Trophic, energetic, and physiological responses of wintering white-winged scoters (*Melanitta fusca*) to habitat variation

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Eric Charles Palm

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Name: **Eric Charles Palm**

Degree: **Master of Science**

Title of Thesis: ***Trophic, energetic, and physiological responses of wintering white-winged scoters (Melanitta fusca) to habitat variation***

Examining Committee:

Chair: Dr. D. Green, Professor

Dr. R. Ydenberg, Professor, Senior Supervisor
Department of Biological Sciences, S.F.U.

Dr. D. Esler, Adjunct Professor
Department of Biological Sciences, S.F.U.

Dr. T. Williams, Professor
Department of Biological Sciences, S.F.U.

Dr. E. Anderson, Instructor
British Columbia Institute of Technology

Dr. P. Baird, Research Associate
External Examiner
Department of Biological Sciences, S.F.U.

Date Defended/Approved: April 20, 2012

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Abstract

I examined diet, body condition, morphology, and physiology of white-winged scoters in relation to widely varying habitat conditions among wintering sites along the Pacific coast of British Columbia and northern Washington. White-winged scoters mainly consumed bivalves across all study sites, but showed flexibility to consume alternative prey in response to temporal changes in food resources. Scoters wintering at a highly exposed and unpredictable offshore site had higher lipid and body masses and different digestive morphology than birds at less exposed sites. Baseline corticosterone and plasma metabolites did not vary in response to differences in habitat conditions across sites. Collectively, these results suggest that wintering white-winged scoters achieve physiological homeostasis by varying diet, endogenous reserves, and gut morphology in response to differences in winter feeding sites.

Keywords: diet; energy management; habitat conditions; physiology; sea ducks; white-winged scoter

To my grandparents, Charles and Esther Oviatt.

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1. Introduction

1.1. Thesis Background

Animals in all habitats must be responsive to an array of factors, including physical habitat attributes, food availability and quality, climate, and densities of predators and competitors (Lima 1986, Hamilton 2000). Habitat use presumably reflects trade-offs among these different conditions and their variation across space and time. As habitat conditions vary, they can have direct and indirect effects on an individual's behaviour, physiological status and energy management, either through adjustments in strategy or through imposed constraints.

Climate and predation danger are two important habitat conditions influencing energetics and physiology in birds, and responses to these factors offer a good example of strategic trade-offs that birds employ. Both climate and predation danger vary widely across space and time. Colder temperatures during winter can increase costs of thermoregulation, which in turn affect energy management (Goudie and Ankney 1986, Lovvorn 1994a). Wintering birds in some areas build fat reserves that can be used during food shortages or prolonged bouts of harsh weather (Olsen and Cox 2003). Similarly, many studies suggest that birds inhabiting areas with unpredictable or variable food sources increase body fat to buffer against the greater risk of starvation (Smith and Metcalfe 1997, Rogers and Reed 2003). However, maintaining greater fat reserves may require an increase in foraging effort, which can increase the likelihood of predation by reducing vigilance effort (Lima 1986). Increased fat reserves also may reduce mobility needed to evade predators by increasing wing loading. In shorebirds, there is considerable evidence that stopover areas represent different trade-offs between food availability and predation danger, and habitat use may be influenced by size of fuel reserves and ability to evade predators (Ydenberg et al. 2002, Pomeroy et al. 2006). The extent to which body condition changes throughout the winter varies widely across latitudes and across different species of waterfowl (Hohman and Weller 1994). To increase chances of surviving winter and emerging in optimal condition for subsequent annual cycle stages, wintering birds must balance predation danger with the risk of starvation (Lima 1986, Witter and Cuthill 1993).

For diving waterfowl, water depth and the degree of exposure to wind and waves also may influence physiological responses. Studies show that variation in water depth affects the amount of time spent foraging, which influences overall foraging profitability and can have subsequent physiological and energetic effects (Lovvorn 1994b, Lovvorn et al. 1996). In a study of feeding harlequin ducks, birds exposed to increased wind and waves shortened dive duration and decreased their foraging effort, which affected overall energy expenditure (Heath et al. 2008)

Diet composition is both a response to food availability and another factor influencing physiology and energy management (Karasov 1990, Janssen et al. 2009). Seasonal or spatial variation in diet composition affects energy intake and digestive physiology (McWilliams and Karasov 2001), and has also been shown to influence body condition in wintering sea ducks (Lovvorn et al. 2003). Further, diet can be used to infer foraging strategies across different habitats. Individuals in areas with stable abundances of preferred prey items, many sea ducks feed mainly on those predictable, readily available prey species. In less productive habitats, some sea duck species increase food intake rates or target specific prey types of higher energetic content to meet demands (Goudie and Ankney 1986).

In response to variation in diet or seasonal energy requirements, birds can quickly modify digestive morphology (McWilliams and Karasov 2001, McWilliams and Karasov 2005). Overall gut size and length can vary in response to changes in prey quality or prey intake rate (McWilliams and Karasov 2005). Increased digestive organ sizes also may allow birds to maximize energy assimilation in areas with poor food quality or low food availability, even if food intake rates do not increase. Gizzard size may be dependent on prey type and size. Marine birds feeding on larger, hard-shelled prey items may need larger gizzards to process food than those feeding on smaller or soft-bodied prey (van Gils et. al 2005). However, a change in gut size may not always be a result of diet composition or quality (Dykstra and Karasov 1992, McWilliams et al. 1999). For example, birds may temporarily increase gut size to maximize digestive efficiency to build reserves prior to migration or in anticipation of cold weather and increased thermoregulatory costs upon arrival at breeding grounds (Piersma and Lindstrom 1997). In many migratory species, strategic reductions in gut size function to reduce wing loading and increase flight efficiency during long-distance migration (Piersma and Gill 1998).

In addition to digestive morphology, plasma metabolites can help indicate variability in habitat conditions such as food availability and quality (Haramis 1986, Johnson 2007). Traditional indices of condition such as size-adjusted body mass and body composition provide indications of the current physiological state of an individual. However, these indices do not indicate the trajectory of an individual's energetic state (Anteau and Afton 2008). Recent studies suggest that plasma metabolite analyses are effective tools in understanding the timing and degree of energy acquisition (Williams et al. 1999, Williams et al. 2007, Anteau and Afton 2008). While body composition analyses reflect changes to nutrient reserves across individuals over days to months, plasma metabolites reflect changes over minutes to hours within an individual. Of particular interest in this study are levels of triglycerides, β-hydroxybutyrate, and uric acid.

Increased triglyceride concentrations in plasma reflect lipid accumulation, while elevated concentrations of β-hydroxybutyrate indicate lipid catabolism (Anteau and Afton 2008). If foraging conditions deteriorate or food availability decline through winter, one might expect to see increasing β-hydroxybutyrate concentrations or decreasing concentrations of triglycerides (Anderson and Lovvorn 2008). Interpretation of plasma uric acid concentration requires consideration of body mass and composition data, as uric acid can reflect elevated dietary protein or protein catabolism (Robin et al. 1987).

Corticosterone is a metabolic hormone released into the bloodstream in response to environmental challenges such as a predatory attack or changes in energetic needs, or food availability (Marra and Holberton 1998, Cockrem 2002). Baseline levels of corticosterone are considered those that are sufficient for animals to carry out normal physiological functions and maintain energetic balance (Romero 2004), and increasingly have been used to infer habitat conditions (Marra and Holberton 1998, Homan et al. 2003). Although baseline corticosterone can be endogenously regulated, it also can vary in response to variation in habitat conditions. In particular, elevated baseline corticosterone may indicated increased predation danger (Clinchy et al. 2004), or decreased food availability and foraging conditions (Buck et al. 2007, Kitaysky et al. 2007).

1.2. Study Species

Where species-specific data are available, numerical trends of white-winged scoters (*Melanitta fusca*) and surf scoters (*M. perspicillata)* at wintering sites along the Pacific coast differ markedly, indicating different ecologies and a need for separate management strategies. Compared to surf scoters, white-winged scoters inhabit far fewer wintering sites in appreciable numbers, yet few studies have specifically addressed factors underlying habitat use of white-winged scoters during the non-breeding period. Recent work on winter ecology of white-winged scoters on the Pacific coast has occurred in relatively protected sites where birds foraged in shallow water, often in close proximity to surf scoters and to potential predators (Lewis et al. 2005, Lewis et al. 2007, Anderson et al. 2008, Anderson and Lovvorn 2011, Lewis et al. 2008, Žydelis et al. 2006). However, a considerable portion of wintering white-winged scoters forages in sites with relatively deep water and a higher degree of exposure to wind and waves (Vermeer and Bourne 1984, Žydelis et al. 2006). In contrast to bays and inlets, these areas may present different site-specific costs and benefits, including differences in predictability of foraging conditions, foraging profitability, degree of predation danger and thermoregulatory costs. It is unclear how white-winged scoters adjust foraging and energy management strategies in response to variation in these trade-offs.

1.3. Conservation Rationale

Physiological and energetic responses to variation in habitat conditions can have direct effects on waterfowl survival, as well as indirect consequences through cross-seasonal effects (Haramis et al. 1986). On wintering grounds, survival rates may decline in response to many habitat changes, including an increase in predator density or a decrease in energy intake due to prolonged harsh weather. Energy management and condition in winter can influence the amount of energy that animals carry over into subsequent seasons (Schoener 1987, Webster et al. 2002). Retention of energy reserves across seasons is particularly important for migratory species because they encounter a wide range of habitats in which conditions vary considerably (Raveling and Heitmeyer 1989). Conditions at wintering areas influence timing of departure and body condition in waterfowl during the ensuing spring migration (Bearhop et al. 2004), which can affect reproductive performance (Lack 1968, Ankney and MacInnes 1978, Rohwer 1992, Perrins 1996). Consequently, habitat conditions at wintering and staging areas may influence overall breeding success, which has subsequent effects on fitness and population dynamics (Jönsson 1997, Anteau and Afton 2004, Anteau and Afton 2008).

Geographic variation in habitat conditions affects the functional value of different sites for individual bird species. Understanding variation in habitat value and function can help identify factors that make sites more or less suitable for a given species and can help determine the range of viable sites that should be considered in protection strategies.

Specifically for white-winged scoters, population declines in recent decades have prompted research to identify potential causes for these declines. White-winged scoters spend a majority of their annual cycle in marine environments, which increasingly are altered for development. By understanding responses to natural habitat variation, we can better predict their responses to future habitat alteration caused by humans.

1.4. Thesis Objective

The purpose of my thesis was to examine effects of habitat conditions on diet, body condition, morphology, and physiology across a number of sites covering a large geographic area and a high degree of variation in conditions. I hypothesized that differences in site-specific costs and benefits across the study area would be reflected in differences in diet, energy management strategies, and physiology. To capture temporal variation in measures of diet and physiological performance throughout the winter, I collected data during two separate time periods at each site. I aimed to identify specific responses to habitat variability that allow white-winged scoters to function under a variety of conditions.

1.5. Thesis Outline

I considered variation in a number of indicators within one stage of the annual cycle, which provides a broader perspective on relationships between habitat conditions and physiology and energetics than examining any single indicator on its own.

In Chapter 2, my first data chapter, I examined spatial and temporal variation in white-winged scoter diet composition over a wide geographic scale and, in subsequent chapters, used these data to determine whether energetics, physiology, or digestive morphology were influenced by diet. I also provided a general assessment of changes in white-winged scoter prey landscapes at two sites by comparing my results to those from past studies.

In Chapters 3 and 4, I considered several factors as potential influences on measures of body condition, physiology and digestive morphology. I determined whether energy management varied in response to varying habitat conditions, endogenously regulated seasonal changes, or both. Using data from corticosterone and plasma metabolites, I assessed whether energy management strategies across sites were largely successful in achieving a physiological homeostasis or if birds in certain areas or periods were physiologically compromised. Additionally, in Chapter 4, I confirmed the utility of a methodological approach to identify baseline corticosterone in lethally collected birds.

In Chapter 5, I presented general conclusions from each of my data chapters, how they relate, and suggested future directions to expand upon this research.

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2. Geographic and temporal variation in diet of wintering white-winged scoters

2.1. Introduction

Food quality and quantity strongly affect habitat use in many species of 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). Even within a particular site, there can be considerable temporal variation in available food resources. 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, Sorenson et al. 2009).

For wintering sea ducks that feed primarily on benthic invertebrates in marine environments, diet composition often varies 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). Sea ducks, like all birds, presumably feed mainly upon prey types that are most profitable. Prey profitability depends on prey energy content and the bird’s ability to detect, capture, handle and digest the prey (Bolnick et al. 2003). Although the optimal foraging theory states that specializing on the most profitable foods will maximize energy gain (Stephens and Krebs 1986), the profitability of specific prey types for individual birds varies across space and time.

There can be considerable variation in foraging strategies and prey consumption between sea duck congeners foraging in the same habitat (Anderson et al. 2008).

