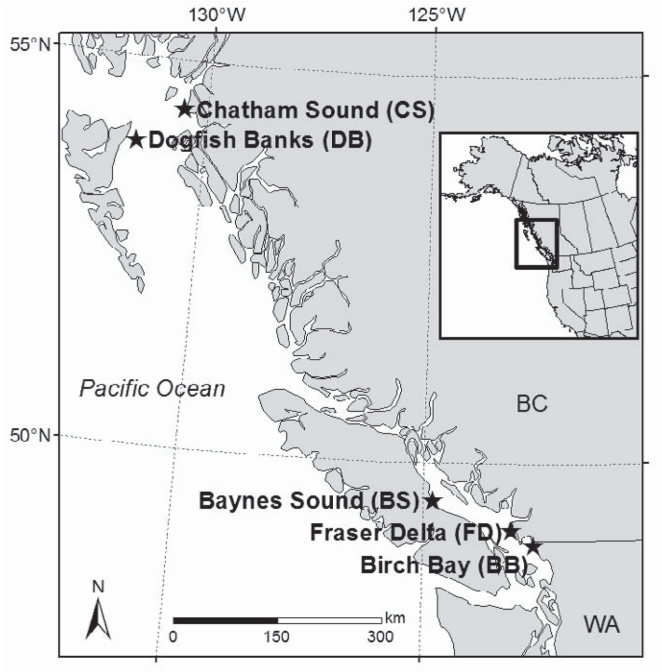

FIGURE 1. Map of the five study sites in British Columbia and Washington.

METHODS

STUDY SITES

Each study site (Fig. 1) represented a different combination of three habitat conditions that we hypothesized might influence physiological measures: exposure to wind and waves, water depth, and predation danger (Table 1). Dogfish Banks (53° 55′ N, 131° 30′ W) is an offshore site that is particularly susceptible to turbulent seas during winter storms because of frequent high winds from the southeast. Savard (1979) described the site as one of only three major wintering areas for scoters in northern BC. In some years, tens of thousands of White-winged Scoters winter at Dogfish Banks; the number fluctuates from year to year (Hodges et al. 2005, LGL Limited et al. 2009; M.T.W., pers. obs.). This site consists mainly of soft-bottom and shallow subtidal habitat, which is rare along the coast of BC. Combined with a mobile substrate of sand or a mixture of sand and gravel, these conditions result in a frequently changing benthic foraging habitat. Water depths on Dogfish Banks range from 4 to 20 m, and the maximal tidal range is approximately 5 m (Amos et al. 1995).

Chatham Sound (54° 27′ N 130° 25′ W) supports hundreds of wintering White-winged Scoters. Situated among many large islands and the mainland coast, the site is more protected from high winds and large swells than Dogfish Banks. At Chatham Sound scoters feed mainly on sandy and muddy substrates located between rock outcrops.

Baynes Sound (49° 39′ N, 124° 53′ W) contains extensive intertidal flats and high densities of wild and cultured bivalves, providing near-shore wintering habitat for a

TABLE 1. Categorical groupings of five sites based on diet composition, exposure, predation danger, and water depth for White-winged Scoters wintering in British Columbia and Washington. Groupings were used to assess the relative importance of these habitat conditions on the birds' physiology and energy management.

Study site	Proportion of bivalves in diet	Exposure	Predation danger	Water depth
Chatham Sound	High–very high	Low–medium	High	High
Dogfish Banks	Medium–high	High	Low	High
Baynes Sound	Very high	Low	High	Low
Fraser R. delta	Very high	Low–medium	Low	Low
Birch Bay	Very high	Low	High	Low

combined total of about 6500 White-winged Scoters and Surf Scoters (*M. perspicillata*) (W. S. Boyd, Environment Canada, unpubl. data). Because it provides an abundant and temporally stable source of bivalve prey and White-winged Scoters wintering in the area expend relatively little effort in foraging, Baynes Sound is considered to be high-quality foraging habitat (Lewis et al. 2007, 2008).

Thousands of White-winged Scoters use the shallow intertidal mudflats of the Fraser River delta (49° 06′ N, 123° 16′ W) for molting, wintering, and staging (E. M. Anderson and J. R. Evenson, unpubl. data). In the winter of 2010–2011, however, numbers of White-winged Scoters in the Fraser River delta were relatively low, ranging from approximately 400–600 in December 2010 to approximately 200–300 in February 2011.

Birch Bay (48° 55′ N, 122° 45′ W) is a small bay located at the northern end of Puget Sound and is characterized by extensive intertidal sandflats and seagrass beds (Anderson and Lovvorn 2011). Approximately 1000 White-winged Scoters winter in Birch Bay annually (Anderson and Lovvorn 2011).

SAMPLE COLLECTION

Under the authority of permits from Environment Canada (BC-09-0182) and Simon Fraser University Animal Care (992B-06), we collected 138 adult male White-winged Scoters by shotgun from a small boat at four areas along the coast of BC (Fig. 1): Dogfish Banks (February 2009 [*n* = 19], December 2009 [*n* = 20], and February 2010 [*n* = 18]); Chatham Sound (December 2009 [*n* = 13] and February 2010 [*n* = 10]); Fraser River delta and Baynes Sound (December 2010 [*n* = 13 and *n* = 15 at the two sites, respectively], and February 2011 [*n* = 15 at each site]), for a total of 9 trips. For analyses of body mass, lipid mass and gizzard mass, we included data from 17 birds previously collected at Birch Bay (December 2005 [*n* = 9] and early March 2006 [*n* = 8]) (Anderson and Lovvorn 2011).

To eliminate potential variation in physiological measures related to age class or sex, we collected only after-hatch-year males, clearly distinguished by plumage from all other cohorts (Brown and Fredrickson 1997). We sampled blood within 10 min of collection and removed the upper gastrointestinal tract within 15 min of collection. Using a sterile 18-gauge needle, we transferred up to 5 mL of heart blood to a heparinized vial for analyses of plasma metabolites. We recorded fresh body mass (±10 g), lengths (±1 mm) of the tarsus, culmen, and wing chord, as well as the fresh mass (±0.1 g) of the empty esophagus and gizzard for use in analyses of digestive morphology and diet. Within 8 hr of collection, we centrifuged whole blood to separate plasma and cells and stored all tissues at –20 ºC until further analyses. Prior to freezing these samples, we kept whole blood and tissues on ice packs in a cooler in the collection boat.

