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Geographic and Temporal Variation in Diet of Wintering White-winged Scoters

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Abstract.—Quantifying variation in diet over time and space is important for understanding patterns of habitat use in marine birds. Diet composition of adult male White-winged Scoters (*Melanitta fusca*) was quantified at five study sites in coastal British Columbia and Washington during mid-winter (December) and late winter (February-March). At four sites where White-winged Scoters fed in nearshore areas, diet varied little between winter periods and birds fed almost exclusively on large infaunal bivalves (B85% of mean ash-free dry mass of esophagus contents for each season × site combination). The main prey of White-winged Scoters in intertidal foraging areas (N = 3 of 5 study sites) were Varnish clams (*Nuttalia obscurata*), which were introduced to the region within the last 25 years. At an offshore site, diet consisted mainly of bivalves except during one period when White-winged Scoters had consumed mainly fish, crustaceans, polychaetes and echinoderms. Greater temporal variation in diet at the offshore site may have been an effect of reduced time available to locate preferred prey items and lower predictability of prey distributions owing to this site's greater exposure to wind and waves. However, neither exposure nor water depth received appreciable support in models of the dietary fraction of bivalves across sites and periods. Our results underscore the importance of marine areas with high densities of infaunal bivalves to White-winged Scoters, but also show that White-winged Scoters exhibit flexibility to adjust diet in response to differences in prey composition across habitats. *Received 6 June 2012, accepted 22 July 2012.*

Key words.—diet, foraging conditions, marine habitat, *Melanitta fusca*, sea duck, White-winged Scoter.

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Food quality and quantity strongly influence habitat use in birds (Fauchald *et al.* 2000; Dorfman and Kingsford 2001). Density, distribution and type of foods available to birds depend on many underlying physical habitat characteristics, which can vary geographically (Goss-Custard 1984). Within a site, considerable temporal variation in prey abundance or diversity may occur at seasonal, annual or decadal time scales. As food resources vary over space and time, birds often respond by altering diet composition (Karasov 1990; Janssen *et al.* 2009; White *et al.* 2009). The degree to which birds modulate diet composition in response to foraging conditions varies widely across species and populations, and can directly affect energy intake, digestive physiology, body condition, reproductive success and survival (Haramis *et al.*

Lok *et al.* 2008). In areas with high densities of sessile, benthic prey, such as mussel beds, high predator consumption rates throughout winter can lead to prey depletion (Lewis *et al.* 2007; Kirk *et al.* 2008) and may force Surf Scoters to switch to alternative prey (Anderson and Lovvorn 2011). Conversely, past studies indicate that infaunal bivalves are a heavily used food by White-winged Scoters (*M. fusca*) in marine environments, irrespective of season (Anderson *et al.* 2008). However, Anderson *et al.* (2008) also found that the methods used in past studies may have underestimated importance of soft-bodied prey such as polychaetes, fish and some crustaceans. Contemporary data describing wintering White-winged Scoter diets are limited, and very few studies have related White-winged Scoter diet composition to physical habitat conditions (Vermeer and Bourne 1984; Lewis *et al.* 2008).

White-winged Scoters are large-bodied sea ducks that spend most of the year in marine environments across a broad range of northern latitudes. Similar to many other sea ducks, they exhibit high site fidelity during the winter (D. Esler, unpublished data). Although the British Columbia (BC) coastline represents a significant portion of their wintering range along the Pacific Coast of North America, there are few areas in BC where White-winged Scoters occur in appreciable numbers during the winter (Savard 1979). This may be due in part to their assumed preference for habitat conditions that are relatively uncommon in BC: intertidal and shallow subtidal areas with soft benthic substrates (Lewis *et al.* 2008). However, even within such habitats, there is considerable variation in water depth and exposure to wind and waves, which may affect prey selection and diet composition by influencing the relative profitability among a range of prey items (Beauchamp *et al.* 1992; de Leeuw and van Eerden 1992; Heath *et al.* 2008). Greater exposure to wind and waves can increase water currents and turbidity, and in areas with soft, mobile substrates, these conditions may result in unpredictable prey distributions and reduced ability to specialize on infaunal bivalve prey.