Recent studies of non-breeding surf scoters (*Melanitta perspicillata*) show 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 a mussel beds, high predator consumption rates throughout winter can lead to prey depletion and force surf scoters to switch to alternative prey (Lewis et al. 2007, Kirk et al. 2008). Conversely, past studies indicate that bivalves are a highly profitable and important food of white-winged scoters (*M. fusca*) in marine environments across a variety of sites, irrespective of season (Anderson et al. 2008). However, Anderson et al. (2008) also found that the methods used in these 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 very 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, unpubl. 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 preference for shallow, subtidal foraging areas with soft substrate, which are relatively uncommon in BC (Lewis et al. 2008). However, even within such habitats, there is considerable variation in prey available to white winged scoters, and in water depth and exposure to wind and waves. Variation in water depths may affect prey selection by influencing profitability of different prey items (Beauchamp et al. 1992, de Leeuw and van Eerden 1992). Increased exposure to wind and waves may affect diet composition, as harsh weather conditions could limit foraging opportunity or shorten dive duration (Heath et al. 2008), which may preclude scoters from forgoing foods that are usually less profitable than bivalves. Further, 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 bivalve prey.

We measured diet composition of white-winged scoters in five wintering areas along the Pacific Coast of BC and WA during mid- and late winter. Our study sites varied markedly in water depth and exposure. The objectives of this study were (1) to quantify white-winged scoter diets across a large geographic area, including spatial and temporal variation in diet composition and bivalve size, and (2) to determine the degree to which diet composition was influenced by general habitat conditions (water depth and exposure) independent of site.

2.2. Methods

2.2.1. Study Sites

We selected sites in which we observed white-winged scoters feeding in relatively large numbers. Each site represented a different combination of latitude, water depth, and exposure to wind and waves (Table 1), each of which might influence foraging behaviour 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 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 is high both at Chatham Sound (5-30 m) and Dogfish Banks (4-20 m) (E. Palm, pers obs.).

2.2.2. Collection Methods

We collected 155 adult male white-winged scoters using a shotgun from a small boat at five wintering areas along the Pacific Coast of BC (Chatham Sound, Dogfish Banks, Baynes Sound, and the Fraser River Delta; Fig. 1), 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) at each study site. There were a total of 11 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.

2.2.3. Laboratory Analyses

For each sample, we rinsed the esophagus contents over a 500-µm sieve and rinsed gizzard contents over a 2-mm sieve. Using a 6−10× dissecting scope, we sorted and identified all food items to the lowest possible taxon. We used digital calipers to measure shell length (±1 mm) of whole prey items along the longest axis. For whole prey in esophagi, we assessed ash-free dry mass by drying items at 60ºC until they reached a constant mass, followed by combustion at 500ºC for 8 hours (Ashkenas et al. 2004). Subtracting the resulting ash mass from dry mass yields ash-free dry mass, which more closely reflects energy content of prey than does wet or dry mass (Ricciardi and Bourget 1998).

We calculated average percent ash-free dry mass (hereafter, AFDM refers to ash-free dry mass of esophagus contents only) 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 (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.

2.2.4. 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. 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 models each of our candidate models.

2.2.4.1. 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 within 500 m of land and generally much closer. Dogfish Banks was the only offshore wintering site 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 subjected to rough seas from prevailing winds that blow out of the southeast for hundreds of kilometers across Hecate Strait during winter. To determine model groupings, we calculated mean fetch lengths for each site (see Chapter 3 for methods), which served as proxies for the degree of exposure. Mean fetch lengths during the 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, in which 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, used the same data groupings by site, but also categorized mid-winter data separately from late-winter data to account for any temporal variation in diet (Table 2).

2.2.4.2. Water Depth

We hypothesized that increased water depth might affect specialization on bivalve prey by limiting the amount of time birds spend at the bottom of their dives searching for bivalves buried within the sediment. To group collection data by 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. We also included a second water depth model that accounted for temporal variation in the proportion of bivalves in diets.

2.2.4.3. Site and Period Models

We included a site model that grouped data from each wintering area 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 assumed 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, based on the idea that diet varied in response to both geographic and temporal differences in prey availability. Finally, our null model was based on the hypothesis that diet did not vary across collection periods or sites.

2.2.5. 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.

2.3. Results

2.3.1. Geographic and Temporal Variation in Diet

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, although the species and size classes of bivalve prey consumed varied among wintering areas. 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, with 23 in Chatham Sound, 12 each in Birch Bay and on the Fraser River Delta, and 11 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 contained 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. 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*). 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 bivalve consumed by white-winged scoters varied according to the dominant species of bivalve consumed in each wintering area (Fig. 2). 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), and in both sites varnish clams were the main prey item. Conversely, white-winged scoters in Chatham Sound consumed much smaller bivalves (8.5 ± 0.1 mm), including mainly divaricate nutclams. 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. Hooked surfclams consumed by birds on Dogfish Banks averaged 27.5 ± 2.0 mm in length (range: 10.5–52.9 mm). The average length of salmon tellin clams (*Tellina nuculoides*), which were more frequently consumed by Dogfish Banks birds during late winter relative to mid-winter, was 7.9 ± 0.4 mm.

Length classes of bivalves consumed by white-winged scoters varied little between winter collection periods in Baynes Sound and on the Fraser River Delta, 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 (Feb 2009: 12.5 ± 2.1 mm, Feb 2010: 16.9 ± 2.4 mm), which reflected similar bivalve composition in diet during these periods. Thus, we pooled bivalve length data from these two collection events in Figure 2. We did not include bivalve length data from Birch Bay in Figure 2 due to very low sample sizes of whole bivalves at this site.

White-winged scoter diets in Baynes Sound and on the Fraser River Delta were very similar between mid-winter and late winter. Conversely, birds on Dogfish Banks and in Chatham Sound fed on a wider variety of prey items during late winter (Fig. 1). Dogfish Banks diets were markedly different in February 2009 compared to December 2009 and February 2010. In both collection periods on Dogfish Banks during winter 2009-2010, scoters consumed primarily bivalves (82-85% of AFDM), as well as smaller quantities of echinoderms (15-18% of AFDM). However, the proportion of bivalves in scoter diets was substantially lower during February 2009, when birds consumed greater numbers of polychaetes, crustaceans and fish. Notably, Pacific sand lance (*Ammodytes hexapterus*) composed 33% of AFDM, while bivalves only composed 25% of AFDM.

Hooked surfclams composed just 16% of AFDM of esophagus contents during February 2009 versus 63% in December 2009 and 59% in February 2010.

2.3.2. 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), indicating that the proportion of bivalves varied across sites and through winter. This model received the most support (w = 0.79) from the data relative to the other candidate models and explained 49% 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. 1). The exposure and period model had a ΔAIC_c score of 2.75 and explained 32% of the variation in the data, but had low support (w = 0.20) relative to the top model. No other models received substantial support; however, each of these remaining models outperformed the null model, indicating that site, period and water depth each explained some of the variation in the proportion of bivalves in diet.

2.4. Discussion

Our study is consistent with past results indicating that bivalves are 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). We demonstrate that species composition of bivalves in diets varies considerably by site, presumably reflecting availability of bivalves. At most marine sites, feeding primarily on bivalve prey is a seasonally stable foraging strategy for white-winged scoters. However, white-winged scoters showed flexibility to consume alternative prey in response to temporal changes in food resources. Most notably, birds during some collection events consumed appreciable amounts of echinoderms and fish, 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

(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 a non-native clam has had a considerable impact on white-winged scoter diet 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 relative proportions of different bivalve species consumed at the two sites have changed markedly over time (Vermeer and Bourne 1984, Lewis et al. 2007). Compared to results from the late 1960s and 1970s, we found a smaller variety of bivalve prey at both sites in 2010-2011, including lower percentages of Manila clams (*Venerupis philippinarium*), Pacific littleneck clams (*Protothaca staminea*), and Nuttall's cockles (*Clinocardium nuttallii*) (Vermeer and Bourne 1984). Baynes Sound birds collected in 2010-2011 contained no Manila clams, a species that occurred in 53% of samples from Baynes Sound in 1968 and constituted nearly 30% of the wet weight of fecal shell fragments from white-winged scoters captured in Baynes Sound in 2001-2004. The varnish clam, an Asian species that was not present on the west coast of North America 25 years ago, is now the main food item at Baynes Sound and Birch Bay, and is almost the sole component of white-winged scoter diets on the Fraser River Delta. These clams are unlikely to appear in white-winged scoter diets on Dogfish Banks or in Chatham Sound, as they occur mainly in intertidal habitats. 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/m^2 (Dudas 2005).

A combination of high densities, low crushing resistance (D. Esler, unpubl. data) and high flesh ratio relative to other bivalve prey make varnish clams an ideal food for white-winged scoters. Past research in Baynes Sound found that densities of varnish clams were positively associated with densities of white-winged scoters (Žydelis et al. 2006) and Tschaekofske (2010) suggested that the presence of varnish clams may have influenced current trends in habitat use by both surf and white-winged scoters in the

Fraser Delta and Puget Sound. In addition to varnish clams, there are other instances of diving ducks altering diet in response to recently introduced bivalve species. Most 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).

We did not find strong support for the idea that either exposure or water depth on their own directly influenced the proportion of bivalves in diet. However, 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 any 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. The February 2009 collection event made diet composition on Dogfish Banks the most temporally variable of the five wintering areas in our study. This may have reflected temporal changes in profitability or availability of bivalves on Dogfish Banks. Most notable during the February 2009 collection event was that roughly one-third of birds collected on Dogfish Banks contained fish in their esophagus and/or gizzard. Although our exposure models did not offer high explanatory power, high exposure on Dogfish Banks potentially reduced foraging opportunity during some periods (Lima 1986). Combined with a mobile sand-gravel substrate (LGL Limited 2009a), exposure to high winds and waves likely resulted in an unpredictable foraging environment, which may have contributed to temporally variable diet composition at this site. Pronounced temporal variation in diet composition on Dogfish Banks influenced different physiological responses relative to those at other wintering areas (Chapter 3), and may have contributed to variable distributions and densities of feeding white-winged scoters between years.

In contrast to results from many studies that showed high philopatry in wintering sea ducks (Robertson et al. 1999, Robertson et al. 2000, Iverson et al. 2004), numbers and distributions of white-winged scoters on Dogfish Banks were inconsistent across years. In some periods, presumably those with relatively low bivalve availability, Dogfish Banks supported fewer white-winged scoters, much like those we observed during February 2009 collections (Hodges 2005, LGL Limited 2009b), when overall densities were considerably lower than during both collection events the following winter (M. T. Wilson, pers. obs.). Conversely, distributions and densities of white-winged scoters in

Baynes Sound were remarkably similar in both the mid- and late-winter collection events. These results suggest that bivalve densities were high enough that prey depletion was not a major issue in Baynes Sound, and they corroborate results of Lewis et al. (2008) who concluded that Baynes Sounds represents high quality, predictable foraging habitat. Although the fraction of bivalve prey in white-winged scoter diets on the Fraser River Delta was consistently high in both collection events, the site unexpectedly had the lowest densities of white-winged scoters of the five wintering areas. This observation, coupled with an observed decrease in overall numbers of birds from December to February and pronounced shifts in bird distribution throughout the winter suggested that bivalve densities and/or distributions may be more variable on the Fraser River Delta than in Baynes Sound and nearby Birch Bay.

Wintering white-winged scoters share Baynes Sound and the Fraser River Delta with large numbers of surf scoters, and both species were frequently observed feeding in close proximity to one another. Surf scoters also were present on Dogfish Banks and Chatham Sound, but occurred in relatively small numbers and in different areas than white-winged scoters. Past data from Birch Bay and Puget Sound showed that in foraging areas where the two species coexisted and potentially shared many of the same sources of prey, white-winged scoters often fed upon larger bivalves, likely because of their larger body and bill sizes relative to surf scoters (Anderson et al. 2008). In the same study, bivalves ≥25 cm in length composed ≤4% of total bivalve prey for surf scoters in Birch Bay and Puget Sound, compared to nearly half (45%) of total bivalve prey for white-winged scoters. Past surveys of bivalves in Baynes Sound found that a majority (72%) of varnish clams were 25-45 mm in length (Lewis et al. 2007), an ideal size for white-winged scoters but too large for most surf scoters. White-winged scoters may largely avoid potential competition for food resources with surf scoters by targeting larger size classes of bivalves, which are relatively abundant in Baynes Sound (Lewis et al. 2007) and likely in Birch Bay. 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 in late summer and early fall (E. M. Anderson and J. R. Evenson, unpubl. data). Heavy use during this time period may deplete prey resources for wintering birds, resulting in lower numbers of white-winged scoters. It is possible that the Fraser River Delta also provides lower densities of large bivalves relative to Baynes Sound and Birch Bay, which may result in relatively lower quality foraging habitat.

2.5. Tables and Figures

Table 1. Latitude and categorical levels of two habitat conditions for five wintering sites of white-winged scoters in BC and WA.

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

Table 2. Candidate models describing variation in proportion of bivalves in diets of male white-winged scoters across five wintering areas in BC and WA. 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.

Explanatory Variable	**Site and Period Grouping**	**K**	**ΔAIC_c**	**w**	**r^2**
site and period	CSM; CSL; DBL09; DBM; DBL10; BSM; BSL; FDM; FDL; BBM	11	0.00	0.79	0.49
exposure and period	CSM=BSM=FDM=BBM; DBM; CSL=BSL=FDL=BBL; DBL	5	2.75	0.20	0.32
water depth and period	CSM=DBM; BSM=FDM=BBM; CSL=DBL; BSL=FDL=BBL	5	8.41	0.01	0.26
exposure	CS=BS=FD=BB; DB	6	10.81	0.00	0.18
period	CSM=DBM=BSM=FDM=BBM; CSL=DBL=BSL=FDL	3	15.36	0.00	0.12
site	CS; DB; BS; FD; BB	6	16.16	0.00	0.20
water depth	CS=DB; BS=DB=BB	3	16.26	0.00	0.11
null	CS=DB=BS=FD=BB	2	21.28	0.00	-

Table 3. Foods of white-winged scoters collected at four sites in BC during winters of 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 included below.