LABORATORY ANALYSES

Analyses of body composition and digestive morphology. The Avian Energetics Lab of Long Point Waterfowl (Port Rowan, Ontario) measured the length (±0.1 cm) and mass (±0.1 g) of intestine and analyzed the body composition (total protein, lipid, water, and ash) of ingesta-free dry carcasses including plumage by the methods described by Afton and Ankney (1991). As did Lovvorn et al. (2003), we adjusted lipid estimates for tissues that were removed in the field and not returned to the carcass prior to composition analyses.

Plasma metabolite assays. For all metabolite assays, we used a microplate spectrophotometer to read samples out of 400-mL flat-bottomed 96-well polystyrene microtitre plates. We measured plasma TRIG concentrations in 5-µL plasma samples in triplicate, using a previously validated colorimetric endpoint assay and by subtracting free glycerol (Sigma-Aldrich, F6428) from total glycerol (Sigma-Aldrich, T2249) (see Williams et al. 1999, Guglielmo et al. 2002, Anteau and Afton 2008). We measured plasma BOHB by a previously validated kinetic assay (Megazyme, K-HDBA; following Guglielmo et al. 2005, Anteau and Afton 2008). Using a chicken hen plasma pool, we calculated intra- and interassay variations of 3.03% and 7.26%, respectively, for TRIG, and 2.04% and 10.28% for BOHB.

Diet analyses. Diet results are reported in Palm et al. (2012). Briefly, we calculated the average percent ash-free dry mass (hereafter, AFDM refers to ash-free dry mass of esophagus contents only) of each prey category (bivalves, crustacea, echinoderms, gastropods, polychaetes, fish) by first assessing the relative percentage of each category in the esophagus of each bird, then averaging those percentages across all samples from the respective collection period (Anderson et al. 2008). We also measured shell length (±1 mm) of whole bivalves along the longest axis.

STATISTICAL ANALYSES

We compared measures of body mass and composition, digestive morphology, and plasma metabolites across study sites and collection periods by least squares analyses in an information-theoretic context. We pooled data from various collecting trips in specific ways to test relative support for various biologically plausible a priori hypotheses describing possible underlying causes of variation in the data. Diet composition, exposure, water depth, predation danger, and collection period were all factors we assessed for influence on body mass, body composition, and plasma metabolites. Because all explanatory variables were categorical, each linear model represented a different way of grouping data from different collecting trips for comparisons (Table 1). This allowed consideration of support for each of the factors as drivers of variation in body mass and composition, digestive morphology, and plasma metabolites. To account for the potential effect of collection period (mid-winter versus late winter) we included models that pooled data by the combination of period and another factor. For example, if the hypothesis was that the response varied by water depth and period, the explanatory variable would have four levels: (1) mid-winter at deep-water sites, (2) mid-winter at shallow-water sites, (3) late winter at deep-water sites, and (4) late winter at shallow-water sites. In addition, we included a null model for all physiological measures, representing the hypotheses that data did not vary geographically or by collection period. We included a model in which all sites were combined within a period, to consider the hypothesis that responses varied seasonally but not geographically (i.e., representing endogenous control irrespective of local conditions). We hypothesized that weather conditions (air temperature, wind, solar insolation, etc.) in the weeks immediately preceding each collecting trip could influence variation in physiological measures. To account for this potential effect, we included a global model that grouped data from each trip separately.

We estimated each bird's structural body size by using the first principal component of measurements of culmen, wing chord, and tarsus. In our set of candidate models, we included models both with and without a body-size covariate for body mass, lipid mass, and digestive morphology to determine whether structural size explained some of the variation in physiological measures. We report results only of models that included a body-size covariate, as they were more parsimonious in all cases (Tables 2 and 3). For analyses of variation in digestive morphology, we limited the candidate set to models representing hypotheses related to diet, excluding those related to other habitat conditions. We found no evidence in past studies suggesting that exposure, water depth, or predation danger directly influence variation in digestive morphology.

As is that of many other sea ducks (Iverson and Esler 2006), the White-winged Scoter's site fidelity from November through March is high, according to satellite-telemetry data (W. S. Boyd, Environment Canada, unpubl. data) and consistent numbers within a winter at some of our sites with survey data (Birch Bay, Anderson and Lovvorn 2011, unpubl. data; Baynes Sound, D. Esler, unpublished data). We assumed that White-winged Scoters remained at each study site through the winter and that variation in different physiological measures largely reflected variation in site-specific habitat conditions. Therefore, we assumed that within a site, we collected from the same population of birds during both mid- and late winter and that sample sizes were adequate to fully represent this population. Below, we describe and justify our predictions for effects of diet composition and three

TABLE 2. Candidate models describing variation in body mass and lipid mass in wintering male White-winged Scoters across five areas in British Columbia and Washington. CS = Chatham Sound, DB = Dogfish Banks, BS = Baynes Sound, FD = Fraser River Delta, BB = Birch Bay, M = mid-winter (December), L = late winter (February–March), 09 = 2009, 10 = 2010. Italics indicate the most parsimonious model for each physiological indicator. Each model (except null) includes a covariate for structural body size.

