POSTBREEDING ECOLOGY OF WHITE-WINGED SCOTERS (*MELANITTA FUSCA*) AND SURF SCOTERS (*M. PERSPICILLATA*) IN WESTERN NORTH AMERICA: WING MOULT PHENOLOGY, BODY MASS DYNAMICS AND FORAGING BEHAVIOUR

by

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Abstract

Waterfowl undergo simultaneous remigial moult, in which flight feathers are shed and then re-grown synchronously. Nutrient and energy demands and vulnerability to predation may be elevated during remigial moult, suggesting that this stage of the annual cycle could pose a constraint on population dynamics. I studied remigial moult in two sea ducks, Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*), in southeast Alaska and the Salish Sea to evaluate evidence of temporal, energetic or nutritional constraints. Scoters exhibited a relatively long flightless period and high inter-individual variation in timing of moult, suggesting there were not strong temporal constraints during this phase of the annual cycle. Increasing body mass during the feather growth period indicated that scoters met costs of moult without relying on endogenous reserves and they did so at moderate levels of foraging effort, strong evidence of lack of energetic or nutritional constraints.

Keywords: postbreeding ecology; remigial moult; phenology; body mass; foraging effort; sea ducks; Surf Scoter; White-winged Scoter; *Melanitta*

I dedicate this work to the memory of my brother,
Jesse Cohen
October 1974 – August 2008

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1: Introduction:

1.1 Thesis Background

Moult is a major component of the annual cycle of all birds (Newton 2011). All phases of the annual cycle have associated costs and constraints, and birds are constantly negotiating shifting trade-offs among time, energy, and safety (Alerstam and Lindstrom 1991).

Much of avian research has focused on the biology and ecology of breeding and migration (Bridge 2011). While these are clearly important fields of research, not every individual in a population will breed in a given year and there are many non-migratory species and populations (Bridge 2011). On the other hand, all birds undergo moult every year and feather quality has direct fitness consequences (Murphy 1996; Dawson et al. 2000; Rohwer et al. 2009). Furthermore, in the typical annual cycle of many adult birds, moult represents the most extensive production of somatic tissue (Walsberg 1983). Despite these factors, moult remains a poorly understood phenomenon within the annual cycle in most species (Bridge 2011).

While there are many variations on the process of moult among avian taxa, most birds undergo at least one complete moult per year, in which all feathers are renewed (Humphrey and Parkes 1959). Nearly all species moult contour feathers gradually, with enough retained while new ones are growing that the body remains covered. Most birds also moult remigial feathers progressively, replacing one to three feathers on each wing at any given time, so that the ability to fly is not lost. However, 11 avian families undergo simultaneous moult of the remiges, in which old flight feathers are lost over a period of a few days (or less) and new feathers grow in synchronously, leaving birds flightless for several weeks (Hohman, Ankney and Gordon 1992).

Waterfowl are among the taxa that exhibit simultaneous wing moult (Hohman, Ankney and Gordon 1992). Remiges are re-grown simultaneously, with the flightless period lasting between 20-40 days, depending on species and individual. The conventional explanation for the evolution of simultaneous wing moult is that 'poor' fliers (e.g. loons, grebes, auks) are unable to fly if lacking just a few primary feathers, so it is advantageous to minimize the length of the flightless period by moulting all the remiges together (Welty 1982). However, many waterfowl can fly when missing one or two primaries, so this hypothesis is not an adequate explanation for anatids. Almost all species that exhibit simultaneous wing moult are either aquatic or marsh-dwelling birds, which are able to feed and escape predators without relying on flight; this observation suggests that simultaneous moulting has advantages when food acquisition and predator avoidance are, at least partially, ameliorated by habitat and/or behaviour.

Although there is general agreement that moult requires extensive physiological and behavioural adjustments (King 1981), quantifying costs of these adjustments is difficult, as it requires segregating them from other components of a bird's energy budget (Walsberg 1983). There is evidence from both wild and captive birds that there are high metabolic costs during the period of wing moult (Murphy 1996; Hoye and Buttemer 2011). For example, Guillemette et al. (2007) found that daily heart rate was elevated throughout wing moult in Common Eiders (*Somateria mollissima*). The majority of this increased energy expenditure does not appear to be directly due to feather synthesis (Schieltz and Murphy 1997), but is related to building associated tissues, as well as increases in amino acid metabolism, cardiovascular activity, daily protein requirements, production of red blood cells, and cyclic osteoporosis (Murphy and King 1982). Increased thermoregulatory costs also may contribute to overall costs, especially in aquatic birds. There is little evidence that plumage disruption during moult interferes with birds' thermoregulatory abilities (Schieltz and Murphy 1997), but there may be evaporative heat loss from increased turnover of body water and possibly from blood-engorged quill sheaths (King 1981). As well, wing-propelled divers may have decreased dive efficiency due to reduced wing area, and thus incur higher foraging costs (Bridge 2004). Non-overlap of moult with breeding activity has been interpreted as indirect evidence that moult is energetically and/or nutritionally costly and so is temporally separated from breeding. However, moult and breeding are not always temporally separated (Gates et al. 1993; Newton 2011) and there are several non-energetic reasons that breeding and moult would not occur simultaneously (Earnst 1992).

In addition to potentially elevated energetic costs during moult, specific nutritional requirements may arise during this period. Feathers are comprised primarily of the protein keratin (Murphy 1996) and the sulphur amino acids (e.g. cyst[e]ine) are often present in higher concentrations in feathers than they are in avian food sources (Hanson 1962; Murphy and King 1992; Murphy 1996; Newton 2011). Additionally, the total amount of protein required during moult is higher than maintenance levels (Murphy 1996).

While evaluating whether Lesser Snow Geese experienced nutritional stress during wing moult, Ankney (1979) noted three ways in which birds can meet nutritional and energetic requirements of this period: (1) increasing daily nutrient intake, (2) reducing other nutrient-demanding functions, and/or (3) drawing on endogenous reserves. When nutrient intake cannot meet demand, then catabolism of tissues can result in stress, if it proceeds to the point that one or more vital physiological functions are impaired (Ankney 1979; King and Murphy 1985).

Remigial moult represents a distinct phase in the annual cycle of waterfowl, generally occurring each year after cessation of breeding activities (Pyle 2005). Some waterfowl remain on breeding grounds during moult, while in some species it occurs after migration to wintering areas. However, many species undergo moult migrations to areas used primarily or exclusively during remigial moult (Salomonsen 1968). Moulting areas may be close to either the breeding or wintering areas, but are sometimes thousands of kilometres distant, and may not be on a direct route from breeding to wintering areas (Robert, Benoit and Savard 2002; Petersen, Bustnes and Systad 2006). The prevalence of moult migration, the high densities of waterfowl found on moulting grounds, and the long distances that may be travelled, suggest that selection of moulting areas can confer significant advantages during the postbreeding period. It is generally thought that moulting areas are chosen on the basis of food availability and protection from predators, because while the birds are flightless they are unable to move far in search of new food supplies and may be more vulnerable than usual to predators (Salomonsen 1968).

Strategies for meeting costs of remigial moult vary considerably among species. Decreases in body mass during remigial moult have been observed in several species of waterfowl: Greylag Geese (*Anser anser*) showed a 22% decrease in body mass, mostly accounted for by use of fat stores (Fox and Kahlert 2005); Pochards (*Aythya farina*) lost 22-24%; and female Tufted Ducks (*A. fuligula*) 12% of their body mass (Fox and King 2011); body mass of male and female Red-billed Teal (*Anas erythroryncha*) decreased by 11% and 21%, respectively (Douthwaite 1976); and male Barrow's Goldeneye (*Bucephala islandica*) lost about 6% of their body mass during the latter half of the period of feather re-growth (van de Wetering and Cooke 2000). However, no significant changes in body mass during the feather growth period were observed in male Mallards (*Anas platyrynchos*) (Young and Boag 1982), Ruddy Ducks (*Oxyura jamaicensis*) (Hohman 1993), and Common Scoters (*Melanitta nigra*) (Fox, Hartmann and Petersen 2008). Increase in body condition index was observed in moulting female Tundra Swans (*Cygnus columbianus*) (Earnst 1992), and male and female Brant (*Branta bernicla*) increased in body mass and total protein during moult (Ankney 1984).