	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	–	–	–	7	–	27	–	53	7	100	20	79	–	15	–	40	–
Nemocardium centifilosum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
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).

	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
Myidae (*Mya arenaria*)	–	–	–	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–
Hiatellidae (*Tresus sp.*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
Gastropoda	7	–	–	–	–	–	13	–	63	3	20	t	58	–	15	–	60	2
Trochidae (*Magarites pupillus*)	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–
Columbellidae	7	–	–	–	–	–	–	–	–	–	5	–	–	–	8	–	–	–
Alia carnata	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–
Alia tuberosa	7	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
Cerithiidae (*Bittium sp.*)	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–
Muricidae	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nassaridae	7	–	–	–	–	–	–	–	11	t	–	–	16	–	8	–	20	–
Nassarius mendicus	–	–	–	–	–	–	–	–	11	t	–	–	16	–	8	–	20	–
Nassarius sp.	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Naticidae (*Natica clausa*)	–	–	–	–	–	–	–	–	32	1	–	–	32	–	8	–	60	2
Buccinidae (*Neptunea sp.*)	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–
Conidae (*Oenopota sp.*)	–	–	–	–	–	–	–	–	5	–	–	–	5	–	–	–	20	–
Olivellidae (*Olivella baetica*)	–	–	–	–	–	–	–	–	53	2	10	–	16	–	8	–	20	–
Unidentified Gastropoda	–	–	–	–	–	–	–	–	–	–	5	t	5	–	–	–	–	–
Crustacea (excluding Pinnotheridae)	7	–	7	–	–	–	–	–	47	14	55	–	37	4	15	2	20	–
Crangonidae	7	–	7	–	–	–	–	–	37	1	25	–	19	4	–	–	–	–
Crangon alaskensis	–	–	–	–	–	–	–	–	32	1	25	–	19	4	–	–	–	–
Crangon nigricauda	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crangon sp.	–	–	7	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–
Pasiphaeidae (*Pasiphaea pacifica*)	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–
Paguridae	7	–	–	–	–	–	–	–	5	–	–	–	–	–	8	2	10	–
Pagurus caurinus	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified Paguridae	7	–	–	–	–	–	–	–	5	–	–	–	–	–	8	2	10	–
Cancridae (*Cancer magister*)	–	–	–	–	–	–	–	–	26	13	40	–	32	–	15	–	20	–
Pinnotheridae	–	–	–	–	7	–	7	–	37	–	42	–	37	t	8	–	10	9
Pinnixa faba	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–
Pinnixa littoralis	–	–	–	–	–	–	–	–	32	–	–	–	–	–	–	–	–	–
Pinnixa tubicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	9
Pinnixa sp.	–	–	–	–	7	–	–	–	5	–	–	–	–	–	–	–	–	–
Faba subquadrata	–	–	–	–	–	–	–	–	26	–	35	–	37	t	–	–	–	–

Table 3 (continued).

	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**
Unidentified Pinnotheridae	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–
Unidentified Amphipoda	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
Unidentified Crustacea	7	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–
Polychaeta	–	–	7	8	13	1	–	–	11	15	–	–	–	–	–	–	10	t
Nephtyidae (*Nephtys sp.*)	–	–	7	8	13	1	–	–	11	15	–	–	–	–	–	–	–	–
Unidentified Polychaeta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	t
Echinodermata	–	–	–	–	–	–	–	–	26	10	45	18	37	15	–	–	20	4
Dendrasteridae (*Dendraster excentricus*)	–	–	–	–	–	–	–	–	26	10	45	18	37	15	–	–	–	–
Ophiuridae (*Ophiura sarsi*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	4
Fish	–	–	–	–	–	–	–	–	32	33	5	–	–	–	–	–	–	–
Ammodytidae (*Ammodytes hexapterus*)	–	–	–	–	–	–	–	–	26	33	–	–	–	–	–	–	–	–
Unidentified Fish	–	–	–	–	–	–	–	–	5	–	5	–	–	–	–	–	–	–

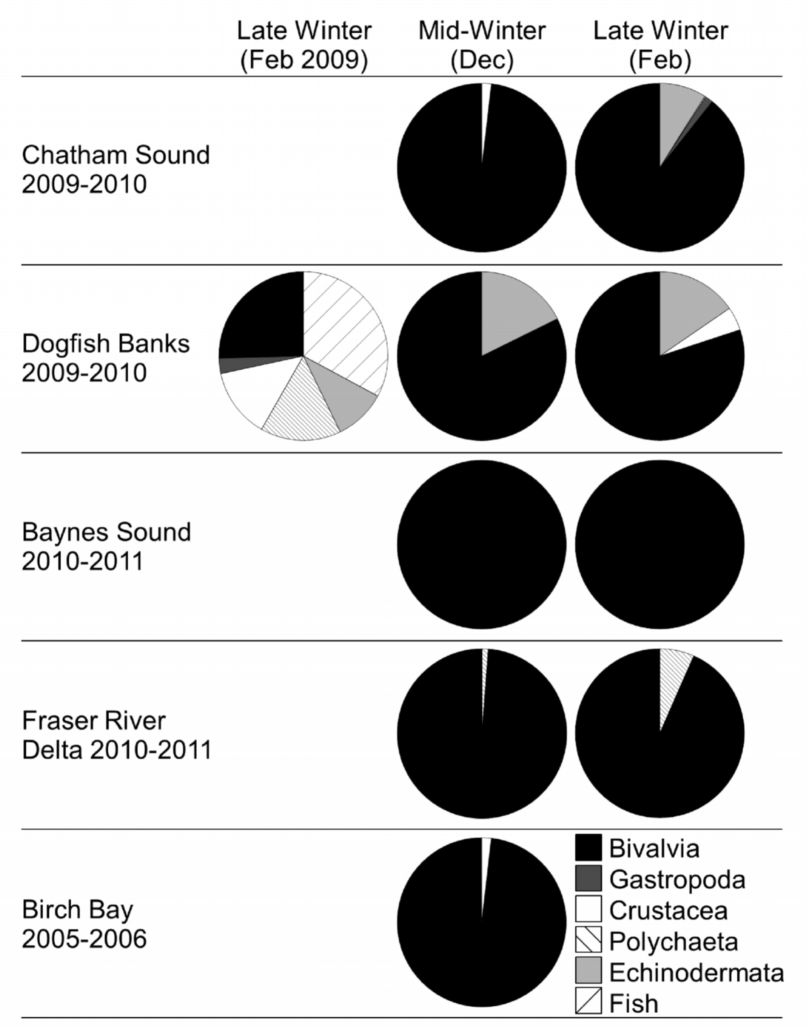

Figure 1. Average percent ash-free dry mass of esophagus contents by prey type for white-winged scoters collected in five Pacific Coast study sites.

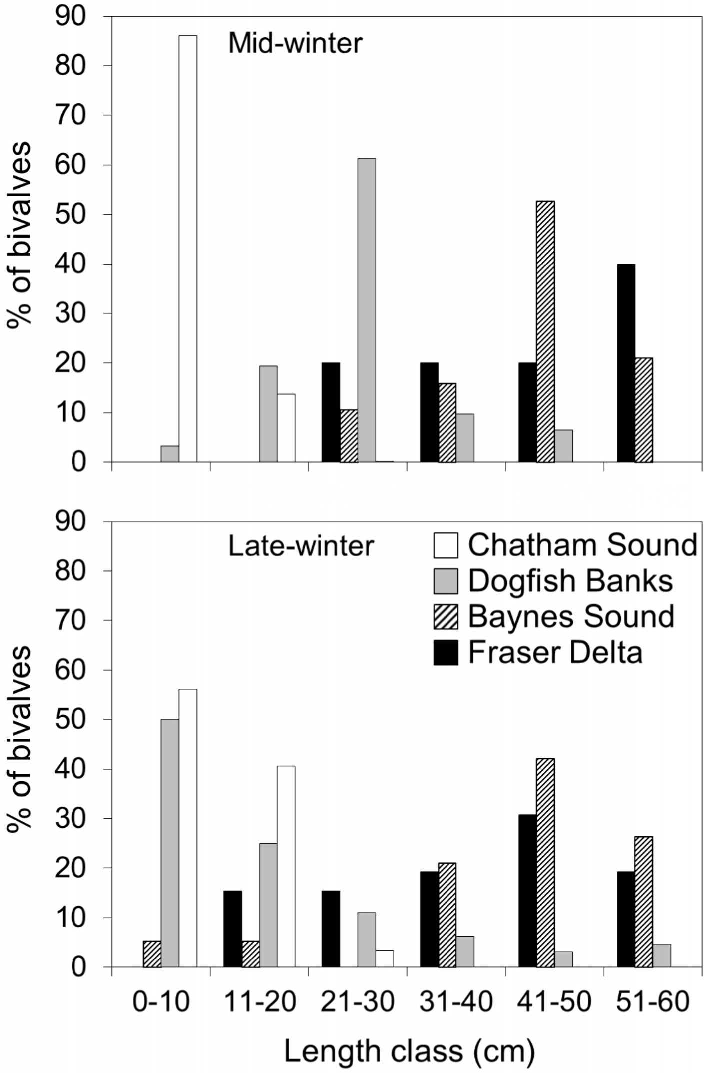

Figure 2. Shell lengths of whole bivalves consumed by white-winged scoters collected in four sites in BC during mid-winter (December) and late winter (February) during 2009-2011.

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3. Geographic variation in physiology and energy management strategies of wintering white-winged scoters

3.1. Introduction

Throughout the annual cycle, birds must be responsive 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 physiology and energy management strategies in birds (Cuthill et al. 2000).

To increase chances of surviving winter and emerging in optimal condition for subsequent annual cycle stages, 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 season and habitat conditions that affect foraging conditions. For example, lipid reserves can be used to buffer against food shortages or to meet costs during periods of increased thermoregulatory demands associated with harsh weather (Smith and Metcalfe 1997, Cuthill et al. 2000, Rogers and Reed 2003). However, maintaining large lipid reserves may require an increase in foraging effort and also may reduce mobility needed to evade predators, which can increase the likelihood of predation (Lima 1986, Bednekoff and Krebs 1995, Cuthill et al. 2000). Birds are generally presumed to balance these trade-offs by employing adaptive strategies of energy management that maximize winter survival and provide sufficient reserves for current and subsequent stages of their annual cycle. Such strategies vary depending on the suite of local habitat conditions. In migratory waterfowl, conditions at wintering areas influence the timing of departure and body condition during the ensuing migration and breeding season (Bearhop et al. 2004).

Measures of body mass and composition have long been used to make inferences about difference in foraging conditions among sites (Gauthier et al. 1993, Hepp et al. 1986, Anderson and Lovvorn 2011). However, in light of the potential costs and benefits of storing reserves described above, higher body and lipid masses do not necessarily indicate better individual condition or higher habitat quality. Body mass and nutrient reserves instead may be optimized to reflect trade-offs associated with local conditions (Lima 1986, Krams et al. 2010, Zimmer et al. 2011). More recently, studies have used plasma metabolites as an additional tool for measuring metabolic response to foraging conditions (Jenni-Eiermann and Jenni 1994, Anteau and Afton 2008). Unlike static measures of nutritional status, such as lipid mass, plasma metabolites can reflect changes in energy status over a very short period of time (hours to days) and provide information on rates of energy acquisition and depletion (Jenni-Eiermann and Jenni 1994). Specifically, triglyceride (TRIG) concentrations in plasma reflect the rate of lipid accumulation, while concentrations of β-hydroxybutyrate (BOHB) indicate the rate of lipid catabolism (Anteau and Afton 2008). Interpretation of plasma uric acid concentration requires consideration of body mass and composition data, as high concentrations of uric acid can reflect either elevated dietary protein or protein catabolism (Robin et al. 1987).

Digestive morphology can also be used as an indicator of variability in foraging conditions. Birds modify digestive morphology in response to seasonal energy requirements, as well as the quantity and types of food they ingest (Piersma and van Gils 2010). Gizzard size and mass varies considerably in relation to prey type and size. Birds feeding on larger, hard-shelled prey items require larger gizzards to process food than those feeding on smaller or soft-bodied prey (Goudie and Ryan 2001, van Gils et. al 2005). Changes to gut size and length can be interpreted in many ways. In response to unpredictable food availability, birds may increase food intake rate during foraging bouts, which requires a larger or longer gut to maintain digestive efficiency (Piersma 2002, Piersma and van Gils 2010). Increased length or mass of the small intestine may also allow for higher nutrient assimilation in areas with poor food quality or low food availability, even if food intake rates do not differ. In either case, maintaining a larger gut is energetically expensive. Birds presumably adjust gut size to balance potential costs and benefits associated with digestive capacity, and these trade-offs may vary with annual cycle stage or local habitat conditions (Piersma and van Gils 2010).

Birds can also endogenously regulate 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, and reflect energy management strategies at an optimized, evolutionary scale. Variations in this pattern, or the absolute levels of body mass, can be proximately influenced by local conditions (Mason et al. 2007).

Different 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 a number of indicators within one stage of the annual cycle provides a broader perspective on relationships between habitat characteristics and physiology than examining any single indicator on its own.

