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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 ($\geq 85\%$ of mean ash-free dry mass of esophagus contents for each season \times site combination). The main prey of White-winged Scoters in intertidal foraging areas ($N = 3$ of 5 study sites) were Varnish clams (*Nuttallia 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.* 1986; Pierotti and Annett 1991; Oro and Furness 2002; Sorensen *et al.* 2009).

For wintering sea ducks that feed primarily on benthic invertebrates in marine environments, diet composition may vary by location, as densities and distributions of available prey types change in relation to physical habitat characteristics (Stott and Olsen 1973; Vermeer and Bourne 1984; Brown and Fredrickson 1997). Birds presumably select prey types based mainly on their profitability, which depends on prey energy content and the bird's ability to detect, capture, handle and digest the prey (Bolnick *et al.* 2003).

There can be considerable variation in foraging strategies and prey consumption between sea duck congeners foraging in the same habitat (Goudie and Ankney 1986; Anderson and Lovvorn 2011). Recent studies of non-breeding Surf Scoters (*Melanitta perspicillata*) showed pronounced diet shifts in late winter from bivalve prey towards seasonally abundant polychaetes and herring spawn (Lacroix *et al.* 2005; Anderson *et al.* 2008;

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

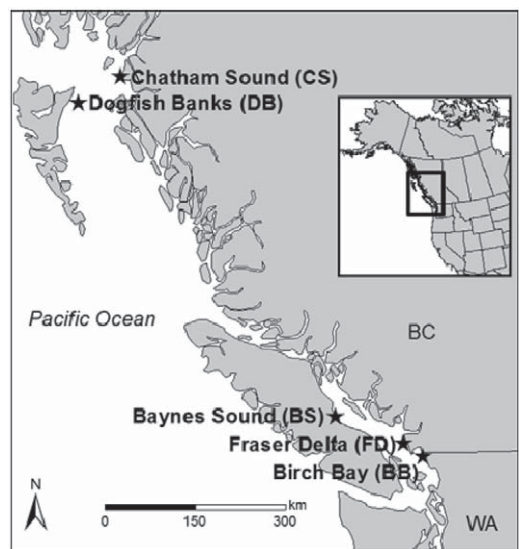


Figure 1. Map of the five study sites in BC and WA for which wintering diets of White-winged Scoters were assessed.

Table 1. Latitude and categorical levels of exposure and water depth for five wintering sites of White-winged Scoters in BC and Washington.

Site	Latitude (°N)	Exposure	Water Depth
Chatham Sound	54.4	Low-Medium	High
Dogfish Banks	54.0	High	High
Baynes Sound	49.6	Low	Low
Fraser River Delta	49.1	Low-Medium	Low
Birch Bay	48.9	Low	Low

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 Sound (5-30 m) and Dogfish Banks (4-20 m) (ECP pers. obs.).

Collection Methods

We collected 155 adult male White-winged Scoters using a shotgun from a small boat, under the authority of permits from Environment Canada (BC-09-0182), U.S. Fish and Wildlife Service (MB111993-0), and Washington Department of Fish and Wildlife (05-608). To assess changes in diet over winter, we collected birds during mid-winter (early December) and late winter (late February-early March) at each study site. There were a total of eleven collection events across the five sites: 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, respectively, and February 2011, N = 15 at both sites), and Birch Bay (December 2005, N = 9 and February-March 2006, N = 8). We attempted to shoot birds that were actively feeding to increase the likelihood that they contained food. Immediately after collection, we removed the esophagus (including the proventriculus and any food items found in the mouth) and gizzard, and preserved the foods they contained separately in 70% isopropyl alcohol for subsequent diet analyses.

Laboratory Analyses

For each sample, we rinsed esophageal contents over a 500- μ m sieve and rinsed gizzard contents over a 2-mm sieve, as gizzard contents were often ground to smaller, less identifiable pieces. Using a 6-10 \times dissecting scope, we sorted and identified all food items to the lowest possible taxon. We used digital calipers to measure length (± 0.1 mm) of whole prey items along the longest axis. For whole prey in esophagi, we measured ash-free dry mass (AFDM) by drying items at 60°C until they reached a constant mass, followed by combustion at 500°C for 8 hr (Ashkenas *et al.* 2004). Subtracting the resulting ash mass from dry mass yielded ash-free

dry mass, which more closely reflects energy value of prey than does wet or dry mass (Ricciardi and Bourget 1998).