The relative amounts of time devoted to major activities can offer important insights into an animal's requirements and the constraints it may be facing (Paulus 1988; Adams, Robertson and Jones 2000). Acquisition of food is a basic element of behaviour and thus study of foraging strategies can contribute to our understanding of potential constraints to populations and the behavioural scope that is available to a species when responding to change (Pyke 1984). Successfully avoiding predators and obtaining sufficient quantities of food are two of the main determinants of an animal's survival (Bednekoff 2007). Animals must often make trade-offs between predator avoidance and foraging efficiency to maximize their overall fitness (Cresswell 2008). The relative importance of these factors can vary throughout an animal's life cycle and may vary among phases of the annual cycle (Witter, Swaddle and Cuthill 1995). To determine if food acquisition or predation pressure are imposing energetic or demographic constraints during the postbreeding period, we can examine the behavioural and physiological responses of ducks during this period. Strategies used by ducks to balance these requirements may include adjustments in 1) the timing or duration of wing moult, 2) body mass, and 3) foraging effort. Differing strategies may be used depending on species or age/sex cohorts and/or physical environment.

The general objective of this thesis is to examine remigial moult in two species of sea ducks, Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*), moulting along the Pacific coast of North America. Specifically, I studied phenology of remigial moult in scoters, to determine feather growth rates, duration of the flightless period, and timing of moult. I also examined differences in timing between species, sites, sexes, age classes, and years. To determine how scoters meet the energetic and nutritional costs of moult, I quantified variation in body mass and foraging effort.

1.2 Study Species

Scoters (genus *Melanitta*) are sea ducks belonging to the tribe Mergini. The genus includes four species: White-winged or Velvet Scoters (*M. fusca*), Surf Scoters (*M. perspicillata*), Black Scoters (*M. americana*), and Common Scoters (*M. nigra*).

In North America, both Surf and White-winged Scoters (hereafter, scoters) breed throughout northern Canada and Alaska and winter along the Atlantic and Pacific coasts. Nonbreeders, including most yearling birds, often spend summers on the coasts and do not return to breeding areas until their second summer. After the breeding season, many scoters migrate to the coast before moulting remiges, and then migrate to other wintering areas or remain at the moulting site through winter (J. Evenson, WDFW, unpublished data).

Scoters feed almost exclusively by diving (Brown and Fredrickson 1997; Savard, Bordage and Reed 1998), with very different prey types exploited on wintering and breeding grounds. In marine waters, scoters feed heavily on molluscs, particularly bivalves, with herring spawn being an ephemerally important food source in some areas (Vermeer 1981; Vermeer and Bourne 1984; Lewis, Esler and Boyd 2007a; Lewis, Esler and Boyd 2007b; Lewis, Esler and Boyd 2008; Lok et al. 2008). Recent work shows that importance of other invertebrates may have been underestimated, especially for Surf Scoters; at times, crustaceans, polychaetes and other invertebrates may be major components of the diet (Anderson, Lovvorn and Wilson 2008; D. Ward, USGS, unpublished data). On freshwater lakes and wetlands of the breeding grounds, scoters feed primarily on aquatic crustaceans, mainly amphipods and insect larvae (Brown and Fredrickson 1997; Savard, Bordage and Reed 1998).

1.3 Study Areas

Field data for this study were collected in two main areas: southeast Alaska and the Salish Sea (southern British Columbia and northern Washington). In southeast Alaska, fieldwork was concentrated in northern Seymour Canal on Admiralty Island (58.0°N, 134.3°W). The Salish Sea study area encompassed sites at the Fraser River Delta (49.2°N, 123.3°W) and Boundary Bay (49.0°N, 123.0°W) in British Columbia, and Padilla Bay (48.5°N, 122.5°W) and Oak Harbor (48.3°N, 122.6°W) in Washington. At both sites, fieldwork was conducted from late July to late September of 2008 and 2009.

Surveys during 1997-2002 showed that about 185,000 scoters were found in southeast Alaska between Cape Spencer and Portland Canal in late July to early August with only one-third that number present during winter (Hodges, Groves and Conant 2008). Some of the highest concentrations of scoters were observed around eastern Admiralty Island and surveys in early August 2008 indicated that at least 16,000 scoters were in the northern half of Seymour Canal on Admiralty Island in an area approximately 25 km by 8km (R. Dickson, unpublished data). The Salish Sea contains the main moulting sites for scoters south of Alaska, with upwards of 20,000 scoters (E. Anderson, SFU and J. Evenson, WDFW, unpublished data). At both sites, flocks of moulting scoters were generally composed of several hundred to several thousand individuals. Larger aggregations of moulting scoters are not known to occur throughout coastal BC (Savard 1988) or south of Puget Sound. Further, telemetry studies indicate that moulting sites in southeast Alaska and the Salish Sea are used by scoters that winter in other regions, including San Francisco Bay, California (J. Evenson, WDFW, unpublished data).

Admiralty Island, the third largest island in southeast Alaska, is located within the Tongass National Forest (administered by the US Department of Agriculture, Forest Service) and is in the northern portion of the Alexander Archipelago. Seymour Canal is a protected inlet, about 65km long and 8km wide and is oriented with the long axis running roughly north to south. It has a diversity of shoreline types with a mix of soft- and hard-bottom habitats and several small river drainages form estuaries with tidal flats. Maximum tidal range is about 4.8m. The upper end of the inlet is 25 km south of the city of Juneau but it is over 100 km by water from Juneau, and consequently the area is relatively undisturbed by boat traffic or other human activity.

The Fraser River Delta is the largest estuary on the coast of British Columbia and supports a diversity and abundance of bird life that is unsurpassed in Canada. Boundary Bay is a 250km^2 area composed of seashore, intertidal mudflats, eelgrass beds, salt marshes, occasional rocky outcrops, farmland, and urban areas. It is located on the southern edge of the delta and receives little fresh water input from the Fraser River. A 4.7m maximum tidal range and gently sloping shorelines give this region extensive tidal flats composed mainly of fine sediments deposited by outflow from the Fraser River.

Padilla Bay is almost entirely intertidal and contains one of the largest contiguous eelgrass (*Zostera* spp.) beds on the Pacific coast of North America (Bulthuis 1995). Maximum tidal ranges are about 4 m (Bulthuis 1995; Thom, Miller and Kennedy 1995). Intertidal flats are drained by many tidal channels that are mainly <5 m deep. Other than drainage from agricultural lands, there is no direct discharge of freshwater into Padilla Bay. Sediments in most areas of Padilla Bay are medium- to fine-grained sands (E. Anderson, SFU, unpublished data). Oak Harbour is largely unvegetated with intertidal substrates ranging from coarse sand to cobble, and subtidal substrates comprised mainly of fine sands.

In contrast to Admiralty Island, there are large urban centres within the Salish Sea and high volumes of commercial and recreational boat traffic throughout much of the region. Portions of Padilla Bay's shorelines were diked for agriculture around the late 1800s, and two oil refineries are located on March Point along the western border of the bay (Thom, Miller and Kennedy 1995).

1.4 Thesis Outline

In light of unexplained decreases in the North American populations of Surf and White-winged scoters, I studied these species during the period of remigial moult to investigate whether constraints during this phase of the annual cycle may be contributing to observed declines. Field studies were conducted concurrently in southeast Alaska and the Salish Sea to obtain a broad geographical scope of inference. Furthermore, at both sites, adult and subadult Surf and White-winged scoters of both sexes were included in the study.

In Chapter 2, my first data chapter, I focused on phenology of remigial moult in Surf and White-winged Scoters. In particular, I calculated species-specific estimates of primary feather growth rates and duration of the flightless period. I assessed variation in timing of moult in relation to site, cohort (sex and age), and year. The degree of individual interannual variation in timing was compared to inter-individual variability. Based on duration of the flightless period for individuals, and variation in timing among individuals, I determined the population-level duration of remigial moult for both species. Finally, I discuss evidence for existence of temporal optima for remigial moult in scoters.

In Chapter 3, I used body mass dynamics and foraging behaviour to evaluate whether scoters were nutritionally or energetically constrained during remigial moult. Body mass was measured on scoters captured throughout the moult period, and foraging effort was monitored both diurnally and nocturnally during the time of primary feather re-growth.

In Chaper 4, I present overall conclusions drawn from this research and highlight directions for continuation or expansion of this work. I also outline some management recommendations for Surf and White-winged scoters, based on my understanding of their moult ecology.

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2: Phenology and duration of wing moult in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) on the Pacific coast of North America

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Author contribution: Rian Dickson is the primary author of this work and was responsible for all data analysis and collection of data in southeast Alaska.

2.1 Abstract

We quantified phenology and duration of remigial moult in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) in southeast Alaska and the Salish Sea. Thousands of flightless scoters were captured using gill nets and their 9th primaries were measured as an indicator of stage of remigial moult. We provide evidence for the occurrence of a pre-emergence interval that occurs after old primaries are shed and before new ones become visible; we estimated this interval to last 7.4 d, indicating that past studies may have underestimated the flightless period for waterfowl by about 20%. To determine dates of remigial emergence for wild-caught scoters (n=3481), we used primary length at capture, estimates of the pre-emergence interval, and species-specific feather growth rates measured directly on a subset of wild birds and a sample of captive birds. All age and sex classes of both scoter species exhibited a wide range of emergence dates (Surf Scoters: 26 June to 22 September, White-winged Scoters: 6 July to 21 September) suggestive of a lack of strong temporal optima for remigial moult. For both species, timing of moult was influenced by site, year, age and sex. Relative to other waterfowl species, scoters have fairly typical remigial growth rates (Surf Scoters: 3.9mm/d, White-winged Scoters: 4.3mm/d) but a long flightless period (34-49 d), in part because their relatively high wing-loading requires a greater proportion of feather re-growth in order to regain flight. These data suggest that moulting scoters are not under strong selective pressure to complete moult quickly.