We measured body mass and composition, digestive morphology, and plasma metabolite concentrations of free-living white-winged scoters (*Melanitta fusca*) from five wintering areas along the coast of British Columbia (BC) and Washington (WA) (Fig. 1). Our study sites varied markedly in habitat conditions, including prey types and diversity, exposure, water depth and predation danger (Chapter 2). We assumed that differences in exposure would affect the degree of predictability across sites, both in terms of weather and foraging conditions. We expected that different local conditions at these sites would contribute to geographic variation in physiology and energy status. Further, we predicted that birds using sites with less predictable foraging conditions would have higher body mass and lipid levels, under the expectation that larger fat reserves would buffer against periods of low food availability or poor foraging conditions (Cuthill et al. 2000, Rogers and Reed 2003). At offshore versus nearshore sites, we expected increased exposure to harsh weather conditions would result in greater thermoregulatory costs, increased rates of food intake and fat catabolism, and elevated levels of plasma TRIG and BOHB. We predicted minimal variation in uric acid across sites, as we did not expect that any birds would face long-term food deprivation that would result in varying rates of muscle catabolism. Finally, we expected that during collection events characterized by a lower degree of specialization on bivalve prey and a higher dietary fraction of soft-bodied foods, we would find lower gizzard masses, intestine masses, and intestine lengths.

White-winged scoters are sea ducks that spend the majority of the year in marine environments across a broad range of northern latitudes. Although the 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 high concentrations during the winter (Savard 1979). This may be due in part to their preference for soft-bottom habitats with large standing stocks of bivalves, which are relatively uncommon in BC. However, even within these habitats, areas used by wintering white-winged scoters vary in available prey types and in a number of conditions, including exposure to wind and waves, water depth and predation danger. We tested whether diets or any of these habitat conditions were related to measures of physiology in wintering white-winged scoters. Widespread population declines in some sea duck species, including white-winged scoters, have prompted efforts to identify functions of habitats used throughout the annual cycle (e.g., Zydelis et al. 2006, Lewis et al. 2008, Anderson and Lovvorn 2011). Our study aims to identify the relative influence of different habitat conditions on white-winged scoter energy management and physiology by examining variation in physiological responses over a wide geographic area.

3.2. Methods

3.2.1. *Study Sites*

Each study site (Fig. 1) represented a different combination of three physical habitat conditions we assessed for their influence on physiological measures: exposure to wind and waves, water depth, and predation danger (Table 1). Dogfish Banks (53°55'N, 131°30'W) 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, Dogfish Banks is a wintering area for tens of thousands of white-winged scoters (Hodges 2005); however, overall abundance and density of wintering sea ducks at Dogfish Banks fluctuates widely between years (Hodges 2005, LGL Limited 2009, M. T. Wilson, pers. comm.).

Along the Pacific Coast, most white-winged scoters winter in somewhat protected nearshore areas. Dogfish Banks is a notable exception because it is an offshore site subject to strong winds and water currents. 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 sand-gravel mixture, these conditions result in a frequently changing benthic foraging habitat. Water depths on the study site 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 a wintering population of hundreds of 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. Birds at Chatham Sound feed in deep water (5-30 m), searching for prey in sandy and muddy substrate situated between rock outcrops (E. Palm, pers obs.).

Baynes Sound (49°39'N, 124°53'W), contains extensive intertidal flats and high densities of wild and cultured bivalves, providing near-shore habitat for approximately 6500 white-winged and surf scoters during winter months (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 show relatively low overall observed foraging effort, Baynes Sound is thought to be high quality foraging habitat

(Lewis et al. 2007, Lewis et al. 2008). Compared to Chatham Sound, this area contains more shallow water habitat, a greater abundance of large bivalves and more protection from high winds and swells.

Thousands of white-winged scoters use the shallow intertidal mudflats on the Fraser River Delta (49°06’N, 123°16’W), annually for moulting, wintering, and staging (E. M. Anderson and J. R. Evenson, unpublished data). However, overall numbers on the Fraser River Delta during winter 2010-2011 were relatively low compared to those at other wintering areas, ranging from approximately 400-600 in December to approximately 200-300 in February (E. Palm, pers. obs.). The area offers less shelter from unfavorable weather than Baynes Sound and nearby Birch Bay. Unlike Chatham Sound, Baynes Sound and Birch Bay, it offers very few potential perches for bald eagles (*Haliaeetus leucocephalus*), which are the most likely predator of white-winged scoters.

Birch Bay (48°55’N, 122°45’W) is a small bay located at the northern extent of Puget Sound characterized by extensive intertidal mudflats and seagrass beds (Anderson and Lovvorn 2011). The bay offers considerable shelter from rough seas and has high densities of bivalves. Approximately 1000 white-winged scoters winter in Birch Bay annually (Anderson and Lovvorn 2011).

3.2.2. Sample Collection

We collected a total of 138 adult male white-winged scoters using a shotgun from a small boat at four wintering areas along the coast of BC (Fig. 1), under the authority of permits from Environment Canada (BC-09-0182) and Simon Fraser University Animal Care (992B-06). There were a total of 9 collection events across the four 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). For analyses of body mass, lipid mass and gizzard mass, we included data from 17 birds previously collected at Birch Bay, WA (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. We verified age class and sex based on plumage, which clearly distinguished after-hatch-year males from all other cohorts (Brown and Fredrickson 1997). We sampled blood within 10 min of collection, and removed the upper gastrointestinal tract within fifteen 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 esophagus and gizzard for use in analyses of digestive morphology and diet. We centrifuged whole blood within 8 hr of collection to separate plasma and cells and stored all tissues at –20 ºC until further analyses.

3.2.3. Analyses of Body Composition and Digestive Morphology

The Long Point Waterfowl's Avian Energetics Lab (Port Rowan, Ontario) conducted measurements of intestine length (±0.1 cm) and intestine mass (±0.1 g), and analyses of body composition (total protein, lipid, water, and ash) of ingesta-free dry carcass mass including plumage using methods described by Afton and Ankney (1991). As in 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. Structural body size, which we estimated separately using measurements of culmen, wing cord, tarsus, and the first principal component of all three, was not correlated with total lipid mass (all $r^2 < 0.05$), and explained less than 11% of variation in body mass. Therefore, we did not correct lipid mass or body mass for body size.

3.2.4. Plasma metabolite assays

For all metabolite assays, we used a microplate spectrophotometer to read samples out of 400 ml flat-bottom, 96-well polystyrene microtitre plates. To calculate plasma TRIG concentrations, we measured total TRIG (TRIG + glycerol) and glycerol by endpoint assay (Williams et al. 1999, Guglielmo et al. 2002, Anteau and Afton 2008) and subtracted glycerol from total TRIG. We used an endpoint assay to measure uric acid (Bentzen et al. 2008) and a kinetic assay to measure BOHB (Guglielmo et al. 2005, Anteau and Afton 2008). We calculated intra- and inter-assay variations of 3.03% and 7.26%, respectively, for TRIG, 2.04% and 10.28% for BOHB and 1.81% and 3.55% for UA.

3.2.5. Diet analyses

As in Chapter 2, we calculated average percent ash-free dry mass (hereafter, AFDM refers to ash-free dry mass of esophagus contents only) 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 also measured shell length (±1 mm) of whole bivalves along the longest axis.

3.2.6. Data analyses

We compared measures of body mass and composition, digestive morphology and plasma metabolites across study sites and collection periods using least squares analyses in an information-theoretic context. We pooled data from separate collection events in specific ways to test relative support for different 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 collection events for comparisons (Table 1), allowing 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 deep water sites, 2) mid-winter shallow water sites, 3) late-winter deep water sites, and 4) late-winter 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 also 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). 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 might directly influence variation in digestive morphology.

Similar to many other sea ducks, white-winged scoters exhibit high site fidelity during the winter (D. Esler, unpubl. data). We worked under the assumption that white-winged scoters remained at each study site throughout the winter with limited movements beyond a local scale, and that variation in different physiological measures largely reflected variation in site-specific habitat conditions and the overall degree of predictability at each site. Although we had no direct measure of predictability at each site, each of our candidate models addressed different factors that could potentially contribute to overall predictability. Below, we describe and justify our predictions for effects of diet composition and three habitat conditions on physiology, body composition, and digestive morphology.

3.2.6.1. Diet Composition

In the absence of prey availability data, we used diet composition as an indicator of prey availability during each of the collection events (Barrett 2002). Diet composition can affect body condition in a number of ways, as prey sources 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 bivalve prey. Bivalves composed 80-85% of AFDM during late-winter 2010 at Chatham Sound, as well as during both Dogfish Banks collection events from winter 2009-2010 (Chapter 2). During February 2009 at Dogfish Banks, bivalves only represented 25% of AFDM, as birds consumed relatively high amounts of fish and polychaetes. In the first diet composition model, we separated data from this February 2009 collection event at Dogfish Banks from all other collection events. Based on 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 relative proportion of bivalve prey in each collection event: (1) medium: Dogfish Banks February 2009, (2) high: Dogfish Banks December 2009, Dogfish Banks February 2010, Chatham Sound

February 2010, (3) very high: Chatham Sound December 2009, Baynes Sound, Fraser River Delta, Birch Bay (Table 1).

3.2.6.2. Exposure

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 within 500 m of land and generally much closer. Dogfish Banks was the only offshore wintering site within our study sites (Table 1). On average, white-winged scoters occurred 8 km (range 2-22 km) from shore at 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 subjected to rough seas from prevailing winds that blow out of the southeast for hundreds of km across Hecate Strait during winter. There is evidence that the presence and relative predictability of wind can affect body and lipid mass in birds (Peach et al. 1992, Witter et al. 1994, Cuthill et al. 2000). Average wind speed (calculated at 30 m above the sea surface) during winter at Dogfish Banks was 19.3 kts, compared to 16.6 kts at Chatham Sound and 10-12 kts at Baynes Sound, the Fraser River Delta and Birch Bay (Canadian Wind Energy Atlas, Environment Canada, 2003).

We used a combination of average wind speed and average fetch length as a proxy for the degree of exposure at each study site. In ArcMap 10 (ESRI 2011), we calculated the geographic centre of collection locations at each study site. At each site's geographic centre, we used Program Fetch (https://sites.google.com/site/davidpfinlayson/Home/programming/fetch, 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 at a site may affect behaviour and energetics in foraging sea ducks (Heath et al. 2008). We used data from the Canadian Wind Energy Atlas to determine the average proportion of time wind blows from each of 12 cardinal directions throughout the winter. For each bearing, we multiplied the fraction of time the wind blows from that direction by its associated fetch length, and 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 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 first exposure model, we pooled data into two groups, in which the first group included data from collection events at Dogfish Banks (high exposure), and the second group consisted of all data from the remaining 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 would have a similar influence on physiology, and that exposure at Dogfish Banks would have a separate effect. Our second exposure model, which pooled data into three groups, still grouped Dogfish Banks data by itself (high exposure), but allowed that birds wintering at Chatham Sound and 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).

3.2.6.3. Water Depth

Variation in water depth across wintering areas has been shown to affect foraging profitability in diving ducks, which can have subsequent physiological and energetic effects (Lovvorn 1994). We used bathymetry data from the General Bathymetric Chart of the Oceans (General Bathymetric Chart of the Oceans, 2010) to estimate water depth at the location of each collected bird. From these values, we estimated average water depth at each study site. 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. To group collection data by water depth, we pooled data from Dogfish Banks and Chatham Sound separately from the remaining sites. We also included 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. Grouping collection data 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 would have more of an impact energetically on foraging white-winged scoters than day length, and therefore did not include a day length model in our candidate set.

3.2.6.4. Predation Danger

Variation in the degree of predation danger across our study sites may have influenced the average size of lipid reserves birds maintained at each site, as well as overall foraging behaviour and food consumption (Lima 1986, Rogers 1987, Zimmer et al. 2011). White-winged scoters wintering in Baynes Sound, Chatham Sound and Birch Bay often foraged in close proximity to forested land or exposed rock outcrops with high densities of bald eagles. Conversely, there were very few potential eagle perches at the Fraser River Delta and virtually no eagle presence at Dogfish Banks. For predation danger models, data from the Fraser River Delta and Dogfish Banks were pooled separately from all other data, which we pooled together in a second group (Table 2). As with exposure and water depth, we included a predation model that allowed for temporal variation in response variables.

3.2.7. 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.

3.3. Results

3.3.1. Body mass and composition

White-winged scoter lipid mass declined from mid- to late-winter at all study sites (Fig. 2), consistent with winter lipid dynamics of many waterfowl. The largest declines occurred at Dogfish Banks, where birds lost an average (±SE) of 81 ± 20 g of lipid mass from December 2009 to February 2010. Baynes Sound birds had the lowest average lipid mass during both mid-winter (160 ± 13 g) and late-winter (112 ± 12 g), while birds collected at Dogfish Banks had the highest mean lipid mass 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 essentially all support (*w* = 1.0) from the data relative to the other candidate models and explained 52% of the variation in the data.