We measured diet composition of White-winged Scoters in five wintering areas along the Pacific Coast of BC and Washington during mid- and late winter. Our study sites varied markedly in water depth and exposure. The objectives of this study were to (1) quantify White-winged Scoter diets across a large geographic area, including spatial and temporal variation in diet composition and the size of bivalves consumed, and (2) determine the degree to which diet composition was influenced by physical habitat conditions (i.e. water depth and exposure).

METHODS

Study Sites

We selected five wintering sites along the Pacific coast of BC (Chatham Sound, Dogfish Banks, Baynes Sound and the Fraser River Delta) and Washington (Birch Bay) in which we observed White-winged Scoters feeding in relatively large numbers (Fig. 1). Each site represented a different combination of latitude, water depth and exposure to wind and waves (Table 1), each of which might influence foraging behavior and resulting diet composition (Vermeer and Bourne 1984; Brown and Fredrickson 1997). Baynes Sound, the Fraser River Delta and Birch Bay are characterized by extensive intertidal to shallow subtidal habitat, mainly of water depths <5 m. Like Baynes Sound, Birch Bay offers considerable shelter from rough seas. The Fraser River Delta is more exposed to wind and water currents than

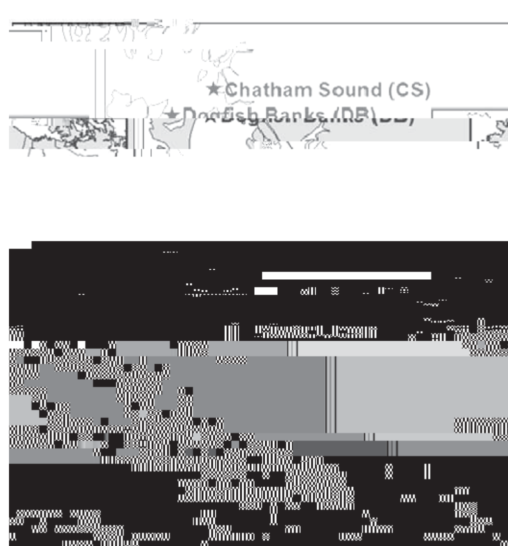

Figure 1. Map of the five study sites in BC and WA for which wintering diets of White-winged Scoters were assessed.

many coastal bays and inlets, but it does not experience frequent high winds and rough seas. Dogfish Banks is a highly exposed, offshore site subject to frequent storms, strong winds and water currents (LGL Limited 2009a). Finally, Chatham Sound is situated between many large islands and the mainland coast, and is more protected from high winds and large waves than Dogfish Banks. Unlike the three southern sites, water depth at which White-winged Scoters fed was high both at Chatham from 80 9 p(4-2(5-30(ECP ot Banks.)T1 Tc0obs.2009a).

Figure 2. Mean percent ash-free dry mass of esophagus contents by prey type for White-winged Scoters collected in five Pacific Coast study sites.

eas. Diets on Dogfish Banks had the highest prey species richness of the five study areas. There were 25 different species of prey in birds collected on Dogfish Banks, 23 in Chatham Sound, twelve each in Birch Bay and the Fraser River Delta, and eleven in Baynes Sound (Table 3). All White-winged Scoters we collected contained either whole bivalves or bivalve shell fragments in their upper gastrointestinal tract. White-winged Scoters consumed over 20 species of bivalves across all sites. Varnish Clams (*Nuttallia obscurata*) were the most frequently consumed bivalve on the Fraser River Delta (92-100% of AFDM), Birch Bay, and in Baynes Sound (55%-71% of AFDM). Hooked Surfclams (*Simomactra falcata*) were the most frequently consumed bivalve species on Dogfish Banks during all three collection periods (16-63% of AFDM). In Chatham Sound, diet composition was slightly more varied than at the three southern sites, and included a wider variety of bivalve species and occasionally echinoderms and gastropods. However, the primary component of scoter diets at Chatham Sound was the small, thick-shelled Divaricate Nutclam (*Acila castrensis*) (63-84% of AFDM). One echinoderm, the Pacific sand dollar (*Dendraster excentricus*) constituted a significant portion of scoter diet on Dogfish Banks during all collection periods (10-18% of AFDM).