2.2 Introduction

Remigial moult is a distinct phase in the annual cycle of waterfowl during which all flight feathers are lost concurrently, leaving individuals flightless. Flight feathers are re-grown synchronously, with the flightless period estimated to last between 20-40 days, depending on species, age, and sex (Hohman, Ankney and Gordon 1992). Remigial moult occurs during the post-breeding period, although the specific timing varies across species, populations, cohorts, and individuals. Temporal optima exist for many events in the annual cycle of birds (Ydenberg, Butler and Lank 2007; Lok et al. 2008; Bridge et al. 2010; Mazerolle, Sealy and Hobson 2011), often resulting in a high degree of synchrony in timing of those events among individuals in a species or population. In many species, timing of wing moult is constrained by breeding or migration phenology (Murphy 1996), although it also may be influenced by needs of individuals during the moult period.

Timing of wing moult is often consistent among years for male ducks, but phenology may be more variable for females if it is contingent upon success of, and therefore time allocated to, breeding activities (Austin and Fredrickson 1986; Savard, Reed and Lesage 2007). In some species with delayed maturity, subadults migrate directly from wintering to moulting areas and therefore typically initiate moult before adults (Salomonsen 1968). Understanding differences in moult phenology among cohorts provides insights on how timing of moult is influenced by other annual cycle events, and is necessary to understand which component of a population is most apt to occur on a moulting area at a given time.

The length of time required to complete remigial moult is determined by primary feather growth rates, which may be controlled by physiological limits (Rohwer et al. 2009). In waterfowl, primary feather growth rates range from 3.0 mm/day to 8.1 mm/day (Hohman, Ankney and Gordon 1992). Most waterfowl are able to fly when primary feathers have reached about 70% of the final length, and the flightless period in most duck species is about 3-4 weeks (Hohman, Ankney and Gordon 1992). Another consideration in determining the duration of flightlessness is that several days may pass after the remiges are shed and before the new primaries are visible (Balat 1970).

However, few studies have attempted to estimate duration of the flightless period prior to emergence of new primaries.

Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) are migratory sea ducks that breed in northern Canada and Alaska, and winter on both Atlantic and Pacific coasts of North America. In spring, scoters generally migrate northwards and move inland to breeding areas mainly in the boreal forest and tundra (Brown and Fredrickson 1997; Savard et al. 1998, Bordage and Reed 1998; Cruz et al. 2009). Male scoters remain on breeding areas for about a month or less, leaving when females begin incubation (Savard et al. 2007, Reed and Lesage 2007). If females fail to nest successfully during the breeding season, they may remain on breeding grounds for some variable amount of time afterward. After leaving breeding areas, most scoters return to the coast and undergo remigial moult. Scoters have a complex age structure in which second-year, non-breeding birds are present in the population, and these subadults may migrate from winter areas directly to moulting areas (Brown and Fredrickson 1997; Savard, Reed and Lesage 2007).

Both Surf and White-winged scoters moult over a large latitudinal range on the Pacific Coast, providing an opportunity to contrast moult phenology across widely separated areas. Basic understanding of moult is lacking for many species (Bridge 2011) and this is particularly true of sea ducks. North American scoter populations have declined by up to 60% since the mid-1900s and the causes remain unknown (Goudie et al. 1994; Hodges et al. 1996; Dickson and Gilchrist 2002; Nysewander et al. 2005). We believe the first step toward understanding possible constraints scoters may face during remigial moult, and the strategies they employ to accommodate them, is quantification of the phenology and duration of the wing moult phase. Our objectives were to determine if timing of moult differed among widely separated moulting areas, evaluate differences in onset of moult among birds in different age and sex classes, contrast moult phenology between two species, and examine the total duration of time that flightless scoters were present at moulting areas.

2.3 Methods

2.3.1 Field methods

We captured White-winged and Surf scoters that were undergoing wing moult in late July to September of 2008 and 2009 in southeast Alaska and the Salish Sea. Capture locations in southeast Alaska were in upper Seymour Canal, on Admiralty Island (58.0°N, 134.3°W). Seymour Canal is a sheltered inlet, about 65 km long and 8 km wide and is oriented with the long axis running roughly north to south. It has a diversity of shoreline types with a mix of soft- and hard-bottom habitats. The Salish Sea study area was much larger, and included the Fraser River Delta (49.2°N, 123.3°W) and Boundary Bay (49.0°N, 123.0°W) in British Columbia, and Padilla Bay (48.5°N, 122.5°W) and Oak Harbor (48.3°N, 122.6°W) in Washington. The Fraser River Delta and Boundary Bay are composed of intertidal mudflats, eelgrass beds, and occasional rocky outcrops. Padilla Bay is almost entirely intertidal and contains one of the largest contiguous eelgrass (*Zostera* spp.) beds on the Pacific coast of North America (Bulthuis 1995). Oak Harbour is largely unvegetated with intertidal substrates ranging from coarse sand to cobble, and subtidal substrates comprised mainly of fine sands.

To capture scoters, we used a floating gill net method, adapted from a submerged mist net technique (Breault and Cheng 1990). This method was a type of drive-trapping in which we used two to three boats to move flocks of scoters toward a free-floating gill net. When the scoters reached the net, we fired a cracker shell to elicit a dive response. We then retrieved the net and any entangled birds. We removed the birds from the net, placed them in small kennels, and then processed them either at a nearby shore station or on the boats. All birds were handled in accordance with protocols approved by the Animal Care Committee at Simon Fraser University (project number 868B).

We marked all captured scoters with a uniquely numbered stainless steel U.S. Geological Survey tarsal band. They were identified to species, sex was determined by plumage and cloacal characteristics, and age class (second-year [SY] or after-second-year [ASY]) by bursal depth (Mather and Esler 1999). For the purposes of this study, SY refers to those scoters that hatched during the previous summer and were beginning their second year, while ASY individuals were two or more years old. We also recorded body mass (± 1 g) and 9th primary length (± 0.1 mm). The length of the 9th primary was used as a metric of the stage of wing moult. In the case of individuals with fully-grown primaries, we examined feather wear to determine if the feathers had been moulted in the current season or if the feathers were from the previous year.

2.3.2 Data analysis

Lengths of primary feathers 1-10 were measured on 14 ASY male Surf Scoters. We examined the degree of correlation among all primaries to evaluate the validity of using the 9th primary length as a metric of wing moult progression. We found that the 9th primary length was highly correlated with all other primary lengths ($r > 0.9$ for all pairwise correlations), so 9th primary length was used as the metric for remigial moult stage in all analyses. The 9th primary was chosen in preference to the 10th primary, as there is a greater chance that the 10th primary will be damaged or missing.

We defined emergence date as the first day on which new primary feathers became visible. While this is often called the moult initiation date, we believe that term is inaccurate, as active feather generation almost certainly begins earlier, before primary growth becomes visible. To estimate emergence date for each captured scoter, we used species-specific feather growth rates (see below) to back-calculate from the 9th primary length at time of capture. For individuals that we captured on multiple occasions within the same year, we based calculations on the first capture date on which new primaries were present. We excluded from our analyses any individuals that had old primaries when captured and that were not recaptured later in the season, as we could not predict when the old primaries would have been shed and new growth initiated.

To estimate primary feather growth rates, we used data from both captive and wild scoters for which primary length was measured on two occasions during wing moult. Measurements of captive scoters included male and female Surf and White-winged scoters held at the Patuxent Wildlife Research Center in Maryland (J-P. Savard, EC, unpublished data) and female White-winged Scoters held at Dry Creek Waterfowl in Washington (E. Anderson, SFU, unpublished data). Measurements of wild scoters included male and female Surf Scoters and male White-winged Scoters captured in the Salish Sea. Feather growth rates for both captive and wild birds were calculated by dividing the change in 9th primary length by the number of days between observations. We then took the average of the estimates across individuals to obtain a single estimate of feather growth rate for each species (there was no evidence that rates differed between sexes or age classes, pers. comm., J-P Savard).

We defined the pre-emergence interval as the time period between the day when old primaries were shed and when new primaries were first visible (i.e. the emergence date). As this period is not well-described in the literature, and few empirical estimates of the duration are available, we used three separate methods to estimate this interval. We did not generate separate estimates for each species, as we did not have sufficient sample sizes.