Declines in lipid mass from mid- to late-winter at all sites accounted for a large portion of the observed declines in total body mass, which occurred at all sites except Baynes Sound (Fig. 2a). Although lipid mass decreased from mid- to late-winter at Baynes Sound, composition analyses from this site showed that birds collected during late-winter had higher protein mass than birds collected in mid-winter, which roughly offset losses in lipid mass and resulted in stable body mass across periods. Birds at Dogfish Banks had the highest body mass (1968 ± 30 g) in mid-winter relative to other sites, and also experienced the greatest body mass declines throughout the winter (89 ± 43 g) (Fig. 2). The best supported model of body mass (Table 2) was the 2-level exposure and period model (*w* = 0.62), 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 only described 10% of the variation in body mass. The 3-level exposure and period model also explained 10% of body mass variation, but received less support in terms of ΔAIC_c and *w* values (Table 2). There was little evidence that lipid or body masses varied in response to either water depth or predation danger

3.3.2. Plasma metabolites

Average concentrations of plasma BOHB increased from mid- to late-winter at Dogfish Banks, Baynes Sound and Fraser River Delta, but not at Chatham Sound (Fig. 2). The most parsimonious model describing variation in BOHB was the period model, which divided all collection data into a mid-winter group and a late-winter group, regardless of geography and habitat conditions (Table 2). However, this model explained <10% of the variation in BOHB. There was a high degree of model uncertainty; 3 other models, all of which accounted for temporal variation in BOHB throughout the winter, had ΔAIC_c values ≤2.

There was little evidence that TRIG concentrations varied in response to habitat conditions (Fig 2). The three-level exposure model was the most parsimonious, yet only marginally outperformed the null model. Greater than 92% of the variation in TRIG was not explained by any of our candidate models. For data describing variation in UA, the water depth model was the most highly supported model ($w = 0.31$) in the candidate set, yet it only explained 2% of the variation in the data. The null model ($\Delta AIC_c = 1.35$) was the second most supported model ($w = 0.16$), indicating that neither diet composition, habitat conditions nor period had an appreciable effect on UA. The average UA concentration across all sites and periods was 1.58 ± 0.04 mmol/L.

3.3.3. Digestive morphology

Intestine mass did not vary in response to habitat conditions, as the null model outperformed both diet models (Fig. 3, Table 3). Conversely, variation in intestine length was correlated with diet, with longer intestines during February 2009 on Dogfish Banks corresponding to a lower fraction of bivalves in diet (Fig. 3, Table 3). The two-level diet model that separated February 2009 at Dogfish Banks from all other collection events was the most parsimonious, and explained 42% of the variation in intestine length. Average intestine length at Dogfish Banks during February 2009 (268 ± 1 cm) was 45 cm longer than at all other collection events (223 ± 2 cm) (Fig. 3). The top supported 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 correlation between increased diet composition and lower gizzard mass.

3.4. Discussion

Overall, we found geographic and temporal variation in a number of physiological indices, suggesting that white-winged scoters exhibit considerable phenotypic plasticity during the winter. This flexibility allows white-winged scoters to use a variety of marine habitats, and to balance potential trade-offs associated with wintering in each area. White-winged scoters employed different energy management strategies across wintering areas depending on local habitat conditions. Lipid mass declined at all sites throughout the winter, suggesting that body composition was endogenously regulated to some degree. However, the magnitude of lipid levels and the decline through winter varied by site, which we interpret as an effect of differences in local habitat conditions at each site.

Our results suggest that the degree of exposure across study sites was the most important factor contributing to variation in both body mass and lipid mass. Likely consequences of high exposure at Dogfish Banks were limited foraging opportunity during periods of extreme winds and high thermoregulatory costs relative to other wintering areas (Wiersma and Piersma 1994). We hypothesize that birds built the largest lipid reserves at Dogfish Banks to buffer against these conditions. Average body and lipid masses from December 2009 at Dogfish Banks were among the highest published values for white-winged scoters during any part of the annual cycle (Brown and Fredrickson 1997, Dickson, 2011). Accumulating large lipid stores early in the season appeared to be an effective energy management strategy at Dogfish Banks; averages of both lipid mass and body mass at Dogfish Banks during February 2010 were remarkably consistent with those from February 2009, suggesting birds targeted a site-specific optimal body mass for late-winter given local conditions. Although our predation danger models explained very little variation in lipid and body mass, birds at Dogfish Banks face virtually no danger of a predatory attack and may have avoided incurring some of the potential cost normally associated with carrying higher mass.

In contrast to Dogfish Banks, Baynes Sound likely provided the most predictable foraging conditions for white-winged scoters. Specifically, relative to Dogfish Banks, Baynes Sound has relatively low exposure and shallow water depths. Baynes Sound likely required lower foraging effort relative to Dogfish Banks, and resulted in the lowest lipid masses during both periods across all sites. In Baynes Sound, costs of maintaining high levels of endogenous reserves, which include a greater danger of predation, may outweigh the benefits.

Results of intestine length and gizzard mass provide further corroboration that physiology varied in response to the degree of predictability in foraging conditions. Increased unpredictability at Dogfish Banks may have forced birds to consume atypical prey during periods of low bivalve availability. The collection event during February 2009 may have been an example of such a period, as diet composition included markedly higher proportions of fish, polychaetes and crustaceans than during other periods (Chapter 2). Higher diet diversity during this period corresponded to longer intestine lengths (but not higher intestine mass), which may have functioned to increase energy assimilation from lower quality foods (Battley and Piersma 2005). Gizzard masses likely varied with a combination of diet composition and the average size of bivalves consumed. At Dogfish Banks, low gizzard masses were likely a result of higher proportion of soft-bodied prey relative to other sites, as well as smaller bivalve sizes relative to southern sites (Chapter 2). Relatively low gizzard masses at Chatham Sound during both collection periods probably reflected the small size of their primary prey source, *Acila castrensis,* despite the fact that mid-winter dietary fractions of bivalves were comparable to those at Baynes Sound, the Fraser River Delta and Birch Bay (Chapter 2).

Contrary to our expectations, TRIG and BOHB concentrations did not vary with physical habitat conditions. Because collection events only lasted 1-3 days, often during extended periods of relatively favorable weather conditions, plasma metabolite data may have failed to reflect long-term variation in trajectories of energy status across sites. If we had collected birds during a period of adverse weather, we speculate that we may have seen stronger signals of BOHB, which would indicate that birds relied on lipid reserves during periods of limited foraging opportunity. Similarly, we may have observed increased plasma TRIG concentrations had we collected immediately following a prolonged stormy period, as birds recovered from limited food access by increasing food intake. We observed a weak correlation between plasma BOHB and period, which indicated that average rates of lipid catabolism during February collections were higher than those during December collections. Coupled with our results of lipid and body mass, which suggest that nutrient reserves peaked sometime around our mid-winter collection events, these results are consistent with declining lipid mass from mid- to late-winter.

A lack of relationship between metabolites and local habitat conditions also may indicate that, irrespective of their energy management strategies, scoters maintained physiological homeostasis at all sites. Past studies showed clear relationships between plasma TRIG, BOHB and daily mass change in a variety of bird species. However, these studies measured metabolites either in captive birds or in actively migrating wild birds that were building reserves to cope with increased energetic demands (Jenni-Eiermann and Jenni 1994, Williams et al. 1999, Afton and Anteau 2008). If rates of nutrient acquisition and depletion in white-winged scoters were lower during winter relative to those observed during periods of hyperphagia or fasting in past studies, variation in metabolites across sites may be more difficult to detect.

3.5. Tables and Figures

Table 1. Variation in diet composition and habitat conditions among four wintering sites for white-winged scoters in BC.

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 River Delta	Very High	Low–Medium	Low	Low
Birch Bay	Very High	Low	High	Low

Table 2. Candidate models describing variation in physiology in male white-winged scoters across five wintering areas in BC and WA. 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. Bold face text denotes most parsimonious model for each physiological indicator. * denotes analyses without data from Birch Bay.

Explanatory Variable	Site and Period Grouping	K	Body Mass n=155			Lipid Mass n=155			BOHB n=138*			TRIG n=138*		
			ΔAIC_c	w	r^2	ΔAIC_c	w	r^2	ΔAIC_c	w	r^2	ΔAIC_c	w	r^2
exposure (2 levels)	CS=BS=FD=BB; DB	3	4.76	0.06	0.05	56.82	0.00	0.26	13.77	0.00	<0.01	3.65	0.04	<0.01
exposure (3 levels)	CS=FD; DB; BS=BB	4	6.53	0.02	0.05	52.68	0.00	0.29	15.70	0.00	<0.01	**0.00**	**0.27**	**0.04**
water depth	CS=DB; BS=FD=BB	3	8.86	0.01	0.02	39.59	0.00	0.34	11.24	0.00	0.02	3.01	0.06	<0.01
predation danger	CS=BS=BB; DB=FD	3	10.13	0.00	0.01	74.00	0.00	0.18	13.28	0.00	<0.01	3.21	0.05	<0.01
diet composition (2 levels)	CS=DBM=DBL10=BS=FD=BB; DBL09	3	11.95	0.00	<0.01	100.24	0.00	0.02	3.49	0.05	0.07	3.43	0.05	<0.01
diet composition (3 levels)	CSM=BS=FD=BB; CSL=DBM=DBL10; DBL09	4	9.79	0.00	0.03	54.19	0.00	0.29	5.25	0.02	0.08	2.67	0.07	0.02
period	CSM=DBM=BSM=FDM=BBM; CSM=DBL09=DBL10=BSL=FDL=BBL	3	5.10	0.05	0.04	91.52	0.00	0.08	**0.00**	**0.28**	**0.09**	1.38	0.14	0.02
exposure (2 levels) with period	CSM=BSM=FDM=BBM; DBM; CSL=BSL=FDL=BBL; DBL09=DBL10	5	**0.00**	**0.62**	**0.10**	19.37	0.00	0.44	2.61	0.08	0.11	4.17	0.03	0.03
exposure (3 levels) with period	CSM=FDM; DBM; BSM=BBM; CSL=FDL; DBL09=DBL10; BSL=BBL	7	3.60	0.10	0.10	**0.00**	**1.00**	**0.52**	0.17	0.26	0.15	2.01	0.10	0.07
water depth with period	CSM=DBM; BSM=FDM=BBM; CSL=DBL09=DBL10; BSL=FDL=BBL	5	5.24	0.05	0.07	16.26	0.00	0.45	0.88	0.18	0.11	4.96	0.02	0.02
predation danger with period	CSM=BSM=BBM; DBM=FDM; CSL=BSL=BBL; DBL09=DBL10=FDL	5	4.14	0.08	0.07	53.93	0.00	0.30	1.37	0.14	0.12	4.11	0.03	0.03
null	CS=DB=BS=FD=BS	2	9.88	0.00	-	102.02	0.00	-	11.98	0.00	-	1.57	0.12	-

Table 3. Candidate models describing variation in digestive morphology in male white-winged scoters across five wintering areas in BC and WA. Site and period abbreviations as in Table 2. Bold face text denotes the most parsimonious model for each physiological indicator. * denotes analyses without data from Birch Bay.

Explanatory Variable	**Site and Period Grouping**	**K**	**Gizzard Mass** *n*=155			**Intestine Mass** *n*=138*			**Intestine Length** *n*=138*		
			ΔAIC_c	***w***	***r^2***	**ΔAIC_c**	***w***	***r^2***	**ΔAIC_c**	***w***	***r^2***
diet composition (2 levels)	CS=DBM=DBL10=BS=FD=BB; DBL09	3	85.43	0.00	0.14	1.32	0.29	<0.01	**0.00**	**0.73**	**0.42**
diet composition (3 levels)	CSM=BS=FD=BB; CSL=DBM=DBL10; DBL09	4	**0.00**	**1.00**	**0.51**	2.49	0.16	0.01	2.04	0.27	0.42
null	CS=DB=BS=FD=BS	2	107.03	0.00	-	**0.00**	**0.55**	**-**	72.32	0.00	-

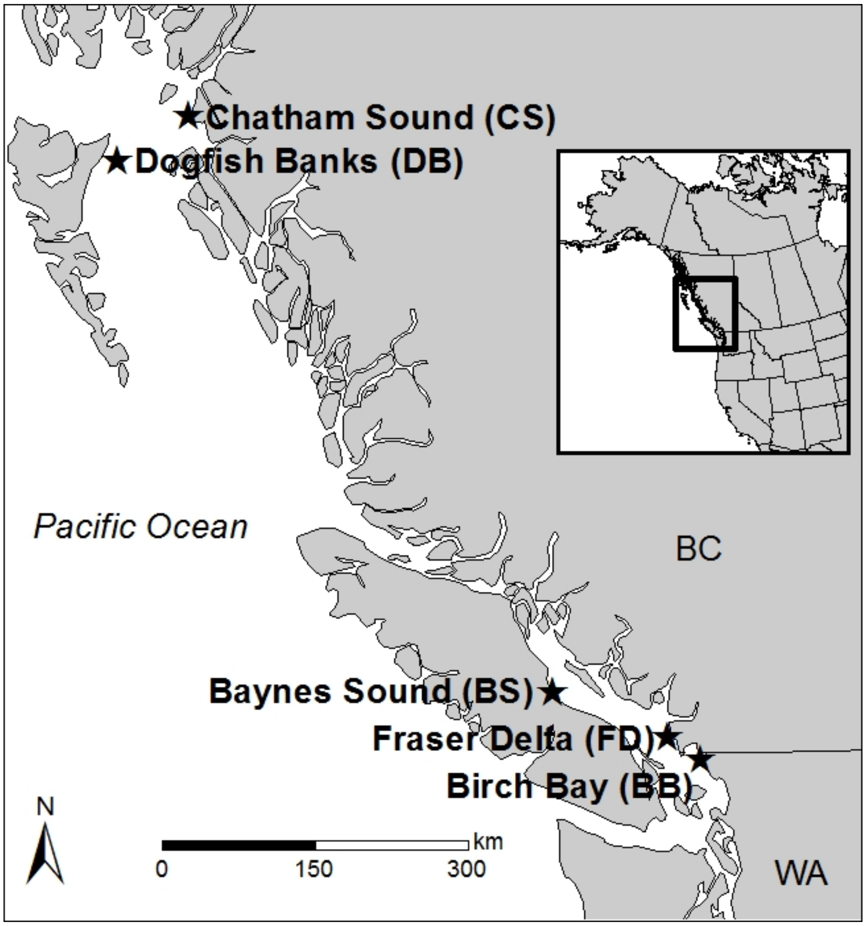

Figure 1. Map of the five study sites in BC and WA.