			Body mass $n = 155$			Lipid mass $n = 155$		
Explanatory variable	Site and period grouping	K	Δ_i^a	w_i	r^2	Δ_i^a	w_i	r^2
Exposure (2 levels)	CS = BS = FD = BB; DB	4	8.87	0.01	0.08	58.85	0.00	0.26
Exposure (3 levels)	CS = FD; DB; BS = BB	5	10.99	0.00	0.08	53.95	0.00	0.30
Water depth	CS = DB; BS = FD = BB	4	12.66	0.00	0.06	39.18	0.00	0.35
Predation danger	CS = BS = BB; DB = FD	4	13.90	0.00	0.05	73.89	0.00	0.19
Diet diversity (2 levels)	CS = DBM = DBL10 = BS = FD = BB; DBL09	4	14.65	0.00	0.05	100.04	0.00	0.03
Diet diversity (3 levels)	CSM = BS = FD = BB; CSL = DBM = DBL10; DBL09	5	13.51	0.00	0.07	54.28	0.00	0.29
Period	CSM = DBM = BSM = FDM = BBM; CSM = DBL09 = DBL10 = BSL = FDL = BBL	4	3.01	0.12	0.12	88.28	0.00	0.10
Exposure (2 levels) with period	CSM = BSM = FDM = BBM; DBM; CSL = BSL = FDL = BBL; DBL09 = DBL10	6	*0.00*	*0.52*	*0.16*	20.64	0.00	0.44
Exposure (3 levels) with period	CSM = FDM; DBM; BSM = BBM; CSL = FDL; DBL09 = DBL10; BSL = BBL	8	3.53	0.09	0.16	*0.00*	*0.91*	*0.53*
Water depth with period	CSM = DBM; BSM = FDM = BBM; CSL = DBL09 = DBL10; BSL = FDL = BBL	6	4.40	0.06	0.14	17.12	0.00	0.46
Predation danger with period	CSM = BSM = BBM; CSL = BSL = BBL; DBM = FDM; DBL09 = DBL10 = FDL	6	1.96	0.20	0.15	52.21	0.00	0.31
Global	CSM; CSL; DBM; DBL09; DBL10; BSM; BSL; FDM; FDL; BBM; BBL	13	11.20	0.00	0.19	4.51	0.09	0.55
Body size	CS = DB = BS = FD = BS	3	12.78	0.00	0.05	101.17	0.00	0.01
Null	CS = DB = BS = FD = BS	2	68.47	0.00	—	146.21	0.00	—

[a] Minimum $AIC_c = 1878.65$ for body mass; 1667.95 for lipid mass.

TABLE 3. Candidate models describing variation in digestive morphology of wintering male White-winged Scoters across five areas in British Columbia and Washington. Site and period abbreviations as in Table 2. Italicized text indicates the most parsimonious model for each physiological indicator. Intestine measurements were not available for Birch Bay. Each model (except null) includes a covariate for structural body size.

			Gizzard mass $n = 155$			Intestine mass $n = 138$			Intestine length $n = 138$		
Explanatory variable	Site and period grouping	K	Δ_i[a]	w_i	r^2	Δ_i[a]	w_i	r^2	Δ_i[a]	w_i	r^2
Diet (2 levels)	CS = DBM = DBL10 = BS = FD = BB; DBL09	4	82.98	0.00	0.14	1.32	0.31	0.01	*0.00*	*0.74*	*0.42*
Diet (3 levels)	CSM = BS = FD = BB; CSL = DBM = DBL10; DBL09	5	*0.00*	*1.00*	*0.51*	2.49	0.13	0.01	2.04	0.26	0.42
Body size	CS = DB = BS = FD = BB	3	102.17	0.00	0.02	*0.00*	*0.55*	*<0.01*	66.10	0.00	0.03
Null	CS = DB = BS = FD = BB	2	137.41	0.00	—	19.79	0.00	—	94.27	0.00	—

[a] Minimum AIC_c = 1316.89 for gizzard mass; 1059.18 for intestine mass; 1175.81 for intestine length.

habitat factors on physiology, body composition, and digestive morphology.

Diet composition. In the absence of data on prey availability, we used diet composition as an indicator of prey resources available during each of our collecting trips (Barrett 2002). Diet composition can affect body condition in a number of ways, as prey vary in energy and nutrient content, as well as in the amount of energy required to locate, handle, and digest them (Anderson et al. 2008). Diets at Baynes Sound, Birch Bay, and the Fraser River delta consisted almost exclusively of bivalves (range 92–100% of AFDM across all collection periods). Bivalves constituted 80–85% of AFDM during February 2010 at Chatham Sound, as well as in both samples from Dogfish Banks in winter 2009–2010 (Palm et al. 2012). During February 2009 at Dogfish Banks, bivalves represented only 25% of AFDM, as birds consumed higher proportions of fish and polychaetes. In the first diet-composition model, we separated data from the February 2009 sample from Dogfish Banks from all other samples. On the basis of the hypothesis that physiological responses could be sensitive to smaller degrees of variation in diet composition, we included a second diet-related model that pooled data into three groups, which corresponded to the proportion of bivalve prey in each sample: (1) medium: Dogfish Banks February 2009, (2) high: Dogfish Banks December 2009, Dogfish Banks February 2010, Chatham Sound February 2010, and (3) very high: Chatham Sound December 2009, Baynes Sound, Fraser River Delta, Birch Bay (Table 1).

Exposure. At Chatham Sound birds generally fed 1–3 km from shore, while at the Fraser River delta they foraged 1–5 km from shore. At Birch Bay and Baynes Sound, scoters fed closer to shore than at the other sites, almost always within 500 m of land and generally much closer. Of our study sites, the only one offshore was Dogfish Banks (Table 1), where White-winged Scoters occurred, on average, 8 km from shore (range 2–22 km). The eastern shore of Haida Gwaii immediately south of Rose Spit offers little to no shelter from prevailing adverse weather. Thus birds at Dogfish Banks were subjected to rough seas from prevailing winds that during winter blow out of the southeast for hundreds of kilometers across Hecate Strait. There is evidence that the presence and predictability of wind can affect body and lipid mass in birds (Peach et al. 1992, Witter et al. 1994, Cuthill et al. 2000).

We used average fetch length and wind direction as a measure of the degree of exposure at each study site. In ArcMap 10 (ESRI 2011), we calculated the geographic center of collection locations at each study site. At each site's geographic center, we used the program Fetch (Finlayson 2009) to calculate values for fetch length, defined as the distance over water that wind from a specific direction can blow unobstructed by land. Fetch length, wind speed, and the resulting amount of exposure to waves may affect the behavior and energetics of foraging sea ducks (Heath et al. 2008). We used data from the Canadian Wind Energy Atlas (Environment Canada 2003) to determine the average proportion of time wind blows through the winter from 12 directions. For each bearing, we multiplied the fraction of time the wind blows from that direction by its associated fetch length, then summed all values to produce a mean fetch length for each site. We calculated mean fetch lengths during the winter of 217.5 km at Dogfish Banks, 13.5 km at the Fraser River delta, 10.6 km at Chatham Sound, 4 km at Baynes Sound, and 2.6 km at Birch Bay.