The first estimate was based on individuals that had no visible primaries when initially captured and that were subsequently recaptured (as per Panek and Majewski 1990). The emergence date was estimated by back-calculating from the second capture date, using estimated feather growth rates. Assuming that there was an equal probability of catching birds on any day between shedding the primaries and first visible growth, the length of the time period between the initial capture date and the estimated emergence date was doubled to obtain an estimate of the total length of the pre-emergence period. This estimate was based upon averages from male and female Surf Scoters and male White-winged Scoters.

For the second estimate of the pre-emergence period, we used ASY Surf Scoters captured in Salish Sea. This group represented our most complete capture effort, with large sample sizes for each sex throughout the moult period. The number of captured individuals with no visible 9th primary was compared to the number with some visible primary growth. The relative numbers of individuals with and without visible newly growing primaries was assumed to be proportional to the amount of time required for each of those stages. Estimates were calculated separately for ASY males and females in each of the two years of the study.

The third method of estimating the pre-emergence interval involved a sample of 30 after-hatch year (AHY) male White-winged Scoters that were collected for a separate project in Georgia Strait during February 2011 (E. Palm, SFU, unpublished data). On each individual, the right 9th primary was marked at the point where it emerged from the skin and then the feather was pulled from the follicle. The base of the feather shaft was measured from the mark to the proximal end to determine the length of the feather shaft that would normally not be visible. This length was then divided by the feather growth rate for White-winged Scoters to determine the number of days that would have elapsed between initiation of growth and visible emergence of the feather.

We calculated a single estimate of the duration of the pre-emergence period by taking the unweighted average of the three point estimates described above (propagation of errors was used to calculate an overall standard error for this estimate). This estimate was then used to predict emergence dates for individuals that did not have visible primaries at the time of capture by adding half of the pre-emergence interval to the capture date (we assumed that, on average, individuals that were captured with no visible primaries were at the midpoint of the pre-emergence period). We also included the pre-emergence period in our estimates of the duration of the flightless period.

After estimating emergence dates for each individual scoter we captured, we used multiple linear regression models to evaluate factors related to variation in remigial emergence dates. Data were analyzed separately for each species, using the same candidate model set. Explanatory variables included cohort (a combination of sex and age class), site (southeast Alaska versus Salish Sea), and year (2008 versus 2009). The four cohorts were female adults (FASY), female subadults (FSY), male adults (MASY), and male subadults (MSY). Each candidate model set included all additive combinations of the main effects and two-way interactions, as well as a null model (Table 2-1and Table 2-2).

To run regression models, we used the *lm* function in R (R Development Core Team 2010). We employed an information-theoretic approach to model selection to evaluate the candidate model sets (Burnham and Anderson 2002). Akaike's information criterion corrected for small sample sizes (AIC_C) was calculated for each candidate model. Candidate models were ranked by their ΔAIC_C values, calculated as the difference between the AIC_C score of each model and of the best-supported model in the candidate set. The relative support for each model in the candidate set was determined by its Akaike weight (w_i), which is a normalized measure of the likelihood of a given model relative to the likelihood of all other models in the candidate set. Parameter likelihood values and weighted parameter estimates based on all candidate models were used in multi-model inference (Burnham and Anderson 2002) to assess the importance of individual variables in the candidate models.

To investigate individual interannual variation in timing of moult, we used individual scoters that were captured in both 2008 and 2009. We calculated the difference between their emergence dates in the two years, and compared it to the difference that would be expected by chance, based on the distributions of emergence dates in both years. This comparison was repeated 1000 times to produce an estimate of the average random difference in initiation dates between the two years. For this analysis of individual interannual variation, we used only ASY female Surf Scoters in the Salish Sea, as there were not sufficient numbers of between-year re-captures for other cohorts (and accordingly, used only distributions of emergence dates for this cohort and location).

To determine length of the flightless period for moulting scoters, we first estimated the minimum 9th primary length required for flight. For that estimate we used the length of the longest newly grown 9th primaries measured on captured scoters, under the assumptions that captured scoters were not capable of flight and that individuals with 9th primaries longer than the maximum we observed for moulting birds were capable of flight and thus would not be captured. The total length of the flightless period was calculated by dividing the length of primary re-growth required for flight by the feather growth rate, and then adding the duration of the pre-emergence interval. We used measurements from scoters captured during previous studies in late fall to early spring to determine length of fully-grown 9th primaries for each species and sex (D. Esler, SFU, unpublished data). The time required to grow primaries to their full length was calculated by dividing 9th primary lengths of these winter-captured birds by the feather growth rate. Using the calculated range of emergence dates and moult duration, we estimated the length of the population-level remigial moult period for each species. For each population (i.e., southeast Alaska or the Salish Sea), the beginning of the remigial moult period is the earliest date of moult initiation for an individual in that population and the end is latest date of remigial feather growth.

2.4 Results

Feather growth rates

Estimated 9th primary growth rates based on combined averages for captive and wild scoters were 3.9±0.22mm/day for Surf Scoters and 4.3±0.25mm/day for White-winged Scoters (all measures of variation are SE unless otherwise noted). Relative to the length of fully grown 9th primaries, these growth rates are equivalent to a daily percent change in length of 2.5% and 2.4% for Surf Scoters and White-winged Scoters, respectively. For wild-caught scoters, primary growth rates were 3.8±0.19mm/day for Surf Scoters (n=9), and 4.7±0.13mm/day for White-winged Scoters (n=8). For captive scoters at Patuxent Wildlife Research Center, primary growth rates were 4.0±0.06mm/day for Surf Scoters (n=5) and 4.4±0.04m/day for White-winged Scoters (n=14) (J-P Savard, EC, unpublished data). Captive White-winged Scoters (n=12) at Dry Creek Waterfowl had a primary growth rate of 3.8±0.35mm/day. Estimated growth rates based on the combined averages for each species were used in further analyses.

Pre-emergence interval

The pre-emergence period was estimated to be 7.4±2.3 days, which was the mean of three methods used to infer the length of this period. The first method, based on recapture of individuals with no primaries visible at first capture (n=9), yielded an estimate of 1.8±0.98 days between loss of old primaries and first appearance of new ones. The second method used proportions of ASY Surf Scoters (Salish Sea only) captured with and without visible growing primaries, and yielded four separate estimates of the pre-emergence interval: estimates for 2008 and 2009, respectively, were 3.1±0.83 and 5.4±0.81 days for male Surf Scoters (n=443) and 10.4±0.70 and 16.3±0.95 days for female Surf Scoters (n=1258). The third method, using measurements on the 9th primaries of collected White-winged Scoters (n=30), yielded an estimate of 7.3±0.038 days for the pre-emergence interval.

Variation in emergence date

Model selection indicated that for Surf Scoters the top-supported model of variation in emergence date included all three main effects (cohort, site, and year) and all two-way interactions (AIC$_C$ w_i = 0.99, Table 2-1). For White-winged Scoters, the two top-supported models included all three main effects and either the cohort × year and site × year interactions (AIC$_C$ w_i = 0.46) or just the cohort × year interaction (AIC$_C$ w_i = 0.40) (Table 2-2). All top-supported models had good explanatory power; in the Surf Scoter analysis, r^2 = 0.62 and for the two top-supported models for White-winged Scoters r^2 = 0.43 and 0.42, respectively. Model-averaged parameter estimates from both models are given in Table 2-3.

Average remigial emergence dates for each species, cohort, site and year are given in Table 2-4. In general, for both species, SY scoters of both sexes began remigial moult earlier than ASY birds, and males started earlier than females (Figure 2-1 and Figure 2-2). The difference between males and females was greater for ASYs than SYs. Overall, SY males moulted first, followed by SY females and ASY males at about the same time, with ASY females beginning much later than all other cohorts. Differences in mean emergence dates among cohorts and the total range in emergence dates were greater for Surf Scoters than for White-winged Scoters (i.e., at the population level, the remigial moult period is longer for Surf Scoters than for White-winged Scoters). For example, based on the model-averaged parameter estimates, the difference in emergence date between SY males and ASY females was 36.7 days in Surf Scoters and only 14.4 days in White-winged Scoters (Table 2-3). Furthermore, emergence dates ranged from 26 June to 22 September for Surf Scoters and from 6 July to 21 September for White-winged Scoters (Table 2-4).