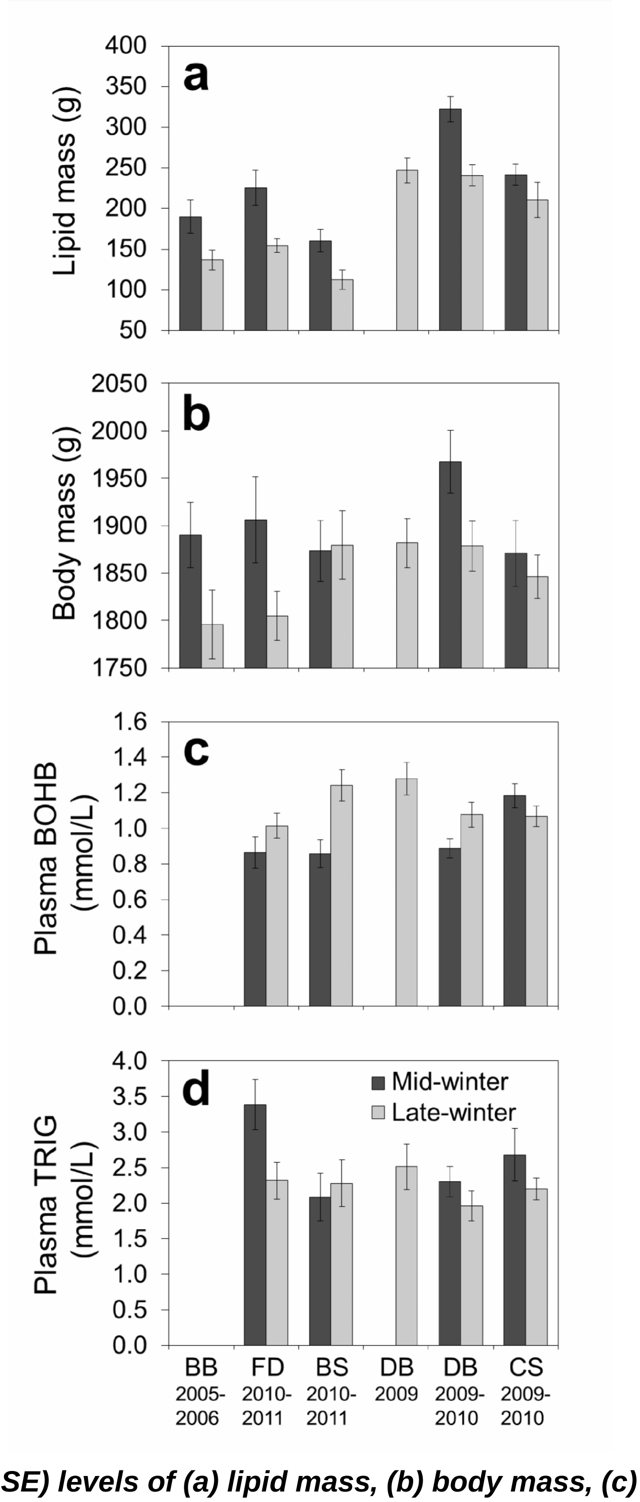

Figure 2. Mean (±SE) levels of (a) lipid mass, (b) body mass, (c) plasma BOHB, and (d) plasma TRIG for white-winged scoters in five sites in BC and WA during mid-winter (December) and late-winter (February-March). Site abbreviations as in Table 2. Plasma metabolites were not available for Birch Bay.

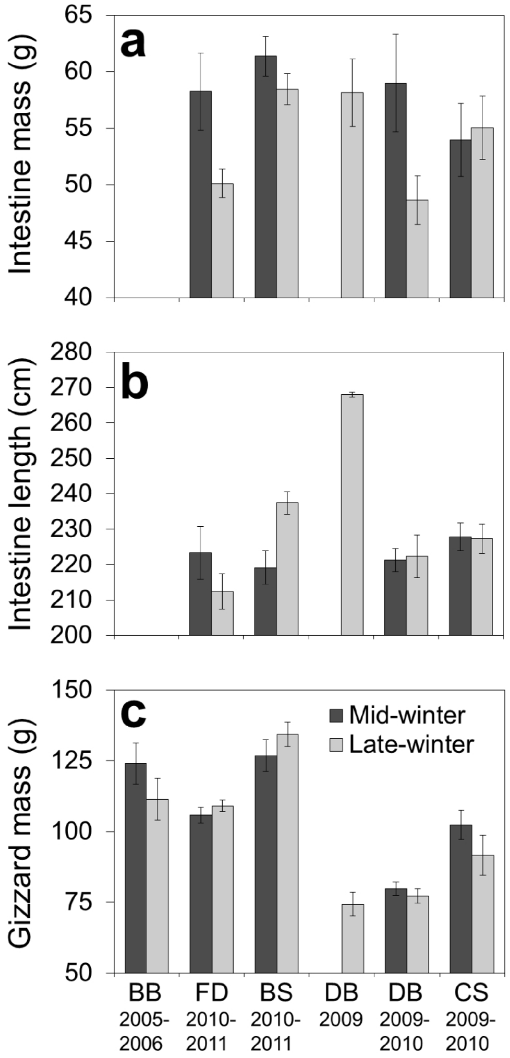

Figure 3. Mean (±SE) levels of (a) intestine mass, (b) intestine length, and (c) gizzard mass for white-winged scoters in five sites in BC and WA during mid-winter (December) and late-winter (February-March). Site abbreviations as in Table 2. Intestine measurements were not available for Birch Bay.

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4. Baseline corticosterone in wintering marine birds: methodological considerations and ecological patterns

4.1. Introduction

Plasma corticosterone (CORT) increasingly has been used as a tool to infer local habitat conditions for birds and to contrast relative condition of individuals and populations (Kitaysky et al. 1999, Walker et al. 2005, Wikelski and Cooke 2006). In response to temporary stressors, such as a predatory attack, a large storm, or capture by researchers, secretion of plasma CORT quickly increases (Breuner et al. 2008). However, behavioural and physiological effects of an acute stress response are markedly different from those associated with variation in baseline CORT. Baseline levels of CORT are considered those that are sufficient for birds to carry out normal physiological functions and maintain energetic balance (Romero 2004). Baseline levels may vary in response to prolonged environmental challenges, such as a decrease in food availability, greater predation danger, or frequent bouts of inclement weather (Kitaysky et al. 1999, Clinchy et al. 2004). Elevation of baseline CORT under persistent challenges presumably serves to modify behaviour and physiology to help overcome these challenges by facilitating increased foraging, movement, and/or mobilization of energy reserves (Landys et al. 2006, Angelier et al. 2007, Sapolsky et al. 2000). However, chronically elevated concentrations of plasma CORT, similar to levels immediately following a temporary stressor, can negatively affect fitness (Romero 2004).

Baseline CORT may vary with environmental conditions or endogenously over the annual cycle. In some species, elevated baseline CORT can drive the accumulation of energetic stores in preparation for long-distance migration (Holberton et al. 1999, Reneerkens et al. 2002). Research on some wintering passerines shows consistently lower CORT concentrations across a wide geographical area during winter compared to levels during spring migration and breeding, suggesting seasonal fluctuations may be endogenously regulated instead of a result of local habitat conditions (Romero et al. 1997). In seabirds, baseline CORT can increase as food availability declines (Kitaysky et al. 1999, Buck et al. 2007). These findings have prompted researchers to suggest that baseline CORT could be used as a proxy for food availability (Buck et al. 2007, Kitaysky et al. 2007). However, a majority of studies relating plasma CORT in seabirds to variation in foraging conditions have focused on the breeding period of the annual cycle (Romero 2002), and it is unclear whether similar relationships between foraging conditions and baseline CORT exist during other life stages.

Measuring blood plasma levels of baseline CORT in the field is challenging because capture and bleeding are both stressors that can result in acute stress responses and elevated levels of plasma CORT (Romero and Romero 2002). The relationship between time since capture and acute CORT response has been well-documented, and it is clear that CORT levels rise within minutes of exposure to stressors; therefore, accurate quantification of baseline CORT requires that time between capture and bleeding must be below the point at which acute CORT responses are detected (Wingfield et al. 1982, Romero and Romero 2002, Romero and Reed 2005). Lethal sampling may represent the only viable means to collect blood samples from some species (e.g., open water seabirds) or during particular stages of the annual cycle. Such sampling eliminates stress associated with capture and handling focal species, but approaching birds may also result in acute effects on baseline CORT. However, the very few studies that have published CORT data from shot birds have not quantified relationships between initial disturbance, time of death, and CORT level (Lisano et al. 1977, Whatley et al. 1977, Wingfield et al. 1982, Marra et al. 1995).

White-winged scoters (*Melanitta fusca*) are sea ducks that spend 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 their wintering range along the Pacific Coast of North America, there are few areas in BC where white-winged scoters occur in high concentrations during the winter (Savard 1979). This may be due in part to their preference for soft-bottom habitats with large standing stocks of bivalves, which are relatively uncommon in BC. However, even among such sites, there is considerable variation in white-winged scoter diet and in water depth, danger of predation, and exposure to wind and waves. We assessed whether these habitat conditions were related to baseline levels of plasma CORT in wintering white-winged scoters. Widespread population declines in some sea duck species, including white-winged scoters, have prompted efforts to identify functional roles of different habitats used throughout the annual cycle through analyses of body condition, prey availability, foraging effort, diet composition and plasma metabolite analyses (e.g., Zydelis et al. 2006, Anderson and Lovvorn 2008, Anderson et al. 2008, Lewis et al. 2008, Anderson and Lovvorn 2011). When combined with these measures, baseline CORT data could provide more insight into the relative habitat values of different sea duck wintering areas.

We measured plasma CORT concentrations from free-living white-winged scoters that were lethally collected at four wintering areas along coastal BC that varied markedly in predictability of weather and foraging conditions (Fig. 1). Our specific objectives were to delineate appropriate methods of identifying baseline CORT from collected birds, and to assess variation in baseline CORT in relation to winter habitat conditions. We predicted that sites with less predictable foraging conditions would have elevated baseline levels of CORT, under the expectation that elevated CORT would be advantageous for triggering behavioural responses to uncertain conditions (Wingfield and Ramenofsky 1997, Reneerkens et al 2002).

4.2. Methods

4.2.1. *Sample Collection*

We collected a total of 119 adult male white-winged scoters using a shotgun from a small boat at four wintering areas along coastal BC (Chatham Sound, Dogfish Banks, Baynes Sound, and the Fraser River Delta; Fig. 1), under the authority of permits from Environment Canada (BC-09-0182) and Simon Fraser University Animal Care (992B-06). There were a total of 8 collection events across the four sites: Dogfish Banks (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). By conducting all collections before the end of February, we assumed that any differences in baseline CORT between wintering areas would be a result of variation in local habitat conditions rather than physiological changes associated with spring migration, which does not occur until April or later (W. S. Boyd, Environment Canada, unpubl. data).

To eliminate potential variation in baseline CORT related to age class or sex (Bonier et al. 2007, Wada et al. 2008), we collected only after-hatch-year (i.e. mature/old) males verified by plumage (Brown and Fredrickson 1997). We recorded the "death time" for each bird, which we defined as the period between initial flush and death. Due to the difficulty of determining when a bird first began to respond to our presence upon our approach, death times were estimated and rounded to the nearest whole minute. We generally approached small flocks at speeds of 15-25 knots and shot flying birds from a moving boat. Within five minutes of retrieval, we sampled heart blood using a sterile 18-gauge needle and transferred up to 5 ml of blood to a heparinized vial for CORT analyses. We centrifuged whole blood within 8 hours of collection to separate plasma and cells and stored all tissues at –20°C. To facilitate examination of relationships between CORT and separate indices of individual condition, Long Point Waterfowl's Avian Energetics Lab (Port Rowan, Ontario) conducted analyses of body composition (total protein, lipid, water, and ash) from ingesta-free dry carcass mass including plumage following methods of Afton and Ankney (1991).

4.2.2. CORT Assay

We determined the concentration of total CORT in non-extracted plasma using a corticosterone Enzyme-linked-Immunoabsorbent Assay (EIA — Assay Designs Inc., Michigan, USA, catalog # 901-097) with a 4-parameter logistic fit based on Love and Williams (2008). We ran all samples in triplicate across 6 assay plates at a total volume of 100 µl with 1:40 dilution and 1.5% steroid displacement buffer. As per kit instructions, we first incubated plates at 26 °C under shaking at 5000 rpm for 2 h and then at 26 °C without shaking for 1 h; we calculated the detection limit of the assay at 0.018 ng/well (0.72 ng/ml), with intra- and inter-assay variations of 6.89% and 10.15%, respectively.