In our first exposure model, we pooled data into two groups, in which the first group included data from Dogfish Banks (high exposure), the second from all other sites (low exposure) (Table 2). This two-level exposure model was based on the hypothesis that the degrees of exposure at the four nearshore sites should have a similar influence on physiology and that exposure at Dogfish Banks should have a different effect. Our second exposure model, which pooled data into three groups, still segregated Dogfish Banks (high exposure) but allowed that birds wintering at Chatham Sound and the Fraser

River delta (medium exposure) were more exposed to wind and waves than birds at Baynes Sound and Birch Bay (low exposure). For each of the two exposure models described above, we included an additional model that featured the same data groupings by site but also categorized mid-winter data separately from late-winter data to account for any temporal variation in responses (Table 2).

Water depth. Variation in water depth has been shown to affect the profitability of foraging in wintering diving ducks, which can have subsequent physiological and energetic effects (Lovvorn 1994). We used the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre 2010) to estimate the depth at the location of each collected bird, then averaged these values for each study site. At Dogfish Banks and Chatham Sound scoters fed exclusively in the subtidal zone at average depths of 10–15 m and 10–20 m, respectively. At Baynes Sound, the Fraser River Delta and Birch Bay they foraged in intertidal and shallow subtidal habitats averaging 2–5 m in depth. To group collection data by water depth, we pooled data from Dogfish Banks and Chatham Sound and those from the remaining sites separately (Table 2). We also considered a second water depth-model that accounted for temporal variation in the response variables.

White-winged Scoters wintering in BC forage almost exclusively during daylight hours (Lewis et al. 2005). However, we did not include day length among our explanatory variables because the difference in the amount of daylight between the northern and southern extremes of our study area was only ~35 min during mid-winter and <10 min during late winter. Models with collection data grouped by day length also would have been confounded with our water-depth models, as the two northern sites also provided the deepest foraging habitat. We assumed that variation in water depth has an effect on the White-winged Scoter's energetics greater than that of day length so did not include a day-length model in our candidate set.

Predation danger. Variation in the danger of predation across our study sites may have influenced White-winged Scoter physiology by affecting overall foraging behavior and food consumption (Lima 1986, Creel and Christianson 2008, Zimmer et al. 2011). White-winged Scoters wintering in Baynes Sound, Chatham Sound, and Birch Bay often foraged near forested land or exposed rock outcrops with high densities of Bald Eagles (*Haliaeetus leucocephalus*), the White-winged Scoter's most likely predator (Anderson et al. 2012).

Conversely, scoters foraged several kilometers from shore at the Fraser River delta, and there were virtually no eagles at Dogfish Banks. For predation danger models, we pooled data from the Fraser River delta and Dogfish Banks separately from all other data (Table 2). As with exposure and water depth, we included a predation-danger model that allowed for temporal variation in response variables.

MODEL SELECTION

We used information-theoretic methods to direct model selection, and for all statistical analyses used the program R (R Development Core Team 2011). To infer the relative support for each model included in the candidate set, we calculated Akaike's information criterion adjusted for small sample sizes (AIC_c), AIC_c differences (Δ_i), and Akaike weights (w_i) (Burnham and Anderson 2002). Both Δ_i and w_i indicate the amount of support for each model in comparison to that for other models in the candidate set. We report values under Results as means ± SE.

RESULTS

BODY MASS AND COMPOSITION

White-winged Scoters' lipid mass declined from mid- to late winter at all study sites (Fig. 2a), consistent with the winter lipid dynamics of many waterfowl. The decline was greatest at Dogfish Banks, where lipid mass decreased by 81 ± 20 g from December 2009 to February 2010. Lipid mass was lowest at Baynes Sound during both mid-winter (160 ± 13 g) and late winter (112 ± 12 g), highest at Dogfish Banks during both periods (mid-winter: 322 ± 14 g; late winter 2009: 247 ± 15 g; late winter 2010: 241 ± 13 g). The most parsimonious model describing variation in lipid mass was the 3-level exposure and period model (Table 2), which received nearly all support ($w_i = 0.91$) and explained 53% of the variation in the data. For lipid mass, body mass, and digestive morphology, we report only the results of models that included a body-size covariate, as they were always more parsimonious than models that did not account for structural size (Tables 2 and 3).

At all sites, declines in lipid mass from mid- to late winter accounted for a large portion of the observed declines in total body mass, which occurred at all sites except Baynes Sound (Fig. 2b). Although lipid mass decreased from mid- to late winter at Baynes Sound, composition analyses showed that an increase in protein mass at this site from December to February and early March roughly offset losses in lipid mass and resulted in a body mass stable through the winter. Birds at Dogfish Banks had body mass (1968 ± 30 g) in mid-winter greater than that at other sites and also experienced the greatest decline in body mass through the winter (89 ± 43 g) (Fig. 2). The best-supported model of body mass was the 2-level exposure and period model ($w_i = 0.52$), which pooled sites into four groups based on levels of exposure (i.e., Dogfish Banks versus all other sites) and period of collection (mid- versus late winter). However, this model described only 16% of the variation in body mass. The 3-level exposure and period model also explained 16% of body-mass variation but received less support in Δ_i and w_i (Table 2).