Average emergence dates for both species were earlier for individuals that moulted in southeast Alaska versus the Salish Sea, with the difference between regions being 15.2 days for Surf Scoters and 10.4 days for White-winged Scoters (Table 2-3). However, the parameter estimate for the Surf Scoter site × year interaction indicated that in 2009 moult initiation occurred only 5 days earlier in southeast Alaska than in the southern site. Year had the opposite effect on initiation date between species. In 2009, Surf Scoters moulted 3.6 days earlier than in 2008, while White-winged Scoters moulted

13.3 days later than the previous year. For White-winged Scoters, the cohort × year interaction terms indicated that this difference was driven by the ASY female cohort; for SYs of both sexes and for ASY males, the mean emergence date was very similar in both years at each site. The difference between years for ASY female White-winged Scoters was extreme in southeast Alaska. In 2008 the two captured ASY females moulted quite early in the season, while in 2009 the single ASY female moulted relatively late. However, in Salish Sea, where there was a much larger sample size of ASY female White-winged Scoters, mean emergence date was 12 days later in 2009.

The site × cohort interaction terms have low parameter likelihoods (and small parameter estimates) in the White-winged Scoter analysis, but higher support in the Surf Scoter analysis. They indicate that for Surf Scoters, although SY males and females initiate moult earlier in southeast Alaska than in the Salish Sea, the difference between sites for SYs was not as large as the site difference for ASY males and females.

Individual interannual variation

Within each cohort at both study sites, there was a large range in emergence dates in both years. For one cohort, ASY female Surf Scoters in the Salish Sea, we had a sufficiently large sample size of individuals (n=11) that were captured in both years of the study to allow a comparison of individual interannual variation in moult phenology relative to the variation in timing exhibited by the entire cohort. The average difference in emergence dates between years for recaptured individuals was 3.0±0.77 days. For the 1000 trials in which random emergence dates were drawn from the distributions of moult emergence dates for ASY female Surf Scoters in Salish Sea in 2008 and 2009, the overall average difference was 12.0±0.1 days (range 4.4 – 26.0 days). Clearly, individuals are more consistent in their timing than would be expected based on chance.

Duration of flightlessness

The amount of remigial growth required by Surf Scoters and White-winged Scoters to allow a return to flight was assessed by examining the distribution of 9th primary lengths among captured moulting scoters (Table 2-5). To obtain a plausible range for the length of 9th primary feather required for flight, the values for the 97.5th and 100th percentiles of 9th primary lengths for captured moulting scoters were determined.

We used the 97.5th percentile as a conservative cut-off, as it is possible that some of the moulting scoters we captured may have been able to fly. Comparing these values to average fully-grown 9th primaries, we found that female Surf Scoters were likely capable of flight when 83-93% of their final 9th primary length had been achieved. Male Surf Scoters required a slightly higher percentage of remigial growth (86-98%). For White-winged Scoters the percentage of growth needed for flight was slightly higher again, for both females (89-97%) and males (88-99%). Using estimates of 9th primary length required for flight, we then calculated the duration of the flightless period, based on feather growth rates for each species and the mean estimate of the pre-emergence period (see above). We calculated a lower estimate based on the number of days needed to grow 9th primaries to the length given by the 97.5th percentile cut-off and an upper estimate using the time required to grow 9th primaries to the maximum length observed for captured moulting individuals. The total duration of the 9th primary growth period, including the pre-emergence interval, was calculated using the estimated feather growth rates and the final length of 9th primary feathers (measured on winter-captured scoters). The time required to complete growth of the 9th primaries was 45.6 days and 48.2 days for female and male Surf Scoters, respectively, and 47.2 days and 49.8 days for female and male White-winged Scoters, respectively. See Table 2-5 for estimates of the length of the growth period excluding the pre-emergence interval. Our estimates of the flightless period do not include the time before the old primaries are shed, when birds may be functionally flightless for several days (Hohman, Ankney and Gordon 1992).

To determine the population-level duration of the remigial moult period for both species, we used the earliest and latest remigial emergence dates, and then added the length of the flightless period to the latter date. Male Surf Scoters began moult in late June at both sites, and finished in late September or early October in southeast Alaska and mid-late October in the Salish Sea. For female Surf Scoters at both sites, there were individuals engaged in remigial moult from early July to late October or early November. White-winged Scoter males began wing moult in early July at both sites, while females started in mid-July. Male White-winged Scoters were likely moulting until late September or early October in southeast Alaska and late October to early November in the Salish Sea. Most females would have completed remigial moult by early-mid October in southeast Alaska and late October to early November in the Salish Sea. Thus, there are over four months during which actively moulting scoters may be found at these sites.

2.5 Discussion

Our results can be broadly generalized, as our two study areas were separated by ten degrees of latitude, and differed in habitat composition, prey species, human activity, climate, and other factors. While our estimates for feather growth rates were similar to those found for other waterfowl, our estimates of the duration of the flightless period in Surf Scoters and White-winged Scoters were longer than most estimates for species of the tribes Anatini, Aythyini or Mergini (Hohman, Ankney and Gordon 1992). This may be partly due to our inclusion of the pre-emergence interval in calculating duration of the flightless period. However, excluding the role of the pre-emergence period, we also found that the percentage of remigial re-growth necessary for flight was higher than reported for other waterfowl in previous studies. Other researchers found that most duck species are able to fly with about 70-80% remex growth (Hohman, Ankney and Gordon 1992), while we estimated that scoters required about 85-99% re-growth before they are capable of flight. Previous work focused largely on dabbling ducks, which tend to have lower wing-loading than diving ducks (Savile 1957), and thus would be able to fly with relatively less primary growth. Also, scoters maintain high body mass during moult relative to other phases of the annual cycle (Chapter 3), which also would contribute to high wing-loading and a high percentage of remex growth required to acheive flight. Scoters presumably could shorten the flightless period by increasing feather growth rates or by decreasing body mass through wing moult. Mass loss has been observed in moulting waterfowl of several species and has been interpreted as an adaptive response to shorten the flightless period (Sjoberg 1988; Brown and Saunders 1998). However, scoters do not appear to be under temporal constraints requiring modifications of moult strategies to reduce the duration of flightlessness. Furthermore, a longer, slower period of remigial moult may result in higher quality feathers and thus may be advantageous (Dawson et al. 2000). In addition to the relatively long flightless period, we found a wide range in emergence dates within each cohort (1.5-2.5 months) and species (2.5-3 months) (Table

2-4), which also suggests that there are not strong temporal constraints on wing moult in scoters.

Despite our evidence that there did not appear to be strong selective pressure for an optimal date of remigial moult initiation, timing for individual ASY female Surf Scoters was highly consistent between years. This is perhaps not surprising, as data from mark-resight and satellite and radio telemetry studies indicate that individual sea ducks often have high site fidelity and are temporally consistent across years during other stages of the annual cycle (Robertson and Cooke 1999; Phillips and Powell 2006; Phillips and Powell 2006; Cruz et al. 2009; Regehr 2011). However, we had expected between-year variation in emergence dates for the ASY female cohort, in particular. Initiation of wing moult occurs shortly after breeding activity ceases, so we hypothesized that an individual’s breeding history (e.g. nest initiation date, success or failure, relative timing of failure) in a particular year would affect timing of moult. The between-year consistency we observed suggests that emergence date is either independent of the cessation of breeding activity or that individual timing of reproduction was similar in consecutive years. Although we did not have enough between-year recaptures from other cohorts to conduct similar analyses, the trend appeared to be consistent and differences in emergence dates between years for individual ASY male Surf Scoters and male White-winged Scoters were 2-4 days.

SY scoters likely do not breed and many probably remain on the coast through spring and summer, rather than migrating to breeding grounds (Brown and Houston 1982; Savard, Reed and Lesage 2007). We therefore expected that SY males and females would undergo remigial moult at about the same time. However, for both species, SY males initiated wing moult earlier than did SY females, by 13 days for Surf Scoters and 6 days for White-winged Scoters. There may be some endogenous control of moult timing that causes females to moult later than males, regardless of external factors. In a study of four species of sea ducks (White-winged Scoters, Surf Scoters, Harlequin Ducks [*Histrionicus histrionicus*] and Long-tailed Ducks [*Clangula hyemalis*]) held in captivity at the Patuxent Wildlife Research Center, females started moult on average 7.2±2.4 days later than males (J-P. Savard, EC, unpublished data). Also, SY scoters usually move northwards on the coast, from wintering to moulting areas and female Surf Scoters generally winter further south than do males (D. Esler, SFU, unpublished data), so perhaps SY females migrate farther and/or migrate more slowly before beginning remigial moult. There is also some evidence that some proportion of SY females migrate to breeding grounds (S. Slattery, DUC, unpublished data), which could influence the average emergence date for that cohort, even though the majority of SY females moult at about the same time as SY males. In particular, see Figure 2-1 for Surf Scoter SY females in the Salish Sea (FemaleSY SALS); especially in 2008, it appears that there may be two "waves" of moult initiation. It may be that the earlier group are SY females that remained on the coast, moving directly from wintering to moulting areas, while the second group migrated to breeding grounds and then returned to coast to undergo remigial moult.