We calculated average percent AFDM of each prey category (bivalvia, crustacea, echinodermata, gastropoda, polychaeta, fish) by first assessing the relative percentage of each food category in the esophagus of each bird, and then averaging those percentages across all samples from the respective collection period (Anderson *et al.* 2008). We calculated the average percent of AFDM for esophagi contents only because gizzard contents are known to be biased towards less digestible foods (hereafter, AFDM refers to esophagus contents only; Anderson *et al.* 2008). However, as a measure of prey species richness in White-winged Scoter diets, we calculated percent frequency of occurrence for each prey species by pooling data from esophagi and gizzards. Because pea crabs (Pinnotheridae) live within the mantle of bivalves, or within polychaete worm burrows (Carlton 2007), we assumed that they were ingested incidentally. Thus, we report them separately from other crustaceans and exclude them from results of AFDM.

Data Analyses

We compared the proportion of bivalves in diets of White-winged Scoters across study sites and collection periods using least squares analyses in an information-theoretic context. We used the proportion of bivalves in diets both as an index of diet composition and as the response variable for each model in our candidate set. We did not arcsine transform proportion data, as the proportions of bivalves in diets were not derived from binomial data (Warton and Hui 2011). To test relative support for different *a priori* hypotheses describing possible sources of variation in proportion of bivalves in diets, we pooled diet data from separate collection events in specific ways. Because all explanatory variables were categorical, each linear model represented a different way of grouping data from different collection events for comparisons, allowing considerations of support for each of the factors as drivers of variation in the proportion of bivalves in diets. Below, we justify and describe each of our candidate models.

Exposure. During our collections, we observed that birds at Chatham Sound generally fed 1-3 km from shore, while Fraser River Delta birds foraged 1-5 km from shore. At Birch Bay and Baynes Sound, scoters fed close to shore relative to other sites, almost always <500 m from land and generally much closer. Dogfish Banks was the only offshore wintering area within our study

sites. On average, White-winged Scoters occurred 8 km (range 2-22 km) from shore on Dogfish Banks. 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 exposed to prevailing southeast winds that travel many hundreds of km across Hecate Strait during winter. To determine model groupings, we calculated mean fetch lengths for each site (see Palm 2012 for methods), which served as proxies for the degree of exposure. Mean fetch lengths during winter were 217.5 km at Dogfish Banks, 13.5 km on the Fraser River Delta, 10.6 km at Chatham Sound, 4 km at Baynes Sound and 2.6 km at Birch Bay.

In our exposure model we pooled data into two groups, where the first group included data from collection events on Dogfish Banks and the second group consisted of all data from the remaining sites (Table 2). This model was based on the hypothesis that high exposure on Dogfish Banks would have a separate effect on diet composition than the lower degrees of exposure at the four remaining sites. For our exposure and period model, we used the same data groupings by site but categorized mid-winter data separately from late-winter data to account for any temporal variation in diet (Table 2).

Water Depth. We hypothesized that increased water depth might affect the degree to which White-winged Scoters can specialize on bivalve prey by reducing the amount of time birds can spend at the bottom. To assess the effect of water depth, we pooled data from Dogfish Banks and Chatham Sound separately from the remaining sites. Scoters at Dogfish Banks and Chatham Sound fed exclusively in the subtidal zone at average water depths of 10-15 m and 10-20 m, respectively. Baynes Sound, the Fraser River Delta and Birch Bay all consisted of intertidal and shallow subtidal foraging habitat averaging 2-5 m in depth. For our water depth and period model, we again used the same data groupings by site but categorized mid-winter data separately from late-winter data to account for any temporal variation in diet.

Site and Period Models. We included a site model that grouped data from each wintering site separately, which represented the hypothesis that variation in diet composition was mainly a result of differences in site-specific prey availability. Our period-only model grouped mid-winter data separately from late winter data, irrespective of site; this model assumes that variation in diet composition across all sites was mainly influenced by differences in prey availability from December to February-March. We also included a model that grouped each collection event separately, representing the hypothesis that diet varied in response to both geographic and temporal differences in prey availability. Finally, our null model was based on the hypothesis that bivalve proportions did not vary across collection periods or sites.

Model Selection

We used information-theoretic methods to direct model selection, and for all statistical analyses used Program R (R Foundation for Statistical Computing 2011). To infer the relative support of each model included in the candidate set, we calculated Akaike's Information Criterion adjusted for small sample sizes (AIC_c), ΔAIC_c values, and Akaike weights (w) (Burnham and Anderson 2002). Both ΔAIC_c and w values indicate the relative amount of support for each model compared to other models in the candidate set.