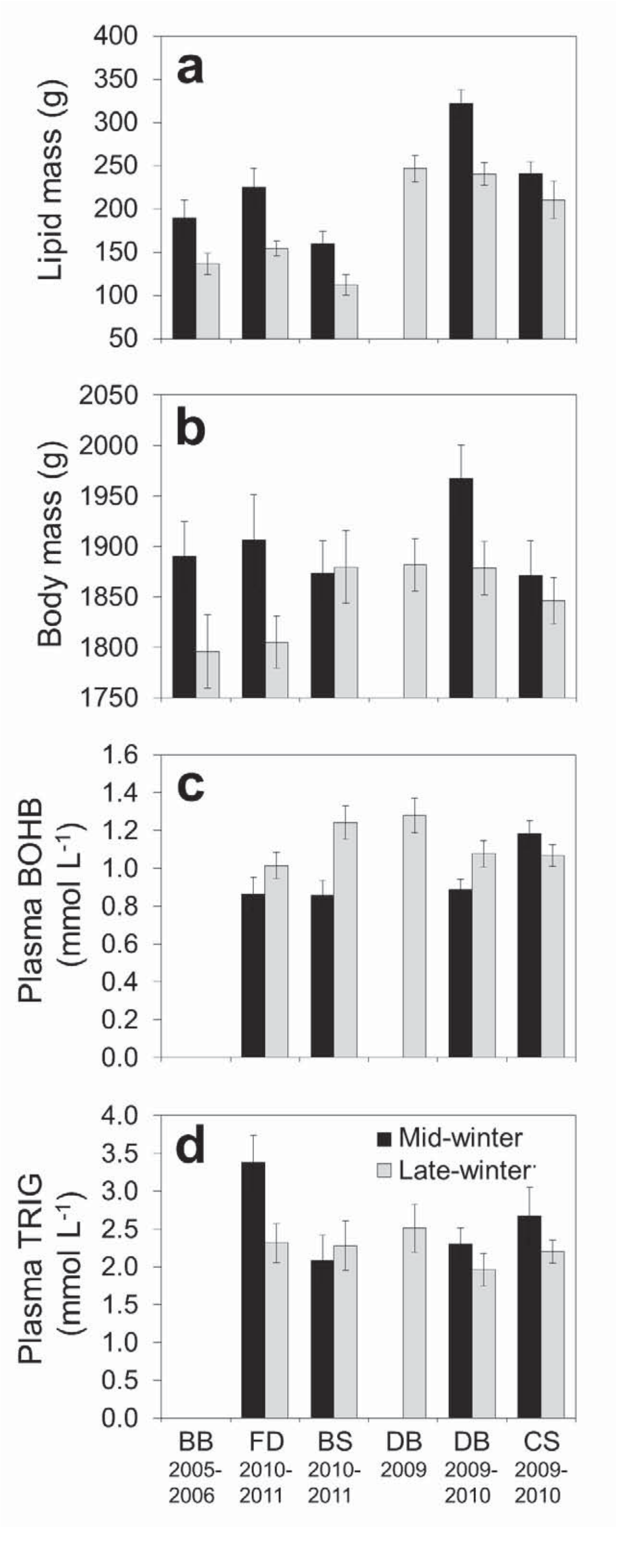

FIGURE 2. Mean (±SE) levels of (a) lipid mass, (b) body mass, (c) plasma β-hydroxybutyrate, and (d) plasma triglyceride for White-winged Scoters at five sites in British Columbia and Washington during mid-winter (December) and late winter (February–March). Site abbreviations as in Table 2. Plasma metabolites were not available for Birch Bay.

PLASMA METABOLITES

Average concentrations of plasma BOHB increased from mid- to late winter at three of four sites; the exception was Chatham Sound (Fig. 2c). The most parsimonious model describing variation in BOHB was the global model (w_i = 0.76), which considered each sample separately and explained 22% of the variation in BOHB (Table 4).

There was little evidence that TRIG concentrations varied in response to habitat conditions (Fig 2d). The three-level exposure model was the most parsimonious, yet it only marginally outperformed the null model. Greater than 89% of the variation in TRIG was not explained by any of our candidate models.

DIGESTIVE MORPHOLOGY

Intestine mass did not vary in response to habitat conditions, as the body-size model outperformed both diet models (Fig. 3, Table 3). Conversely, variation in intestine length was correlated with diet (Fig. 3, Table 3). The two-level diet model that separated February 2009 sample from Dogfish Banks from all others was the most parsimonious, explaining 42% of the variation in intestine length. In February 2009 (268 ± 1 cm), intestine length at Dogfish Banks was 45 cm longer than in any other sample (223 ± 2 cm) (Fig. 3). The top model describing variation in gizzard mass was the 3-level diet model, which explained 51% of variation in the data (Table 3). These results show a strong positive correlation between fraction of bivalves in the diet and gizzard mass.

DISCUSSION

Overall, we found geographic and temporal variation in several metrics of physiology and energetics, indicating that White-winged Scoters have considerable phenotypic flexibility in trophic level and energy management during the winter. This flexibility allows White-winged Scoters to use a variety of marine habitats and to balance trade-offs associated with wintering in each.

Our results suggest that the degree of exposure was the most important factor contributing to variation in both body mass and lipid mass. Likely consequences of the greater exposure of Dogfish Banks included reduced time for foraging and elevated thermoregulatory costs during high winds (Wiersma and Piersma 1994). We hypothesize that at Dogfish Banks the birds accumulated the largest lipid reserves to buffer themselves against these conditions. Average body and lipid masses from December 2009 at Dogfish Banks are among the highest published for the White-winged Scoter during any part of its annual cycle (Brown and Fredrickson 1997, Dickson 2011). Accumulating large stores of lipid early in the season appeared to be an effective energy-management response at Dogfish Banks, where averages of both lipid mass and body mass in February 2010 were remarkably consistent

TABLE 4. Candidate models describing variation in plasma metabolites in wintering male White-winged Scoters across four areas in British Columbia and Washington. Site and period abbreviations as in Table 2. Italicized text indicates the most parsimonious model for each physiological indicator. Data on plasma metabolites were not available for Birch Bay.

			β-Hydroxybutyrate $n = 138$			Triglycerides $n = 138$		
Explanatory variable	Site and period grouping	K	Δ_i^{a}	w_i	r^2	Δ_i^{a}	w_i	r^2
Exposure (2 levels)	CS = BS = FD = BB; DB	3	18.64	0.00	<0.01	3.65	0.04	<0.01
Exposure (3 levels)	CS = FD; DB; BS	4	20.56	0.00	<0.01	*0.00*	*0.26*	*0.04*
Water depth	CS = DB; BS = FD	3	16.10	0.00	0.02	3.01	0.06	<0.01
Predation danger	CS = BS; DB = FD	3	18.14	0.00	<0.01	3.43	0.05	<0.01
Diet diversity (2 levels)	CS = DBM = DBL10 = BS = FD; DBL09	3	8.36	0.01	0.07	3.43	0.05	<0.01
Diet diversity (3 levels)	CSM = BS = FD; CSL = DBM = DBL10; DBL09	4	10.11	0.00	0.08	2.67	0.07	0.02
Period	CSM = DBM = BSM = FDM; CSM = DBL09 = DBL10 = BSL = FDL	3	4.87	0.07	0.09	1.38	0.13	0.02
Exposure (2 levels) with period	CSM = BSM = FDM; DBM; CSL = BSL = FDL; DBL09 = DBL10	5	7.47	0.02	0.11	4.17	0.03	0.03
Exposure (3 levels) with period	CSM = FDM; DBM; BSM; CSL = FDL; DBL09 = DBL10; BSL	7	5.04	0.06	0.15	2.01	0.10	0.07
Water depth with period	CSM = DBM; BSM = FDM; CSL = DBL09 = DBL10; BSL = FDL	5	6.24	0.03	0.11	4.96	0.02	0.02
Predation danger with period	CSM = BSM; CSL = BSL; DBM = FDM; DBL09 = DBL10 = FDL	5	5.74	0.04	0.12	4.11	0.03	0.03
Global	CSM; CSL; DBM; DBL09; DBL10; BSM; BSL; FDM; FDL	10	*0.00*	*0.76*	*0.22*	3.96	0.04	0.10
Null	CS = DB = BS = FD	2	16.84	0.00	—	1.57	0.12	—