Moult initiation dates for scoters on the Pacific coast generally correspond to timing of involvement in breeding activities for each of the cohorts. Overall, SY scoters of both sexes began remigial moult first, followed shortly thereafter by ASY males, with most ASY females moulting considerably later. Many ASY female Surf Scoters do not begin remigial moult until late August or September, so these females could have successfully hatched and raised broods before leaving the breeding grounds. Phenology of breeding and moult migration have been studied in Surf Scoters breeding in Quebec and moulting in the St. Lawrence estuary (Savard, Reed and Lesage 2007), but similar data are not available for Surf Scoters that moult on the Pacific coast. While dates may differ between the Atlantic and Pacific coasts, the relative timing of events is likely similar. In Quebec, female Surf Scoters began incubation in mid to late June, and at this time most male Surf Scoters left the breeding areas, after having been there for only three weeks (Savard, Reed and Lesage 2007). Numbers of lone females on breeding lakes increased from mid-June through July as females failed in their breeding attempts, and many of these females departed in late July. Females that failed early in reproduction or lost their broods after hatching left breeding areas earlier than females that remained with their broods (Savard, Reed and Lesage 2007). Successful females may remain with their broods until late August or September, when they abandon their ducklings before they fledge (Savard, Reed and Lesage 2007; Lesage, Reed and Savard 2008). Surveys in the St. Lawrence estuary indicate that male Surf Scoters arrive on the coast in late June and begin remigial moult in late July (Savard et al. 1999) while increased proportions of females are observed in August (Savard, Bordage and Reed 1998).

For White-winged Scoters, timing of various breeding activities has been documented at several sites in western North America, including Redberry Lake, Saskatchewan, Cardinal Lake, Northwest Territories, and Yukon Flats, Alaska. Links between breeding and wintering areas have been established through stable isotope analyses and 79% of female White-winged Scoters nesting at Redberry Lake wintered on the Pacific coast (C. Wood, USask, unpublished data) and 92% of White-winged Scoters (both males and females) breeding at Cardinal Lake wintered on the Pacific coast (K. Gurney,USask, unpublished data). Similar data are not available for the Yukon Flats, but it is likely that most scoters breeding there wintered in the Pacific. Thus, breeding phenology at these sites is relevant to our understanding of moult initiation dates for White-winged Scoters on the Pacific coast. In Alberta and Saskatchewan, near the southern extent of the breeding range, incubation initiation dates ranged from 19 June to 13 July, with most females beginning incubation in late June or early July (Brown and Fredrickson 1997). At Cardinal Lake and Yukon Flats, females also began incubating in late June to early July and the range in dates may be smaller than it is further south (Safine 2005; S. Slattery, DUC, unpublished data). Generally, breeding phenology is quite synchronous across a large geographic area and 15 degrees of latitude. Males leave breeding areas shortly after females begin incubation (Brown and Fredrickson 1997). The earliest moult initiation dates for ASY White-winged Scoter males were 6 July in southeast Alaska and 12 July in the Salish Sea, 3-4 weeks after the earliest incubation initiation dates. Average emergence dates for ASY White-winged Scoter males were 24-28 July in southeast Alaska and 3-5 August in the Salish Sea, again about a month later than peak incubation initiation (24 June to 3 July). Latest dates of remigial emergence were late August to mid-September in the Salish Sea. Latest incubation initiation is in mid July, so some ASY males are not beginning moult until two months after the latest incubation initiation dates. While scoters can migrate from breeding grounds to coastal moulting areas in just a few days, most individuals take several weeks, with numerous stops and/or circuitous routes (J. Evenson, WDFW, unpublished data). There is considerable variation in the amount of time that ASY males spend on the coast before beginning remigial moult. Some individuals likely begin remigial moult just a week or two after arriving from breeding grounds, while others may be on the coast for close to two months before shedding their remiges. Males may be undergoing body moult prior to initiating wing moult, so varying schedules of body moult may affect timing of remigial moult. As well, some individuals may take longer to migrate to the coast, or they may arrive on the coast but delay moult initiation for some period of time. For male diving ducks breeding and moulting in Idaho, about six weeks elapsed between desertion of their mates and the onset of flightlessness (Oring 1964) and Barrow's Goldeneye arrive at moulting areas over a month before shedding primary feathers (Robert, Benoit and Savard 2002).

Salomonsen (1968) suggested that adult females that migrate to the same moulting locations as males and subadults are likely non-breeders (in that year).. However, our data suggest that many adult females moulting on the coast have at least migrated to breeding grounds in the current year, and either did not successfully nest, or may have hatched ducklings but not remained with them until fledging. Most White-winged Scoter nests in Saskatchewan, the Northwest Territories, and Alaska hatch in mid to late July (Brown and Brown 1981; Brown and Fredrickson 1997; Safine 2005; Traylor and Alisauskas 2006; S. Slattery, DUC, unpublished data), and the ducklings fledge at about 56-70 days (Brown and Brown 1981; Brown and Fredrickson 1997; Traylor and Alisauskas 2006) so earliest fledge dates would be in mid September. The latest emergence dates we recorded for ASY females were in mid to late September (6 September 2008 and 21 September 2009), and these females probably would have arrived on the moulting grounds at least one week before remigial growth first became visible. Therefore, it is likely that most female White-winged Scoters moulting on the coast would not have successfully fledged young before leaving the breeding grounds; however many female scoters abandon their broods before fledging, even if their ducklings have survived (Brown and Brown 1981; Traylor, Alisauskas and Kehoe 2008). Brood amalgamation commonly occurs in scoters, and thus if females leave surviving ducklings, they may be associated with remaining females and other ducklings (Brown and Fredrickson 1997; Traylor, Alisauskas and Kehoe 2008).

Our estimates of scoter primary feather growth rates are similar to those obtained for adults of other duck species (4.22 – 5.2mm/day) and fall within the typical range of 2-3% daily change in length, relative to final primary length (Hohman, Ankney and Gordon 1992). However, they are higher than values obtained from allometric equations (Rohwer et al. 2009), which give values of 3.3mm/day and 3.5mm/day for Surf Scoters and White-winged Scoters, respectively. These equations yield estimates of a species' expected feather growth rates based on mass, and were developed from a database that included 43 species, but only 10 of which were waterfowl (Rohwer et al. 2009). It appears that scoters grow flight feathers faster than would be expected based on mass alone, although that might be expected for synchronous remigial moulters.

Estimates of the pre-emergence period are lacking in most published descriptions of remigial moult, whether for waterfowl or other species. Balat (1970) reported that 2-4 days elapsed between the shedding of old primaries and appearance of the new in captive Mallards and Bowman (1987) used a value of three days of no visible primary growth in American Black Ducks (*Anas rubripes*). However, our data indicate that the pre-emergence period may last a week or more. Our estimates using the proportional time calculation method produced very different values for male and female Surf Scoters. On average, male Surf Scoters moult earlier than females, our capture effort did not coincide with the earliest moulting males nor the latest females. Therefore, we believe that these estimates are likely biased in opposite directions for each of the sexes; that is, the male values probably underestimate the pre-emergence interval and the female estimates are likely high. This time period is difficult to quantify in free-ranging birds, and more precise estimates from captive birds would be useful. Measurements on captive Harlequin Ducks indicate that the pre-emergence interval for this species is ≥ 7 days (E. Anderson, SFU, unpublished data) and for Spectacled Eiders it may be as long as 14 days or more (T. Hollmenn, pers. comm.), so we believe that our estimate of 7.4 days is reasonable. Furthermore, primary feather growth appears to be slightly slower during the earlier stages (J-P Savard, pers.comm.), so our estimates of the pre-emergence interval should be conservative, and in reality, this period may be even longer.

This interval is generally not included in estimates of the length of the flightless period for waterfowl but may be a significant amount of time, representing about twenty percent of the flightless period. This stage in the moult process has perhaps been overlooked as it is commonly believed that old feathers are “pushed out” by the growth of new feathers (Voitkevich 1966). While the loss of the old feathers may coincide with the initiation of new growth, a variable amount of time may pass before those new growing feathers actually emerge from the follicles and become visible. For many species and/or feather types, this time may be negligible, but for remiges and rectrices of larger birds it is likely that several days elapse before new feathers visibly emerge from follicles.

Our study indicates there is a wide temporal window during which scoters undergo remigial moult on the coast. If there were strong disadvantages to moulting later, then we would not expect to see such a large gap in timing between the end of involvement in breeding activities and initiation of remigial moult. It is possible that scoters are building reserves after they arrive on the coast and before they shed flight feathers, in which case there may be some trade-off between body mass and moult initiation. However, we have recorded a large degree of individual variation in body mass during moult, and it does not appear that there is a threshold mass that must be attained before moult is commenced (Chapter 3).