RESULTS

Geographic and Temporal Variation in Diet

Infaunal bivalves were the most commonly consumed prey type for wintering White-winged Scoters at all study sites along the coast of BC and far northern WA (Fig. 2), although the species and size classes of bivalve prey consumed varied among wintering ar-

Table 2. Candidate models describing variation in the proportion of bivalves in diets of male White-winged Scoters across five wintering areas in BC and Washington. CS = Chatham Sound, DB = Dogfish Banks, BS = Baynes Sound, FD = Fraser River Delta, BB = Birch Bay, M = mid-winter, L = late winter, 09 = 2009, 10 = 2010. Number of parameters includes +1 for intercept and +1 for model variance. Candidate models are listed by ΔAIC_c .

Model	Data grouping	Number of parameters	ΔAIC_c	w	r^2
Site and period	CSM; CSL; DBL09; DBM; DBL10; BSM; BSL; FDM; FDL; BBM	11	0.00	0.87	0.51
Exposure	CS = BS = FD = BB; DB	6	5.10	0.07	0.30
Exposure with period	CSM = BSM = FDM = BBM; DBM; CSL = BSL = FDL = BBL; DBL	5	5.44	0.06	0.34
Water depth and period	CSM = DBM; BSM = FDM = BBM; CSL = DBL; BSL = FDL = BBL	5	14.59	0.00	0.25
Site	CS; DB; BS; FD; BB	6	14.60	0.00	0.27
Water depth	CS = DB; BS = DB = BB	3	19.44	0.00	0.13
Period	CSM = DBM = BSM = FDM = BBM; CSL = DBL = BSL = FDL	3	22.65	0.00	0.09
Null	CS = DB = BS = FD = BB	2	27.10	0.00	—

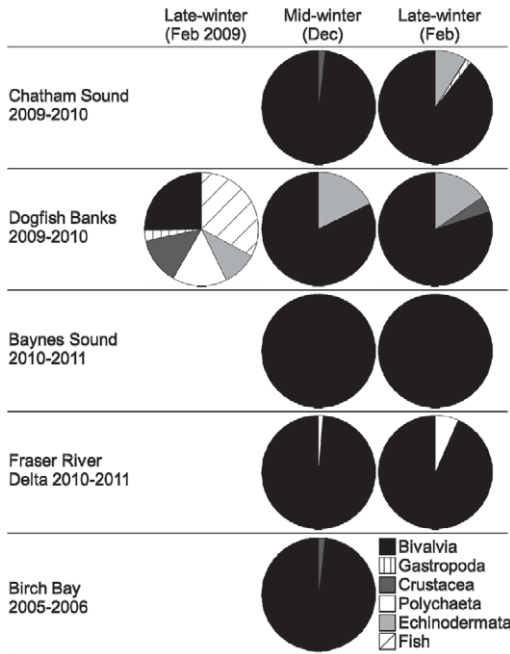


Figure 2. Mean percent ash-free dry mass of esophagus contents by prey type for White-winged Scoters collected in five Pacific Coast study sites.

eat. 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 (*Simomastra 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 (\pm 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 nutculoides*) 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. (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 ≥1% 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		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 = 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
Myidae (<i>Mya arenaria</i>)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hiatellidae (<i>Thesua</i> sp.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—
Gastropoda	7	—	—	—	13	—	—	63	3	20	t	—	—	15	—	60	2
Trochidae (<i>Maganites pupillus</i>)	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Columbellidae	7	—	—	—	—	—	—	—	—	5	—	—	—	8	—	—	—
<i>Alia carnata</i>	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
<i>Alia tuberosa</i>	7	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—
Cerithiidae (<i>Bititium</i> sp.)	—	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—
Muricidae	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nassaridae	7	—	—	—	—	—	—	11	t	—	—	—	—	8	—	20	—
<i>Nassarius mendicis</i>	—	—	—	—	—	—	—	11	t	—	—	—	—	8	—	20	—
<i>Nassarius</i> sp.	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Naticidae (<i>Natica clausa</i>)	—	—	—	—	—	—	—	32	1	—	—	—	—	8	—	60	2
Buccinidae (<i>Nephtaea</i> sp.)	—	—	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—
Conidae (<i>Oenopota</i> sp.)	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	20	—
Olivellidae (<i>Olivella baetica</i>)	—	—	—	—	—	—	—	53	2	10	—	—	—	8	—	20	—
Unidentified Gastropoda	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Crustacea (excluding Pinnotheridae)	7	—	7	—	—	—	—	47	14	55	—	—	—	15	2	20	—
Crangonidae	7	—	7	—	—	—	—	37	1	25	—	—	—	—	—	—	—
<i>Crangon alaskensis</i>	—	—	—	—	—	—	—	32	1	25	—	—	—	—	—	—	—
<i>Crangon nigricauda</i>	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Crangon</i> sp.	—	—	7	—	—	—	—	5	—	—	—	—	—	—	—	—	—
Pasiphaeidae (<i>Pasiphaea pacifica</i>)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Paguridae	7	—	—	—	—	—	—	5	—	—	—	—	—	8	2	10	—
<i>Pagurus caurinus</i>	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Paguridae	—	—	—	—	—	—	—	5	—	—	—	—	—	8	2	10	—
Canceridae (<i>Cancer magister</i>)	—	—	—	—	—	—	—	26	13	40	—	—	—	15	—	20	—