[a] Minimum $\text{AIC}_c = 73.90$ for BOHB; 437.769 for TRIG.

with those in February 2009, suggesting birds targeted a site-specific body mass for late winter optimal for local conditions.

In contrast to Dogfish Banks, Baynes Sound likely provided the most predictable foraging for White-winged Scoters, and it supported the highest densities of scoters. Specifically, at Baynes Sound exposure was less, the water was shallower and stocks of bivalves were more abundant, stable, and predictable than at Dogfish Banks (Lewis et al. 2008). Foraging likely required less effort at Baynes Sound than at Dogfish Banks, and lipid masses at Baynes Sound were the lowest of all sites. In Baynes Sound, the costs of maintaining high levels of endogenous reserves appear to outweigh the benefits.

Analyses of intestine length and gizzard mass provide further corroboration that physiology varied in response to local habitat conditions. Greater exposure on Dogfish Banks may have depressed the fraction of bivalves in the diet by reducing the scoters' ability to select the most profitable prey (i.e., bivalves) or by altering benthic sediments so that distributions of bivalves were less predictable. February 2009 may have been an example of such a period, as the sample of the diet taken then included markedly higher proportions of fish, polychaetes, and crustaceans than during other periods (Palm et al. 2012). A more diverse diet during this period corresponded to longer (but not more massive) intestines, which may have functioned to increase energy assimilation from these foods (Battley and Piersma 2005). Gizzard masses likely varied with a combination of diet composition and average size of bivalves consumed. At Dogfish Banks, low gizzard masses corresponded to a higher proportion of soft-bodied prey than at other sites, as well as bivalves smaller than at sites farther south. Relatively low gizzard masses in both samples from Chatham Sound probably reflected the small size of the scoter's primary prey at this site, *Acila castrensis*, even though the fraction of bivalves in the mid-winter diet was comparable to those at Baynes Sound, the Fraser River delta, and Birch Bay (Palm et al. 2012).

Contrary to our expectations, TRIG concentrations did not vary with habitat conditions. Collecting trips only lasted 13 days, mainly during extended periods of favorable weather. We speculate that plasma TRIG may increase immediately after a prolonged stormy period if White-winged Scoters accelerate their foraging to compensate for a period when feeding was not possible. Plasma BOHB also may increase during periods of adverse weather if foraging time declines and the birds rely more heavily on lipid reserves. Indeed, we found that BOHB varied by sample, but the increase in average BOHB from December to February at three of four sites indicated that average rates of lipid catabolism during February were higher than those during December. Coupled

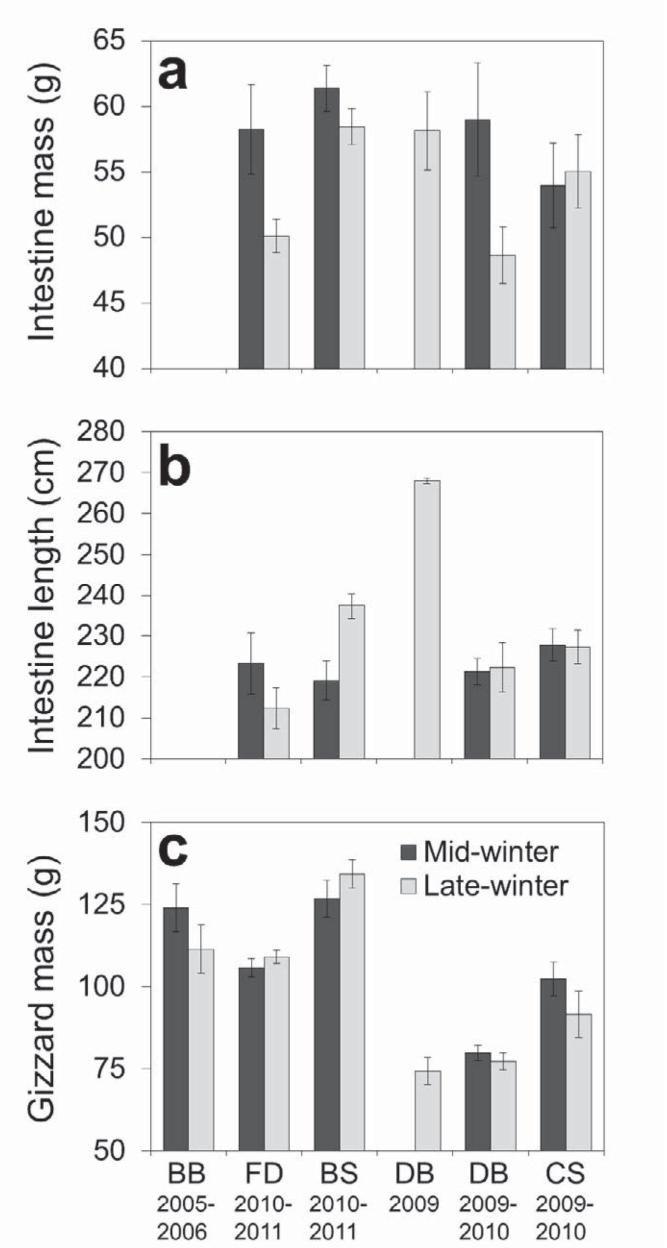

FIGURE 3. Mean (±SE) levels of (a) intestine mass, (b) intestine length, and (c) gizzard mass for White-winged Scoters at five sites in British Columbia and Washington during mid-winter (December) and late winter (February–March). Site abbreviations as in Table 2. Intestine measurements were not available for Birch Bay.

with our results for lipid and body mass, these results are consistent with body condition declining from December to February.