The average (±SE) length of bivalves consumed by White-winged Scoters varied according to the dominant species of bivalve consumed in each wintering area (Fig. 3). Shell lengths of ingested bivalves were greatest in Baynes Sound (43.1 ± 1.8 mm) and on the Fraser River Delta (38.7 ± 2.5 mm), two of the sites where Varnish Clams were the main prey item. Conversely, White-winged Scoters in Chatham Sound consumed much smaller bivalves (8.5 ± 0.1 mm). Lengths of bivalves consumed by scoters on Dogfish Banks varied widely within and between bivalve species, but the average length across all species was 18.4 ± 1.3 mm. On Dogfish Banks, Hooked Surfclams consumed by White-winged Scoters averaged 27.5 ± 2.0 mm in length. On Dogfish Banks the average length of Salmon Tellin clams (*Tellina nuculoides*) consumed was 7.9 ± 0.4 mm, and this prey species appeared more frequently in late winter relative to mid-winter diets.

Length classes of bivalves consumed by White-winged Scoters in Baynes Sound and on the Fraser River Delta varied little between winter collection periods, with slight shifts towards smaller bivalves in late winter (Fig. 2). On Dogfish Banks, a marked shift towards consumption of smaller bivalves from mid- to late-winter was due to greater consumption of Salmon Tellin clams in late winter. Average lengths of bivalves were similar during both late winter collection events on Dogfish Banks (February 2009: 12.5 ± 2.1 mm, February 2010: 16.9 ± 2.4 mm), which reflected similar bivalve species composition in diet during these periods. Thus, we pooled bivalve length data from these two collection events in Fig. 3. For Birch Bay, we did not assess lengths of bivalves consumed because of the small number of birds that contained foods at this site.

White-winged Scoter diets in Baynes Sound and on the Fraser River Delta were

Table 3. Foods of White-winged Scoters collected at four sites in BC during 2009-2011. Results include percent frequency of occurrence for pooled esophagus and gizzard contents (%FO), and average percent ash-free dry mass for foods comprising B1% of esophagus contents (%AFDM); a dash indicates that foods were not observed in the sample and t (trace) indicates that foods were present but composed <1% AFDM of esophagus contents. Sample sizes indicate the number of birds that contained food for each category. Relatively few birds in Birch Bay contained foods, and thus those data are not shown here.

	Fraser River Delta				Baynes Sound				Dogfish Banks						Chatham Sound			
	December 2010		February 2011		December 2010		February 2011		February 2009		December 2009		February 2010		December 2009		February 2010	
	N = 14	N = 3	N = 15	N = 7	N = 15	N = 9	N = 15	N = 7	N = 19	N = 8	N = 20	N = 7	N = 19	N = 7	N = 13	N = 9	N = 10	N = 8
	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM
Bivalvia	100	100	100	92	100	99	100	100	100	25	100	82	100	80	100	98	100	85
Nuculidae (*Acila castrensis*)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	84	90	63
Nuculanidae (*Nuculana taphria*)	—	—	—	—	—	—	—	—	5	t	—	—	—	—	8	9	20	—
Pectinidae (*Chlamys rubida*)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Cardiidae	7	—	—	—	7	—	27	—	53	7	100	20	79	—	23	—	40	—
Clinocardium nuttallii	7	—	—	—	—	—	27	—	53	7	100	20	79	—	15	—	40	—
Nemocardium centifilosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—
Clinocardium sp.	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—	—	—	—
Mactridae	7	—	—	—	—	—	—	—	95	16	100	63	84	59	—	—	—	—
Simomactra falcata	—	—	—	—	—	—	—	—	95	16	100	63	84	59	—	—	—	—
Unidentified Mactridae	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cultellidae (*Siliqua patula*)	—	—	—	—	—	—	—	—	16	—	—	—	5	t	—	—	—	—
Tellinidae	—	—	—	—	20	22	20	2	53	1	10	—	21	21	23	5	40	16
Tellina modesta	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—
Tellina nuculoides	—	—	—	—	—	—	—	—	47	1	10	—	21	21	—	—	—	—
Macoma eliminata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	5	40	16
Macoma moesta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	t	—	—
Macoma nasuta	—	—	—	—	20	22	20	2	—	—	—	—	—	—	—	—	—	—
Psammobiidae (*Nuttallia obscurata*)	93	100	100	92	87	55	80	71	—	—	—	—	—	—	—	—	—	—
Semelidae (*Semele rubropicta*)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	—
Veneridae	7	—	—	—	33	22	60	27	26	1	—	—	5	—	15	1	50	6
Compsomyax subdiaphana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	1	20	6
Humilaria kennerleyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—
Protothaca staminea	—	—	—	—	20	15	60	27	21	1	—	—	—	—	—	—	—	—
Saxidomus gigantea	—	—	—	—	13	7	—	—	—	—	—	—	—	—	—	—	—	—
Nutricola tantilla	—	—	—	—	—	—	—	—	5	—	—	—	5	—	—	—	—	—
Unidentified Veneridae	7	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	30	—