4.2.3. Study Sites

Each study site (Fig. 1) represented a different combination of three physical habitat conditions we assessed for their influence on baseline CORT: exposure to wind and waves, water depth, and predation danger (Table 1). Dogfish Banks (53°55'N, 131°30'W) 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, Dogfish Banks is a wintering area for tens of thousands of white-winged scoters (LGL Limited 2009a); however, overall abundance and density of wintering sea ducks at Dogfish Banks fluctuates widely between years (LGL Limited 2009a, Hodges 2005, E. Palm pers obs.).

Dogfish Banks consists mainly of soft-bottom and shallow subtidal habitat, which is rare along the coast of BC. Along the Pacific Coast, most white-winged scoters winter in somewhat protected nearshore areas. Dogfish Banks is a notable exception because it is an offshore site subject to strong winds and water currents. Combined with a mobile substrate of sand or a sand-gravel mixture, these conditions result in a frequently changing benthic foraging habitat. Water depths on the study site 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 a wintering population of hundreds of 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. Birds at Chatham Sound feed in deep water (5-30 m), searching for prey in sandy and muddy substrate situated between rock outcrops (E. Palm, pers obs.).

Baynes Sound (49°39'N, 124°53'W), contains extensive intertidal flats and high densities of wild and cultured bivalves, providing near-shore habitat for approximately 6500 white-winged and surf scoters during winter months (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 show relatively low overall observed foraging effort, Baynes Sound is thought to be high quality foraging habitat (Lewis et al. 2007, Lewis et al. 2008). Compared to Chatham Sound, this area contains more shallow water habitat, a greater abundance of large bivalves and more protection from high winds and swells.

Thousands of white-winged scoters use the shallow intertidal mudflats on the Fraser River Delta (49°06'N, 123°16'W), annually for moulting, wintering, and staging (E.M. Anderson, J.R. Evenson, unpublished data). However, overall numbers on the Fraser River Delta during winter 2010-2011 were relatively low compared to those at other wintering areas, ranging from approximately 400-600 in December to approximately 200-300 in February (E. Palm, pers. obs.). The area offers less shelter from unfavorable weather than Baynes Sound and nearby Birch Bay. Unlike Chatham

Sound, Baynes Sound and Birch Bay, it offers very few potential perches for bald eagles (*Haliaeetus leucocephalus*), which are the most likely predator of white-winged scoters.

4.2.4. Data Analysis

4.2.4.1. Quantification of timeline to acute stress CORT

Prior to running the models corresponding to each of our *a priori* hypotheses describing possible sources of variation in baseline CORT, we quantified the average amount of time between when targeted birds were initially flushed until they exhibited an acute stress response, represented by an increase in plasma CORT concentration. We excluded a single data point from all analyses, with a CORT concentration of 151.3 ng/ml and an associated death time of 1 min, because it far exceeded baseline values found in a separate study of wintering sea ducks, which ranged from approximately 15-50 ng/ml (Nilsson et al. 2008). An initial plot of CORT versus death time showed average CORT to be relatively stable until approximately 3-4 minutes, after which it increased (Fig. 2). We ran a series of multiple linear regressions in program R to determine the appropriate cutoff time that would separate baseline values from values of potentially stressed birds (Nickerson et al. 1989). We log-transformed CORT data to meet assumptions of normality in our linear models, but we report untransformed data in their original units of measurement for presentation in this paper.

Using 1 min as the first potential cutoff time, we separated CORT data into two groups based on associated death times: 1) 0 to 1 min and 2) >1 min*.* For each of the two groups in the linear model, we allowed both the intercept and the slope to vary. We then repeated the process using every death time from 2 to 6 min as the potential cutoff time between the two groups. We expected to see a relatively flat line for baseline values, followed by a linear increase in CORT, which would represent acute stress. To choose the cutoff time that provided the best fits of both baseline CORT and the acute stress response, we calculated Akaike's Information Criterion adjusted for small sample size (AIC_c) for each of the models and chose the model with the lowest value (Burnham and Anderson 2002).

4.2.4.2. Geographic variation in CORT:

Based on the analysis described above, we excluded any birds whose death time exceeded the determined cut-off and thus may have exhibited acute CORT response.

Eliminating these birds ensured that values included in subsequent analyses represented baseline levels. We compared baseline CORT data across study sites and collection periods using least squares analyses in an information-theoretic context. We pooled data from the 8 separate collection events in specific ways to test relative support for different biologically plausible, *a priori* hypotheses describing possible sources of variation in baseline CORT. Exposure, water depth, diet composition, predation danger and collection period were all factors potentially influencing baseline CORT, and these factors varied across study sites (Table 1). Each model represented a different way of grouping data from different sites for comparisons, allowing considerations of support for each of the factors as drivers of variation in baseline CORT. 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 baseline CORT varied by water depth and period, the explanatory variable would have four levels: 1) mid-winter deep water sites, 2) mid-winter shallow water sites, 3) late winter deep water sites, and 4) late winter shallow water sites. In addition, we included a null model, representing the hypothesis that CORT did not vary geographically or by collection period.

Based on past studies that found relationships between baseline CORT and measures of body condition (Kitaysky et al. 1999, Müller et al. 2007), we ran a post-hoc analysis to test the hypotheses that baseline CORT varied by body mass, lipid mass or protein mass. Structural body size, which we estimated separately using measurements of culmen, wing cord, tarsus, and the first principal component of all three, explained <16% of variation in body mass, and was not correlated with total lipid mass (all $r^2 < .06$) or total protein mass (all $r^2 < .03$). Therefore, we did not correct measures of individual condition for body size.

4.2.4.3. Exposure

Dogfish Banks stands out as the only offshore wintering site within our study area (Table 1). On average, white-winged scoters occurred 8 km (range 2-22 km) from shore at Dogfish Banks. The eastern shore of Haida Gwaii immediately south of Rose Spit offers little to no shelter from adverse weather. Birds at Dogfish Banks are subjected to rough seas from prevailing winds that blow out of the southeast for hundreds of kilometers across Hecate Strait during the winter months. At more exposed sites, baseline CORT in seabirds may vary in response to a greater frequency in storms, which can limit access to food resources (Smith et al. 1994). Birds at the remaining three wintering areas occur within 2 km from shore and can find shelter in bays and inlets. For exposure hypotheses, we pooled Dogfish Banks data separately from data from other sites (Table 2).

4.2.4.4. Water Depth

Scoters at Dogfish Banks and Chatham Sound fed exclusively in the subtidal zone at depths of 5 to 25 m. Variation in baseline CORT may trigger increased explorative behaviour for locating food resources (Reneerkens 2002). At greater depths, where locating benthic prey may require more time and effort, such a behavioural response could be beneficial for white-winged scoters. To group CORT data by water depth, we pooled data from Dogfish Banks and Chatham Sound separately from the remaining two sites (Table 2), which consisted predominantly of intertidal and very shallow subtidal foraging habitat.

4.2.4.5. Predation Danger

Increased predation danger has been associated with variation in baseline CORT in a number of bird species (Scheuerlein et al. 2001). White-winged scoters wintering in Baynes Sound and Chatham Sound forage within 1 km of shore, often in close proximity to forested land with high densities of bald eagles, which are the most likely predator for white-winged scoters. Conversely, there were very few potential eagle perches at the Fraser River Delta and virtually no eagle presence at Dogfish Banks. For predation danger hypotheses, Fraser River Delta and Dogfish Banks data was pooled together separately from Baynes Sound and Chatham Sound (Table 2).

4.2.4.6. Diet composition

Lacking prey sampling, we used diet composition as an indicator of food availability at each site. Diets in Baynes Sound and the Fraser River Delta consisted almost entirely of bivalve prey during mid and late winter. Similarly, birds in Chatham Sound fed nearly exclusively on bivalves during mid-winter collections. During late winter, white-winged scoters at Chatham Sound consumed a wider variety of foods, including echinoderms and crustaceans. Dogfish Banks birds during both collection periods also fed on a more diverse suite of prey. Diet composition can be used as another indicator of the relative predictability of food resources in that area, which can influence baseline CORT levels (Reneerkens et al. 2002). We grouped data from both mid and late winter at Dogfish Banks with late winter collection data from Chatham Sound in diet composition hypotheses (Table 2).

4.2.4.7. Model Selection

We used information-theoretic methods to direct model selection, and used Program R (R Foundation for Statistical Computing, 2011) for all statistical analyses. To infer the relative support of each model included in the candidate set, we calculated $AIC_{c,}$ ΔAIC_c values and Akaike weights (*w*) (Burnham and Anderson 2002). Both ΔAIC_c and *w* values measure the relative amount of support for each model compared to other models in the candidate set.

4.3. Results

4.3.1. Quantification of timeline to acute stress CORT

The model using 3 min as the cutoff time ($r^2 = 0.31$) to separate baseline values from values representing acute stress provided the best fit of the observed data relative to the other models. Therefore, we excluded all CORT values with associated death times (*t*) of greater than 3 minutes in subsequent analyses. The regression equations [parameter estimates (SE)] for this model generally reflected our expectations (Fig. 2), which were that baseline CORT values would form a relatively flat line below a certain death time (3 min), after which CORT would increase linearly, corresponding to acute stress:

$$\text{Baseline CORT} = 6.97\ (5.55) - 0.61\ (3.01)t$$

$$\text{Collected after 3 minutes: } 0.39\ (9.65) + 4.24\ (3.20)t$$

4.3.2. Geographic variation in CORT

Across all sites, average (±SE) baseline CORT was 6.64 ± 1.19 ng/ml. Five models describing variation in baseline CORT had ΔAICc scores ≤2. However, >95% of the variation in our data was not explained by models in our candidate set (Table 2).

There was no evidence indicating that exposure, water depth, predation danger or diet composition influenced baseline CORT. In addition, baseline CORT did not vary between mid-winter and late winter collection periods. In our post-hoc analysis examining relationships between individual condition and baseline CORT, all three measures of condition outperformed the null model. The protein mass model was most parsimonious, explaining 12% of the variation in baseline CORT. The weak correlation between protein mass and baseline CORT suggested that elevated CORT may be associated with lower protein mass.

4.4. Discussion

Our results demonstrate that it is possible to obtain baseline CORT from lethally-collected marine birds if the time from initial flush until death is measured. We found increasing CORT values above a death time of 3 min, presumably reflecting acute stress response. That result is consistent with past studies indicating that blood samples taken within 3 min of capture represent baseline CORT (Wingfield et al. 1982, Romero et al. 1997, Silverin and Wingfield 1998, Romero and Romero 2002). Our methods, which determine the appropriate cutoff time between baseline and stressed concentrations of CORT in shot birds, can be applied in subsequent studies requiring lethal collection of birds.

Despite perceived differences in habitat predictability across white-winged scoter wintering areas, baseline CORT did not vary in response to habitat conditions. These results suggest either that (1) overall foraging conditions were not markedly different among our study sites, or that (2) fluctuations in baseline CORT levels are largely endogenously regulated and dependent on season, and/or that (3) baseline CORT was not affected by the different factors that we hypothesized might be influential. If baseline CORT levels in wintering white-winged scoters were driven primarily by predictability of foraging conditions, values should have been greatest at Dogfish Banks due to its frequent storms, strong currents, mobile substrate, and relatively low density of bivalves (LGL Limited 2009b).

Combining baseline CORT with data on body condition may provide more insight into differences in habitat conditions than either metric on its own (Kitaysky et al. 1999).

White-winged scoters employed different energy management strategies across sites based on habitat conditions (Chapter 3). Wintering birds at Dogfish Banks maintained relatively high lipid mass, which likely functioned as an “insurance policy” to cope with frequently changing foraging conditions. During both mid and late winter, average lipid mass at Dogfish Banks was over twice as high as at Baynes Sound, which has an abundant, predictable source of prey and more favorable weather (Lewis et al. 2008). Our results suggest that individual condition of birds may have influenced baseline CORT; however, irrespective of their energy management strategy, birds were largely successful in maintaining homeostasis and avoiding physiological stress across sites.

In waterfowl, there is evidence that adult male birds often compose high proportions of populations wintering in northern sites or sites with relatively harsh weather (Jorde et al. 1982, D. Esler, Simon Fraser University, unpubl. data). Greater body size of male white-winged scoters relative to females confers lower mass-specific energy demands, making males better equipped to handle cold or windy environments (Goudie and Ankney 1986). Larger birds also may be more resistant to fluctuations in energy status as a result of variable foraging conditions (Richman and Lovvorn 2009). Further, older, more experienced birds may be more likely to find food resources in an unpredictable foraging environment. Relative to other sites, we saw a higher ratio of adult males to other cohorts at Dogfish Banks. Among male white winged scoters, the ability to manage site specific costs may vary by individuals or phenotypes, and a lack of variation in our baseline CORT data may reflect those differences (Wada et al. 2008). For example, individuals at Dogfish Banks may have been better at managing increased costs of foraging in an unpredictable habitat and could maintain baseline CORT at levels similar to those at other sites. Thus, winter habitat selection in white-winged scoters may be an adaptive process based in part on individual phenotype. Similar baseline CORT levels across our study sites may indicate that white-winged scoters select wintering areas where they can successfully maintain physiological homeostasis.

4.5. Tables and Figures

Table 1. Variation in habitat conditions and diet composition among four wintering sites for white-winged scoters in BC.