The lack of relationship between absolute levels of plasma metabolites across sites may indicate that, irrespective of their energy-management responses, scoters maintained physiological homeostasis at each site. Past studies used plasma TRIG and BOHB to show marked geographic variation in habitat conditions in a variety of bird species (e.g., Guglielmo et al. 2005, Seaman et al. 2006, Williams et al. 2007, Anteau and Afton 2008). However, these studies measured metabolites either in captive birds or in actively migrating wild birds that were building reserves to fuel coming energetic demands. If rates of nutrient acquisition and depletion in the White-winged Scoter are lower during winter than those observed during periods of hyperphagia or fasting in past studies, variation in metabolites across sites may be more difficult to detect.

While all five study sites are tenable for wintering White-winged Scoters, the functional value of each site may vary by age and sex. If we had included all cohorts in our analyses, we speculate that there would have been clearer patterns in body size across sites. Compared to other cohorts of the White-winged Scoter, adult males may be able to exploit a wider variety of habitats. Males' larger body size decreases mass-specific energy demands, making males better equipped than females to handle cold or windy environments and more resistant to fluctuations in energy status as a result of variable foraging conditions (Goudie and Ankney 1986, Richman and Lovvorn 2009). Further, older, more experienced birds may be more likely to find food resources in an unpredictable foraging environment. Consistent with this hypothesis, we observed the ratio of adult males to other cohorts was higher at Dogfish Banks than at the other sites, indicating that Dogfish Banks has more functional value for adult males than for other cohorts. We speculate that birds wintering in Dogfish Banks may benefit from decreased competition for food resources relative to other wintering areas.

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LITERATURE CITED

Afton, A. D., and C. D. Ankney. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: a test of competing hypotheses. Condor 93:89–97.

Amos, C. L., J. V. Barrie, and J. T. Judge. 1995. Storm enhanced sand transport in a macrotidal setting, Queen Charlotte Islands, British Columbia, Canada, p. 53–68. *In* Flemming, B. W. and Bartolomä [eds.], Tidal signatures in modern and ancient sediments. Blackwell, Oxford, UK.

Anderson, E. M., and J. R. Lovvorn. 2011. Contrasts in energy status and foraging strategies of White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*). Auk 128:248–257.

Anderson, E. M., J. R. Lovvorn, and M. T. Wilson. 2008. Reevaluating marine diets of Surf and White-winged Scoters: interspecific differences and the importance of soft-bodied prey. Condor 110: 285–295.

Anderson, E. M., D. Esler, W. S. Boyd, J. R. Evenson, D. R. Nysewander, D. H. Ward, R. D. Dickson, B. D. Uher-Koch,

C. S. VanStratt, and J. W. Hupp. 2012. Predation rates, timing, and predator composition for scoters (*Melanitta* spp.) in marine habitats. Canadian Journal of Zoology 90:42–50.

Anteau, M. J., and A. D. Afton. 2008. Using plasma-lipid metabolites to index changes in lipid reserves of free-living Lesser Scaup (*Aythya affinis*). Auk 125:354–357.

Barboza, P. S., and D. G. Jorde. 2002. Intermittent fasting during winter and spring affects body composition and reproduction of a migratory duck. Journal of Comparative Physiology B 172:419–434.

Barrett, R. T. 2002. Atlantic Puffin (*Fratercula arctica)* and Common Guillemot (*Uria aalge)* chick diet and growth as indicators of fish stocks in the Barents Sea. Marine Ecology Progress Series 230:275–287.

Battley, P. F., and T. Piersma. 2005. Adaptive interplay between feeding ecology and features of the digestive tract, p. 201–227. *In* J. M. Starck and T. Wang [eds.], Physiological and ecological adaptations to feeding in vertebrates. Science Publishers, Enfield, NH.

Bednekoff, P. A., and J. R. Krebs. 1995. Great Tit fat reserves: effects of changing and unpredictable feeding day length. Functional Ecology 9:457–462.

British Oceanographic Data Centre [online]. 2010. Gebco gridded global bathymetry data. <http://gebco.net> (22 February 2012).

Brown, P. W., and L. H. Fredrickson. 1997. White-winged Scoter (*Melanitta fusca*), no. 274. *In* A. Poole and F. Gill [eds.], Birds of North America. Academy of Natural Sciences, Philadelphia.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Springer-Verlag, New York.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Cuthill, I. C., S. A. Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. Behavioral Ecology 11:189–195.

Dickson, R. D. 2011. Postbreeding ecology of White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*) in western North America: wing moult phenology, body mass dynamics and foraging behaviour. M.Sc. thesis, Simon Fraser University, Burnaby, BC.

Environment Canada [online]. 2003. Canadian wind energy atlas. <http://www.windatlas.ca/en/index.php> (22 February 2012).

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, CA.

Finlayson, D. P. [online]. 2009. Program Fetch. <https://sites.google.com/site/davidpfinlayson/home/programming/fetch> (22 February 2012).

Gauthier, G., J.-F. Giroux, and J. Bédard. 1992. Dynamics of fat and protein reserves during winter and spring migration in Greater Snow Geese. Canadian Journal of Zoology 70:2077–2087.

Goudie, R. I., and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

Goudie, R. I., and P. C. Ryan. 1991. Diets and morphology of digestive organs of five species of sea ducks wintering in Newfoundland. Journal of the Yamashina Institute of Ornithology 22:1–8.

Guglielmo, C. G., P. D. O'Hara, and T. D. Williams. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free living Western Sandpipers. Auk 119:437–445.

Guglielmo, C. G., D. J. Cerasale, and C. Eldermire. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116–125.

Hamilton, D. J. 2000. Direct and indirect effects of predation by Common Eiders and abiotic disturbance in an intertidal community. Ecological Monographs 70:21–43.