Due to the wide range in moult initiation dates, there is a correspondingly long period during which flightless scoters occur in both southeast Alaska and the Salish Sea. Based on captures of scoters at both of these study sites, the earliest emergence dates that we have calculated are in late June (for SY and ASY male Surf Scoters). These individuals most likely shed their primaries about a week prior to the emergence date, and may have been flightless for some time before that as well. The latest emergence dates were 21-22 September, for adult females of both species, and those individuals would not have completed remigial growth until late October or early November. There may have been individuals in these populations that began remigial moult even later than this, and were not detected because our capture effort had ended. Remigial moult occupies about ten percent of the year for an individual scoter, but at the population level the process occurs over a period of more than four months.

2.6 Figures

Figure 2-1. Remigial emergence dates for Surf Scoters (n = 2671) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009. Each point represents the emergence date for an individual scoter. SY = second year, ASY = after-second year.

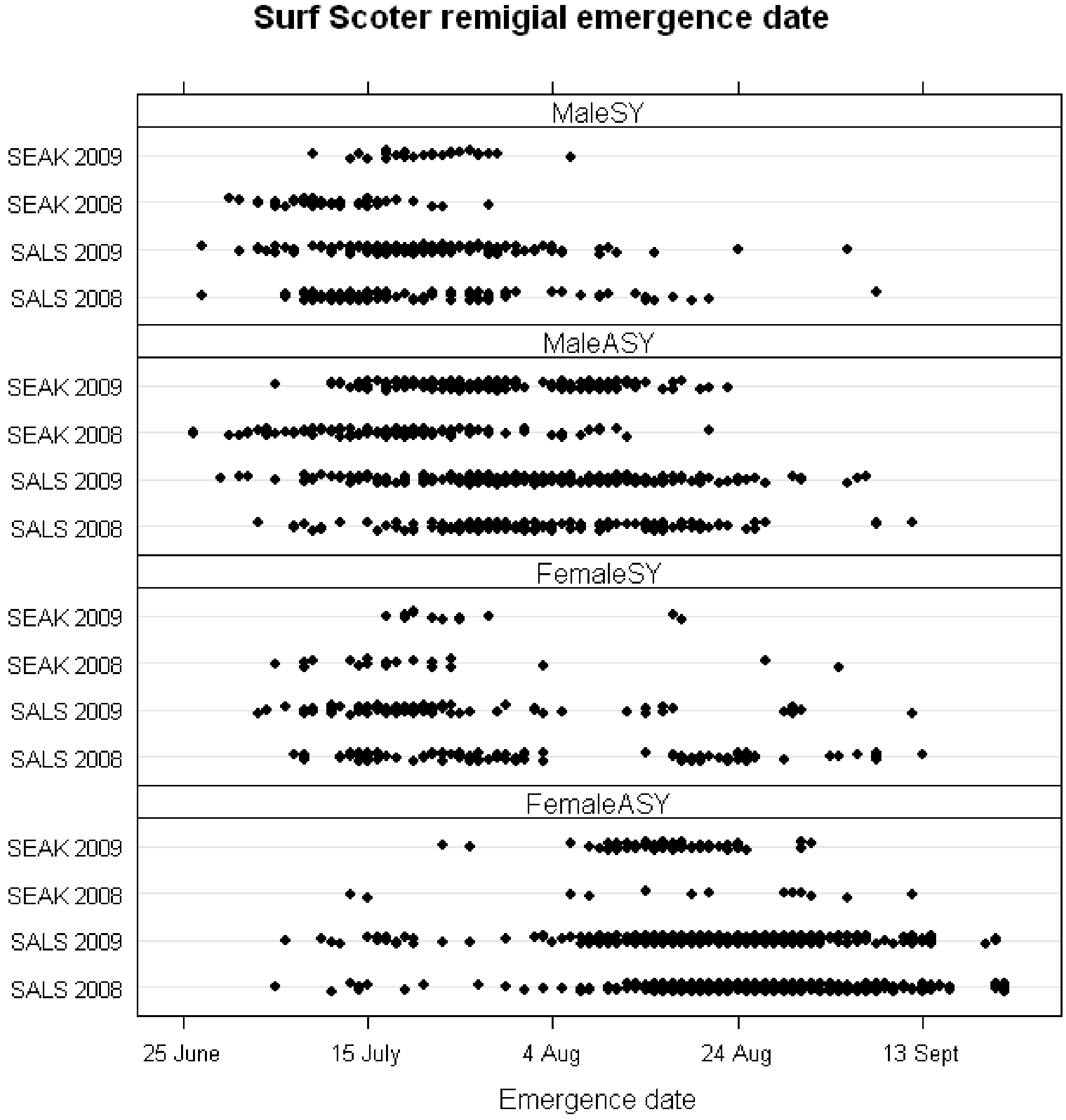
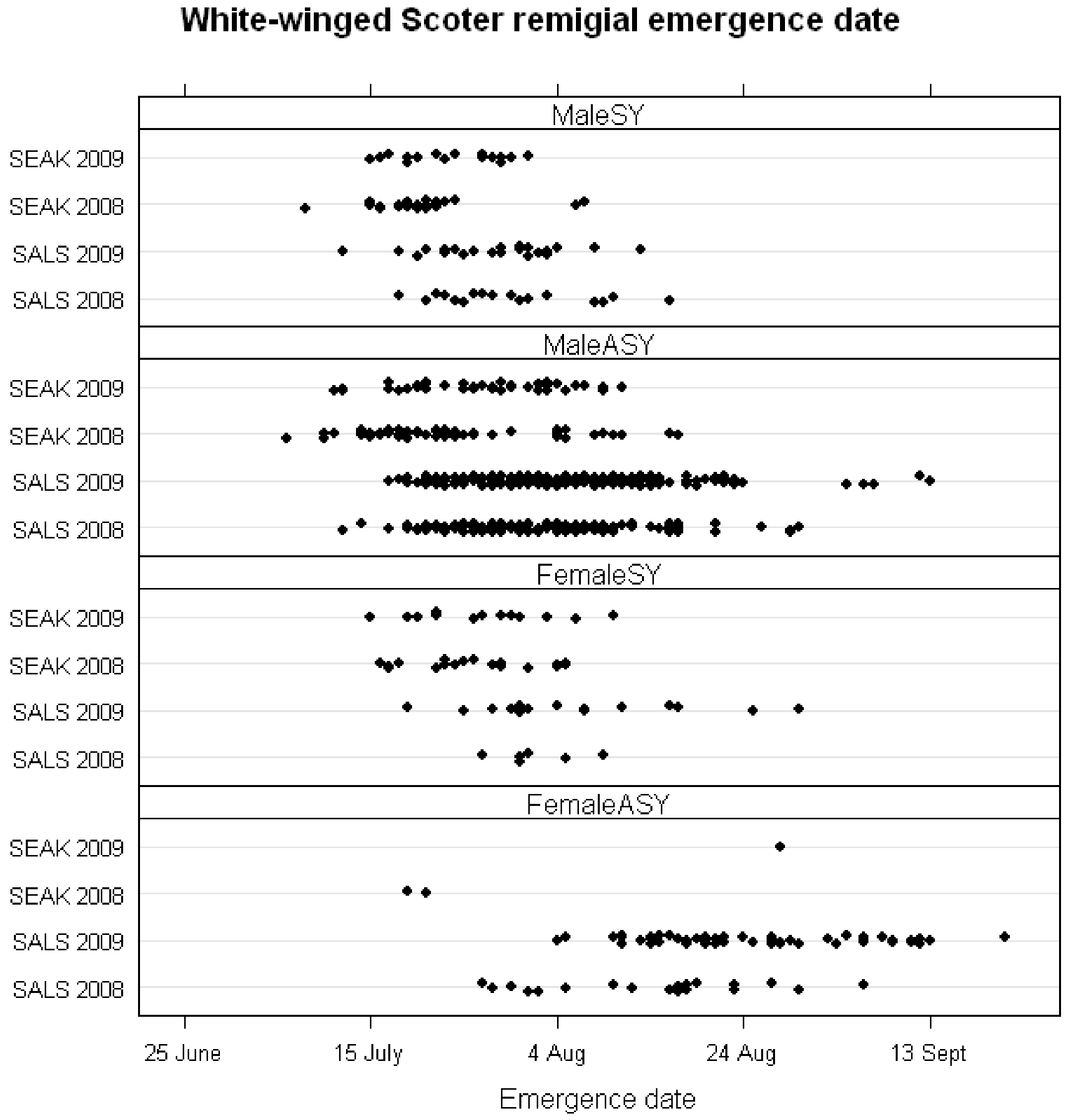


Figure 2-2. Remigial emergence dates for White-winged Scoters (n = 810) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009. Each point represents the emergence date for an individual scoter. SY = second year, ASY = after-second year.



2.7 Tables

Table 2-1. Multiple linear regression model results assessing variation in 9th primary feather emergence dates in Surf Scoters in southeast Alaska and the Salish Sea.