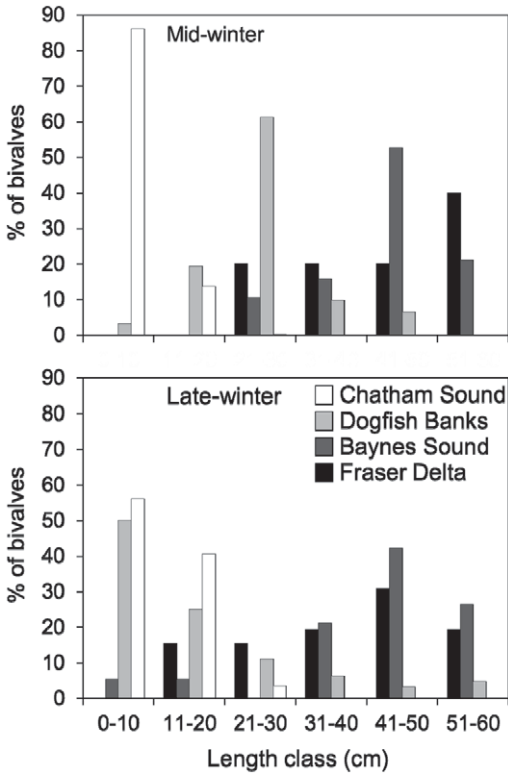


Figure 3. Shell lengths of whole bivalves consumed by White-winged Scoters collected in four sites in BC during mid-winter (December) and late-winter (February) during 2009-2011.

very similar between December and February-March. Conversely, birds on Dogfish Banks and in Chatham Sound fed on a greater diversity of prey items in late winter compared to mid-winter (Fig. 2). On Dogfish Banks during December 2009 and February 2010, scoters consumed primarily bivalves (80-82% of AFDM) and secondarily echinoderms (15-18% of AFDM). However, during February 2009 compared to the other two periods on Dogfish Banks, White-winged Scoters consumed a lower fraction of bivalves and greater fractions of polychaetes, crustaceans, and fish. Notably, Pacific sand lance (*Ammodytes hexapterus*) composed 33% of AFDM during February 2009 on Dogfish Banks. At the same site, Hooked Surfclams composed just 16% of AFDM during February 2009 versus 63% in December 2009 and 59% in February 2010.

Relative Influence of Habitat Conditions on Diet Composition

The most parsimonious model describing variation in the proportion of bivalve prey in diets was the site and period model (Table 2). This model received the most support ($w = 0.87$) from the data relative to the other candidate models and explained 51% of the variation in the data. Bivalves composed >80% of AFDM during all collection periods except February 2009 on Dogfish Banks. During that period, which was highly influential in the model results, bivalves composed just 25% of AFDM while four other categories of prey each composed >10% of AFDM (Fig. 2). No other models received substantial support; however, each of these remaining models outperformed the null model, indicating that site, period, exposure and water depth each explained some of the variation in the proportion of bivalves in diet.

DISCUSSION

Our study was consistent with past results indicating that infaunal bivalves were an important prey type for White-winged Scoters across wintering sites (Yocum and Keller 1961; Grosz and Yocum 1972; Stott and Olson 1973; Hirsch 1980; Vermeer and Bourne 1984; Anderson *et al.* 2008). Species composition of bivalves in diets varied considerably across study sites, presumably reflecting differences in availability among sites. At most of our study sites, feeding mainly on bivalves appeared to be a seasonally stable foraging strategy for White-winged Scoters. However, White-winged Scoters showed flexibility to consume alternative prey during one collection event (February 2009 on Dogfish Banks), presumably in response to temporal changes in food availability. Most notably, birds during this collection event consumed appreciable amounts of fish and echinoderms, which have not previously been described as major parts of their diets. Only two other studies documented fish consumption in wintering White-winged Scoters; specifically, scoters consumed sand lance (*Ammodytes* sp.) in Long Island Sound,