Heath, J. P., W. A. Montevecchi, and G. J. Robertson. 2008. Allocating foraging effort across multiple time scales: behavioral responses to environmental conditions by Harlequin Ducks wintering at Cape St. Mary's, Newfoundland. Waterbirds 31:71–80.

Hepp, G. R., R. J. Blohm, R. E. Reynolds, J. E. Hines, and J. D. Nichols. 1986. Physiological condition of autumn-banded Mallards and its relationship to hunting vulnerability. Journal of Wildlife Management. 50:177–183.

Hodges, J. I., D. Groves, and A. Breault [online]. 2005. Aerial survey of wintering waterbirds in the proposed Nai Kun Wind Farm Project Area of Hecate Strait. <http://alaska.fws.gov/mbsp/mbm/waterfowl/surveys/pdf/Nai%20Kun%202005%20Report.pdf> (22 February 2012).

Iverson, S. A., and D. Esler. 2006. Site fidelity and the demographic implications of winter movements by a migratory bird, the Harlequin Duck. Journal of Avian Biology 37:219-228.

Jenni-Eiermann, S., and L. Jenni. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. Auk 111:888–899.

Krams, I., A. Bērziņš, T. Krama, D. Wheatcroft, K. Igaune, and M. J. Rantala. 2010. The increased risk of predation enhances cooperation. Proceedings of the Royal Society B 277: 513–518.

Lewis, T. L., D. Esler, W. S. Boyd, and R. Žydelis. 2005. Nocturnal foraging behavior of wintering Surf Scoters and White-winged Scoters. Condor 107:636–646.

Lewis, T. L., D. Esler, and W. S. Boyd. 2007. Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. Marine Ecological Progress Series 329:131–144.

Lewis, T. L., D. Esler, and W. S. Boyd. 2008. Foraging behaviors of Surf and White-winged Scoters in relation to clam density: inferring food availability and habitat quality. Auk 125:149–157.

LGL Limited, KS Biological Services, and P.G.E.C. Ltd. [online]. 2009. Technical volume 8 of the environmental assessment application for the Naikun offshore wind energy project: marine birds and sea turtles in the Naikun offshore wind energy project area. <http://a100.gov.bc.ca/appsdata/epic/documents/p230/d29856/1242852284826_65f01eb6ca8c72dd6b6b913184fc3f67b13510f066a1689fbf7098ea323ed76c.pdf> (22 February 2012).

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67:377–385.

Lovvorn, J. R. 1994. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 279/280:223–233.

Lovvorn, J. R., S. E. Richman, J. M. Grebmeier, and L. W. Cooper. 2003. Diet and body condition of Spectacled Eiders wintering in pack ice of the Bering Sea. Polar Biology 26:259–267.

Mason, D. D., P. S. Barboza, and D. H. Ward. 2007. Mass dynamics of wintering Pacific Black Brant: body, adipose tissue, organ, and muscle masses vary with location. Canadian Journal of Zoology 85:728–736.

Palm, E. C., D. Esler, E. M. Anderson, and M. T. Wilson. 2012. Geographic and temporal variation in diet of wintering White-winged Scoters. Waterbirds 35:577–589.

Peach, W. J., D. P. Hodson, and J. A. Fowler. 1992. Variation in the winter body mass of starlings (*Sturnus vulgaris)*. Bird Study 39: 89–95.

Perry, M. C., W. J. Kuenzel, B. K. Williams, and J. A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive Canvasbacks in winter. Journal of Wildlife Management 50: 427–434.

Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. Integrative and Comparative Biology 42: 51–67.

Piersma, T., and J. A. van Gils. 2011. The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour. Oxford University Press, New York.

R Development Core Team [online]. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org> (22 February 2012).

Richman, S. E., and J. R. Lovvorn. 2009. Predator size, prey size, and threshold food densities of diving ducks: does a common prey base support fewer large animals? Journal of Animal Ecology 78:1033-1042.

Rogers, C. M., and A. K. Reed. 2003. Does avian winter fat storage integrate temperature and resource conditions? A long-term study. Journal of Avian Biology 34:112–118.

Savard, J.-P. L. 1979. Marine birds of Dixon Entrance, Hecate Strait and Chatham Sound, B.C. during fall 1977 and winter 1978 (number, species, composition and distribution). Canadian Wildlife Service, Delta, BC.

Seaman, D. A. A., C. G. Guglielmo, R. W. Elner, and T. D. Williams. 2006. Landscape-scale physiology: site differences in refueling rates indicated by plasma metabolite analysis in free-living migratory sandpipers. Auk 123:563–574.

Smith, R. D., and N. B. Metcalfe. 1997. Diurnal, seasonal and altitudinal variation in energy reserves of wintering Snow Buntings. Journal of Avian Biology 28:216–222.

Van Gils, J. A., P. F. Battley, T. Piersma, and R. Drent. 2005. Reinterpretation of gizzard sizes of Red Knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. Proceedings of the Royal Society B 272: 2609–2618.

Wiersma, P., and T. Piersma. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. Condor 96:257–279.

Williams, T. D., C. G. Guglielmo, O. Egeler, and C. J. Martyniuk. 1999. Plasma lipid metabolites provide information on mass change over several days in captive Western Sandpipers. Auk 116:994–1000.

Williams, T. D., N. Warnock, J. Y. Takekawa, and M. A. Bishop. 2007. Flyway-scale variation in plasma triglyceride levels as an index of refueling rate in spring-migrating Western Sandpipers (*Calidris mauri)*. Auk 124:886–897.

Witter, M. S., and I. C. Cuthill. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society B 340:73–92.

Witter, M. S., I. C. Cuthill, and R. H. C. Bonser. 1994. Experimental investigations of mass-dependent predation risk in the European Starling (*Sturnus vulgaris*). Animal Behaviour 48:201–222.

Zimmer, C., M. Boos, N. Poulin, A. Gosler, O. Petit, and J.-P. Robin. 2011. Evidence of the trade-off between starvation and predation risks in ducks. PLoS One 6:e22352.

Žydelis, R., D. Esler, W. S. Boyd, D. Lacroix, and M. Kirk. 2006. Habitat use by wintering Surf and White-winged Scoters: effects of environmental attributes and shellfish aquaculture. Journal of Wildlife Management 70:1754–1762.