Study Site	Exposure	Water Depth	Proportion of bivalves in diet	Predation Danger
Chatham Sound	Low	High	High–Very High	High
Dogfish Banks	High	High	Medium–High	Low
Baynes Sound	Low	Low	Very High	High
Fraser River Delta	Low	Low	Very High	Low

Table 2. Candidate models describing variation in baseline CORT levels in male white-winged scoters across four wintering areas in BC. CS=Chatham Sound, DB=Dogfish Banks, BS=Baynes Sound, FD=Fraser River Delta, M=mid-winter, L=late winter.

Explanatory Variable	Site and Period Grouping	K	ΔAIC_c	*W*	r^2
null	CS=DB=BS=FD	2	0.00	0.22	-
diet composition	CSM=DB; CSL=BS=FD	3	0.23	0.20	0.03
predation danger	CS=BS; DB=FD	3	0.23	0.20	0.03
water depth	CS=DB; BS=FD	3	0.84	0.15	0.02
season	CSM=DBM=BSM=FDM; CSL=DBL=BSL=FDL	3	2.02	0.08	<0.01
exposure	DB; CS=BS=FD	3	2.19	0.07	<0.01
exposure, period	CSM=BSM=FDM; CSL=BSL=FDL; DBM; DBL	5	3.80	0.03	0.04
water depth, period	CSM=DBM; CSL=DBL; BSM=FDM; BSL=FDL	5	3.96	0.03	0.04
predation danger, period	CSM=BSM; CSL=BSL; DBM=FDM; DBL=FDL	5	4.47	0.02	0.03

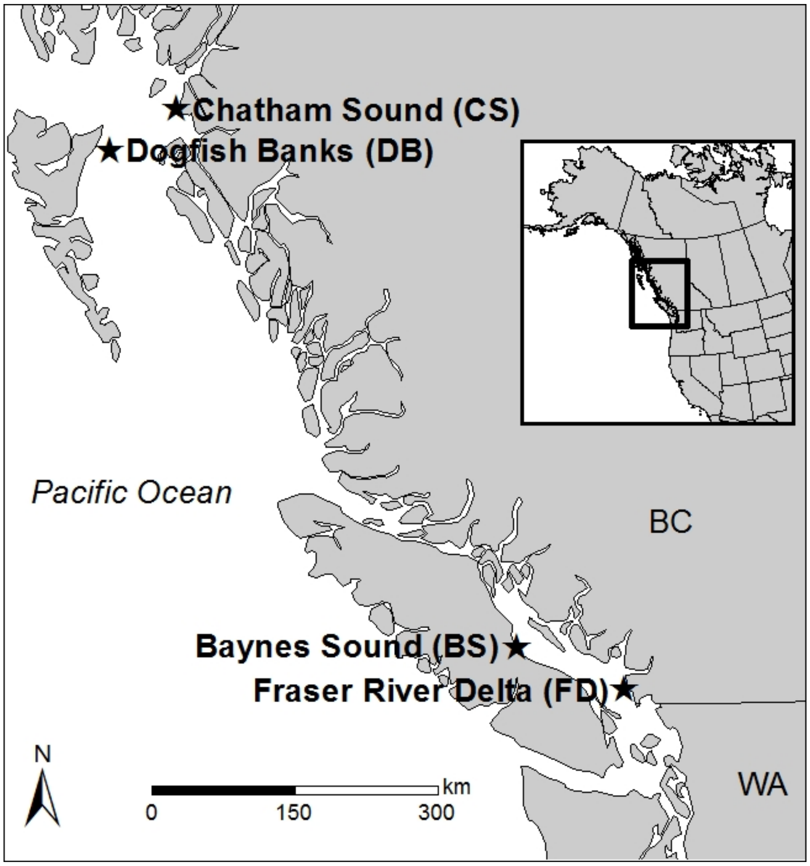

Figure 1. Map of the four study sites along coastal BC.

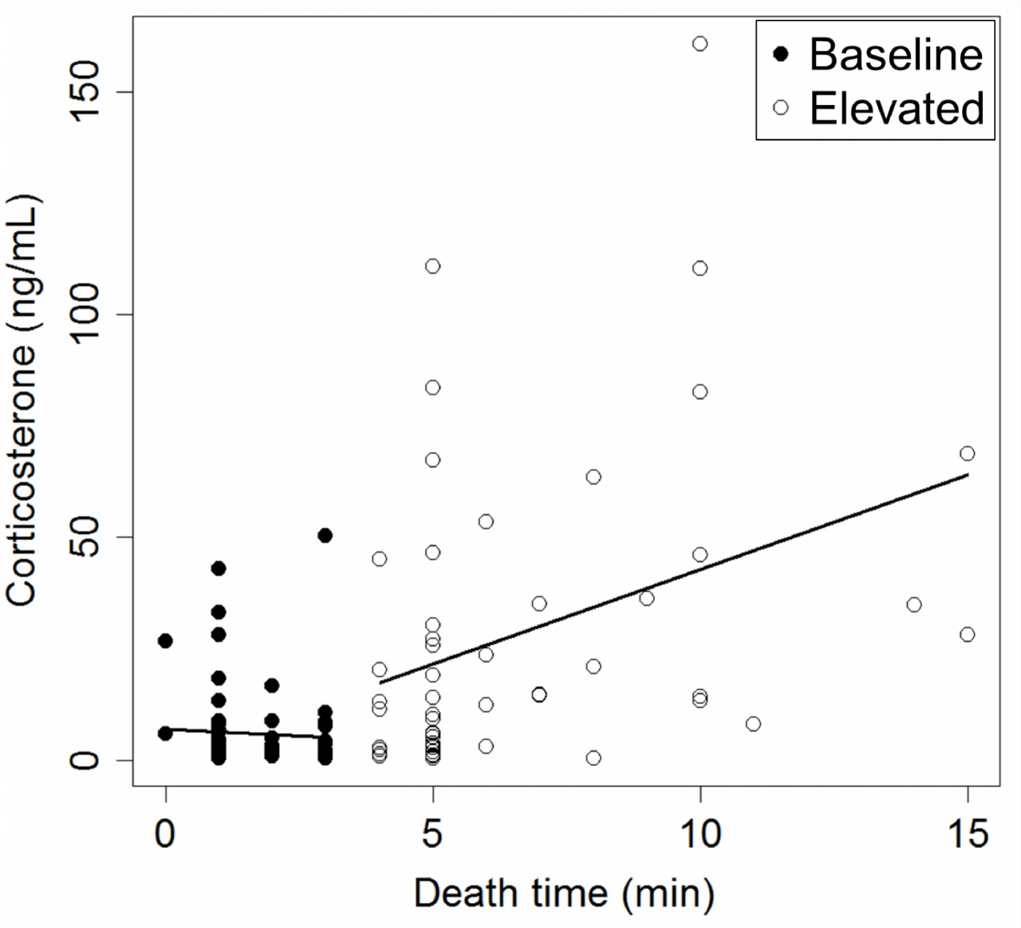

Figure 2. Plasma CORT concentrations as a function of death time, with separate regression lines for baseline levels (0-3 min) and elevated levels (>3 min).

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5. General Conclusions

5.1. Thesis Summary

In this thesis, I examined geographic variation in diet, body condition, morphology and physiology at five sites in British Columbia and Washington, and related those to differences in habitat attributes across sites. Because individual measures of condition and physiology vary by a number of factors (Anderson and Lovvorn 2011), I concurrently evaluated a broad suite of indicators to enhance interpretation and draw inferences about habitat function.

By including study sites that spanned a large geographic area and a variety of habitat conditions, my intention was for my results to apply broadly to white-winged scoters, which typically have been studied in sheltered, nearshore sites but occur in appreciable numbers in other habitats. In many aspects of diet, digestive morphology and energy management, a highly exposed, offshore site in Hecate Strait showed different patterns than other white-winged scoter wintering areas.

In Chapter 2, I confirmed that white-winged scoters are generally bivalve specialists, although the species of bivalves consumed and their relative contributions to overall diet varied by site. Diet composition was more temporally variable at an offshore site, indicating that birds adjusted prey consumption in response to changes in food resources at this site. During some periods, presumably those with relatively low bivalve availability, white-winged scoters at the offshore site fed on a wide variety of prey items, which included substantial dietary fractions of fish, crustaceans, polychaetes and echinoderms. At other sites, with intertidal foraging habitat and high bivalve densities, white-winged scoters fed almost exclusively on large bivalves, particularly varnish clams, and diet composition remained stable through winter. The invasion of varnish clams has markedly altered the prey landscape at some white-winged scoter wintering sites, and illustrates plasticity that white-winged scoters demonstrate in foraging strategies under modified conditions. Our findings also corroborate those from previous studies, which suggest that soft-bottom, marine habitats with high densities of infaunal invertebrates offer favorable, reliable foraging conditions for some sea duck species.

In Chapter 3, I assessed how white-winged scoters adjust foraging and energy management strategies in response to variation in these tradeoffs. Specifically, I used several physiological indicators to quantify geographic and temporal variation in physiology and energy status of wintering scoters in five sites in British Columbia and Washington. Scoters employed different energy management strategies depending on habitat conditions. Total body mass and lipid mass were greatest at an exposed offshore site. I interpreted this increased energy storage as an adaptive response used to buffer against unpredictable foraging conditions and increased thermoregulatory costs at this site. At nearshore sites where exposure was lower, scoters had the smallest lipid masses in mid-winter and experienced the smallest lipid declines from December to late February. At most sites, scoters displayed overwinter declines in body condition as lipid mass declined and levels of plasma β-hydroxybutyrate increased. However, levels of plasma metabolites varied little across sites suggesting that, irrespective of body composition, birds at all sites maintained a physiological homeostasis. I found that digestive morphology was strongly related to diet, as smaller gizzards were associated with a greater dietary fraction of soft-bodied foods. Similarly, intestine length varied in relation to diet, and increased length may have functioned to increase nutrient assimilation during poor foraging conditions.

In Chapter 4, I observed increasing CORT values above a death time, defined as the period between initial flush and death, of 3 min, presumably reflecting acute stress response. This result was similar to those from studies of live-captured birds (Wingfield et al. 1982, Romero et al. 1997, Silverin and Wingfield 1998, Romero and Romero 2002), and demonstrated that it was possible to obtain baseline CORT from lethally-collected marine birds. Despite differences in foraging conditions and habitat predictability among wintering areas, baseline CORT of white-winged scoters did not vary across sites. I interpreted this lack of variation as further evidence that white-winged scoters selected wintering areas where they could successfully manage site specific costs.

Collectively, my results indicate that white-winged scoters achieved physiological homeostasis across all sites by varying diet, endogenous reserves, and gut morphology in response to spatial and temporal differences in habitat conditions. This flexibility allows them to use a variety of marine habitats, and to balance potential trade-offs associated with wintering in each area.

Recent research on black brant (*Brant bernicula*) and surf scoters found pronounced differences in foraging effort, morphology, physiology and sex/age ratios between the northern and southern peripheries of their wintering range (Mason et al. 2006, Mason et al. 2007, VanStratt 2011). These differences likely reflected strategies for coping with variation in trade-offs between foraging opportunity, nutrient acquisition, and predation danger across latitudes. My findings indicate that even within the range core, variation in habitat conditions across sites can influence physiology and energy management in white-winged scoters. Like wintering black brant, white-winged scoters exhibit phenotypic flexibility by feeding on a wide variety of prey during some periods, and by varying lipid mass, body mass and digestive morphology to meet site-specific costs (Mason et al. 2007).

5.2. Future Directions

I suggest that future studies of white-winged scoters more thoroughly examine sex/age ratios and foraging effort across sites, which would help determine the extent of differential habitat use across cohorts and further clarify functional value of wintering habitats for this species. I did not formally document variation in sex/age ratios or foraging effort across sites. However, observations indicated a higher proportion of adult males at the highly exposed, deep water site, which may indicate differential habitat use among cohorts during the winter. Adult males are generally heavier and have lower mass-specific energy demands than other cohorts (Brown and Fredrickson 1997, D. Esler, unpubl. data), and may therefore be best suited to withstand unpredictable foraging conditions or harsh weather. Winter habitat selection in white-winged scoters may be an adaptive process based in part on individual phenotype. Foraging effort data would help elucidate any differences in prey availability and overall foraging conditions across sites (Lewis et al. 2008, Reed and Flint 2007, VanStratt 2011), allowing explicit tests of hypotheses about foraging conditions. I also would expect these data to corroborate my results on energy management by lending support to the idea that white-winged scoters using exposed sites build extra lipid reserves in anticipation of increased or variable foraging effort required to meet relatively high energy demands.

In conjunction with foraging effort data, winter satellite telemetry data also would clarify the function of these habitats for foraging birds, and provide an assessment of inter-site movements through the winter. Research on surf scoters in Puget Sound and in the Strait of Georgia showed that birds departed traditional wintering sites in response to declining foraging conditions (Anderson and Lovvorn 2008, Kirk et al. 2008). Although movement data for white-winged scoters suggest that they exhibit high site fidelity during winter (J. R. Evenson, unpubl. data), similar data do not exist for highly exposed winter feeding sites such as Dogfish Banks. In fact, variable numbers of birds observed on Dogfish Banks in 2009-2010 suggest low inter- or intra-annual fidelity at this site. Satellite data from highly exposed sites, where traditional survey data showing temporal movements are difficult to obtain, would clarify whether or not white-winged scoters move to more sheltered areas during bouts of harsh weather or in response to variable foraging opportunity. Finally, future research relating diet and physiological measures to habitat conditions would help determine whether our findings are consistent with those from white-winged scoters wintering in other regions.

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