New York (McGivrey 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's cockles (*Clinocardium nuttallii*) and introduced Manila clams (*Venerupis philippinarum*) (Vermeer and Bourne 1984). In 2010-2011, Baynes Sound birds contained no Manila clams. Conversely, in this same site, Manila clams occurred in 53% of White-winged Scoters in 1968 and constituted nearly 30% of the dry weight of fecal shell fragments of White-winged Scoters in 2001-2004 (Lewis *et al.* 2007). The Varnish Clam, an Asian species that was not present on the Pacific coast of North America 25 years ago, is now the main food item of White-winged Scoters at Baynes Sound and Birch Bay, and is almost the sole component of their diets on the Fraser River Delta. These clams did not appear in White-winged Scoter diets on Dogfish Banks or in Chatham Sound, probably because they occur mainly in intertidal habitats that we did not consider for these two sites (Dudas 2005). Varnish Clams were likely introduced to Vancouver Harbor in the late 1980s to early 1990s and have since spread north along Vancouver Island and south into Puget Sound and the southern coast of Oregon (Gillespie *et al.* 1999). The ability to reproduce within a year of recruitment, compared to 2-3 years for most native bivalves, has aided dispersal throughout the region, where they reach densities of up to 800/m² (Dudas 2005).

A combination of high densities, low crushing resistance (D. Esler, unpublished data), and high flesh-to-shell ratio relative to other bivalve prey make Varnish Clams a high quality food for White-winged Scoters. Past research in Baynes Sound indicated that distributions of White-winged Scoters were positively associated with densities of Varnish Clams (Žydelis *et al.* 2006). Further, Varnish Clam distributions may influence current trends in habitat use by moulting Surf and White-winged scoters in the Fraser River Delta and parts of Puget Sound (Tschaekofske 2010). Other introduced bivalve species have appreciably altered the diets of diving ducks. Notably, Lesser Scaup (*Aythya affinis*) in San Francisco Bay prefer *Corbula amurensis* clams, an Asian species that was introduced in 1986 (Poulton *et al.* 2002).

Our results were strongly influenced by the February 2009 collection event on Dogfish Banks, during which White-winged Scoters fed on a much higher proportion of non-bivalve prey types than during the other collection events. The site and period model received the most support in the candidate set because it was the only model that separated data from this collection event into its own group. Largely as a result of the February 2009 collection event, diet composition on Dogfish Banks was the most temporally variable of the five wintering areas in our study. This may have reflected temporal changes in the profitability of bivalves at this site. Most notable during the February 2009 collection event on Dogfish Banks was that roughly one-third of birds contained fish in their esophagus or gizzard. Although our exposure models did not offer high explanatory power, high exposure on Dogfish Banks may have constrained consumption of bivalves in two ways. Specifically, periods of extreme wind and waves may reduce foraging time and thus the ability of White-winged Scoters to locate preferred prey items (Lima 1986), while the mobile sand-gravel substrate (LGL Limited 2009a) of this site likely reduces the predictability of prey distributions. White-winged Scoters on Dogfish Banks met this pronounced seasonal variation in diet with different physiological responses

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 Sound found that most (72%) Varnish Clams were 25-45 mm in length (Lewis *et al.* 2007), a size range commonly consumed by White-winged Scoters but larger than most bivalves consumed by Surf Scoters (Anderson *et al.* 2008). White-winged Scoters may avoid potential competition with Surf Scoters by targeting larger sizes of bivalves, which are relatively abundant in Baynes Sound and Birch Bay (Lewis *et al.* 2007; Anderson 2009). Unlike these two areas, the Fraser River Delta serves as a major moulting site for both White-winged and Surf Scoters with up to 10,000 total scoters present each

year during July to September (J. R. Evenson, Washington Department of Fish and Wildlife, unpublished data). Heavy use of the Fraser River Delta during moult may deplete bivalves and other prey in some years, thereby contributing to lower numbers of wintering White-winged Scoters at this site.

Population declines in many sea duck species in recent decades have prompted research intended to identify potential causes for these declines. Because White-winged Scoters spend a majority of their annual cycle in marine environments, identifying important marine habitats should be a priority. Our diet results underscore the importance marine areas with high densities of infaunal bivalves to White-winged Scoters, and also show that White-winged Scoters exhibit flexibility to adjust diet in response to changes in food availability across habitats.

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