Table 3. (Continued) Foods of White-winged Scoters collected at four sites in BC during 2009-2011. Results include percent frequency of occurrence for pooled esophagus and gizzard contents (%FO), and average percent ash-free dry mass for foods comprising B1% of esophagus contents (%AFDM); a dash indicates that foods were not observed in the sample and t (trace) indicates that foods were present but composed <1% AFDM of esophagus contents. Sample sizes indicate the number of birds that contained food for each category. Relatively few birds in Birch Bay contained foods, and thus those data are not shown here.

	Fraser River Delta				Baynes Sound				Dogfish Banks						Chatham Sound			
	December 2010		February 2011		December 2010		February 2011		February 2009		December 2009		February 2010		December 2009		February 2010	
	N = 14	N = 3	N = 15	N = 7	N = 15	N = 9	N = 15	N = 7	N = 19	N = 8	N = 20	N = 7	N = 19	N = 7	N = 13	N = 9	N = 10	N = 8
	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM	%FO	%AFDM
Pinnotheridae	—	—	—	—	7	—	7	—	37	—	42	—	37	t	8	—	10	9
Pinnixa faba	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Pinnixa littoralis																		

New York (McGilvrey 1967) and off the Lithuanian coast (Žalakevicius 1995). No previous studies measured such a large degree of temporal variation in diet composition within a site as we did on Dogfish Banks.

The invasion of the non-native Varnish Clam has greatly impacted White-winged Scoter diets in the three southern sites. Similar to study results from the late 1960s, 1970s, and early 2000s, our data show that White-winged Scoters are bivalve specialists in Baynes Sound and on the Fraser River Delta. However, the proportions of bivalve species consumed at the two sites have changed markedly over time. Specifically, compared to results from these two sites in the late 1960s and 1970s, our results from 2010-2011 show lower species richness of bivalve prey, as well as lower dietary percentages of Pacific littleneck clams (*Protothaca staminea*), Nuttall' compared to those they displayed at the remaining four wintering areas (Palm 2012).

In contrast to results of many studies that show high philopatry in wintering sea ducks (Robertson *et al.* 1999; Robertson *et al.* 2000; Iverson *et al.* 2004), we observed variable numbers and distributions of White-winged Scoters on Dogfish Banks and on the Fraser River Delta between collection events. Consistent with our observations, survey data from recent years at Dogfish Banks showed marked variation in White-winged Scoter densities and distributions (Hodges *et al.* 2005; LGL Limited 2009b). During 2010-2011 we observed only a few hundred White-winged Scoters on the Fraser River Delta, yet many thousands winter at this site in some years. Periods with lower densities of White-winged Scoters at these two sites were characterized by different patterns in their diet: birds consumed lower dietary fractions of bivalves on Dogfish Banks but not on the Fraser River Delta. We speculate that the lower degree of exposure and more stable substrate on the Fraser River Delta allowed White-winged Scoters to be more selective in their diets relative to birds at Dogfish Banks.

Wintering White-winged Scoters share Baynes Sound, the Fraser River Delta, and Birch Bay with large numbers of Surf Scoters, and we observed both species frequently feeding in close proximity to one another. Past data from Birch Bay showed that White-winged Scoters often fed on larger bivalves, likely because of their larger body and bill sizes relative to Surf Scoters (Anderson *et al.* 2008). Past surveys of bivalves in Baynes

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