Response	Model	k	ΔAIC_C	w_i
SUSC emergence date	Cohort[a] + Site[b] + Year[c] + Cohort × Site + Cohort × Year + Site × Year	14	0.00	0.99
	Cohort + Site + Year + Cohort × Year + Site × Year	11	8.39	0.01
	Cohort + Site + Year + Cohort × Site + Site × Year	11	22.88	0.00
	Cohort + Site + Year + Site × Year	8	31.68	0.00
	Cohort + Site + Year + Cohort × Year	10	53.09	0.00
	Cohort + Site + Year + Cohort × Site + Cohort × Year	13	54.28	0.00
	Cohort + Site + Year	7	101.47	0.00
	Cohort + Site + Year + Cohort × Site	10	104.08	0.00
	Cohort + Site	6	109.39	0.00
	Cohort + Site + Cohort × Site	9	111.19	0.00
	Cohort + Year + Cohort × Year	9	174.31	0.00
	Cohort + Year	6	231.09	0.00
	Cohort	5	242.15	0.00
	Site + Year + Site × Year	5	2091.88	0.00
	Site + Year	4	2215.36	0.00
	Site	3	2235.83	0.00
	Year	3	2515.85	0.00
	Null	2	2550.99	0.00

Note: *The number of parameters (k) includes +1 for intercept and +1 for model variance estimated for each model.*

[a] *Cohort = FemaleASY, FemaleSY, MaleASY or MaleSY (ASY = after second year, SY = second year)*

[b] *Site = Southeast Alaska or Salish Se*

a[c] *Year = 2008 or 2009*

Table 2-2. Multiple linear regression model results assessing variation in 9th primary feather emergence dates in White-winged Scoters in southeast Alaska and the Salish Sea.

Response	**Model**	**k**	**ΔAIC_C**	**w_i**
WWSC emergence date	Cohort[a] + Site[b] + Year[c] + Cohort × Year + Site × Year	11	0.00	0.46
	Cohort + Site + Year + Cohort × Year	10	0.28	0.40
	Cohort + Site + Year + Cohort × Site + Cohort × Year + Site × Year	14	3.76	0.07
	Cohort + Site + Year + Cohort × Site + Cohort × Year	13	3.77	0.07
	Cohort + Site + Year	7	17.07	0.00
	Cohort + Site + Year + Cohort × Site	10	17.71	0.00
	Cohort + Site + Year + Site × Year	8	18.83	0.00
	Cohort + Site + Year + Cohort × Site + Site × Year	11	19.48	0.00
	Cohort + Site	6	31.87	0.00
	Cohort + Site + Cohort × Site	9	32.23	0.00
	Cohort + Year + Cohort × Year	9	98.54	0.00
	Cohort + Year	6	109.88	0.00
	Cohort	5	141.65	0.00
	Site + Year	4	258.23	0.00
	Site + Year + Site × Year	5	260.25	0.00
	Site	3	276.05	0.00
	Year	3	388.84	0.00
	Null	2	431.07	0.00

Note: The number of parameters (k) includes +1 for intercept and +1 for model variance estimated for each model.

[a] *Cohort = FemaleASY, FemaleSY, MaleASY or MaleSY (ASY = after second year, SY = second year)*

[b] *Site = Southeast Alaska or Salish Se*

a[c] *Year = 2008 or 2009*

Table 2-3. Parameter likelihoods and weighted parameter estimates ± unconditional standard error (SE) from multiple linear regression models evaluating variation in remigial emergence dates in Surf Scoters and White-winged Scoters in southeast Alaska and the Salish Sea. Parameter estimates are for emergence date with June 25=0.

	Surf Scoter		White-winged Scoter	
Explanatory variable	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Intercept	1.00	62.0 ± 0.44	1.00	48.9 ± 2.02
Cohort(FSY)	1.00	-23.3 ± 1.20	1.00	-8.5 ± 2.95
Cohort(MASY)	1.00	-22.2 ± 0.96	1.00	-9.9 ± 2.11
Cohort(MSY)	1.00	-36.7 ± 1.15	1.00	-14.4 ± 2.61
Site (SEAK)	1.00	-15.2 ± 1.72	1.00	-10.4 ± 2.4
Year(2009)	1.00	-3.6 ± 0.64	1.00	13.3 ± 2.36
Cohort(FSY) × Site(SEAK)	0.99	5.6 ± 2.64	0.14	1 ± 2.13
Cohort(MASY) × Site(SEAK)	0.99	0.4 ± 1.52	0.14	0.9 ± 1.87
Cohort(MSY) × Site(SEAK)	0.99	6.1 ± 2.15	0.14	1.2 ± 2.37
Cohort(FSY) × Year(2009)	1.00	-6.4 ± 1.71	1.00	-12.9 ± 3.61
Cohort(MASY) × Year(2009)	1.00	2.0 ± 1.20	1.00	-11.5 ± 2.5
Cohort(MSY) × Year(2009)	1.00	3.9 ± 1.44	1.00	-13.4 ± 3.21
Site(SEAK) × Year(2009)	1.00	10.2 ± 1.37	0.53	1.4 ± 1.76

Note: *Parameter likelihoods closest to 1 have the greatest relative support.*

FSY = Female second year, MASY = male after-second year, MSY = male second year

SEAK = Southeast Alaska

All variables are categorical; references cases are cohort(FASY), site(SALS) and year(2008).

Table 2-4. Remigial emergence dates (mean ± SE) for Surf and White-winged scoters moulting in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009.

			Surf Scoter			**White-winged Scoter**		
Cohort	Site	Year	n	Mean	Range	n	Mean	Range
Male SY	SEAK	2008	43	11 Jul ± 0.94	30 Jun - 28 Jul	30	20 Jul ± 1.05	8 Jul - 7 Aug
Male SY	SEAK	2009	27	21 Jul ± 1.12	9 Jul - 6 Aug	18	23 Jul ± 1.22	15 Jul - 1 Aug
Male SY	SALS	2008	107	20 Jul ± 1.17	27 Jun - 8 Sep	18	29 Jul ± 1.86	18 Jul - 16 Aug
Male SY	SALS	2009	174	20 Jul ± 0.71	27 Jun - 5 Sep	24	27 Jul ± 1.46	12 Jul - 13 Aug
Male ASY	SEAK	2008	108	19 Jul ± 1.03	26 Jun - 21 Aug	63	24 Jul ± 1.15	6 Jul - 17 Aug
Male ASY	SEAK	2009	198	29 Jul ± 0.66	5 Jul - 23 Aug	42	27 Jul ± 1.23	11 Jul - 11 Aug
Male ASY	SALS	2008	159	4 Aug ± 1.08	3 Jul - 12 Sep	174	3 Aug ± 0.73	12 Jul - 30 Aug
Male ASY	SALS	2009	284	1 Aug ± 0.72	29 Jun - 7 Sep	306	4 Aug ± 0.55	17 Jul - 13 Sep
Female SY	SEAK	2008	20	23 Jul ± 3.91	5 Jul - 4 Sep	20	26 Jul ± 1.52	16 Jul - 5 Aug
Female SY	SEAK	2009	13	25 Jul ± 2.93	17 Jul - 18 Aug	13	27 Jul ± 2.09	15 Jul - 10 Aug
Female SY	SALS	2008	101	2 Aug ± 1.94	7 Jul - 13 Sep	6	1 Aug ± 1.85	27 Jul - 9 Aug
Female SY	SALS	2009	83	23 Jul ± 1.62	3 Jul - 12 Sep	17	5 Aug ± 2.74	19 Jul - 30 Aug
Female ASY	SEAK	2008	13	18 Aug ± 5.25	13 Jul - 12 Sep	2	20 Jul ± 1.00	19 Jul - 21 Jul
Female ASY	SEAK	2009	83	16 Aug ± 0.67	23 Jul - 1 Sep	1	28 Aug	NA
Female ASY	SALS	2008	683	25 Aug ± 0.41	5 Jul - 22 Sep	20	14 Aug ± 2.54	27 Jul - 6 Sep
Female ASY	SALS	2009	575	22 Aug ± 0.46	6 Jul - 21 Sep	56	26 Aug ± 1.51	4 Aug - 21 Sep

Table 2-5. Estimates of the duration of the flightless period during remigial moult for Surf and White-winged scoters. Estimates are calculated using feather growth rates of 3.9mm/day for Surf Scoters and 4.3mm/day for White-winged Scoters. The length required for flight is based on the distributions of primary lengths of flightless scoters captured during remigial moult.

			Length required for Flight[a] (mm)		**Pre-emergence interval (days)**	**Length of flightless period[b] (days)**		**9th primary growth period (days)**	
Species	Sex	Final 9th primary length[c] (mm)	97.5th percentile	100th percentile	Mean Estimate ± SE	Lower estimate	Upper estimate	From emergence date	Including pre-emergence interval
SUSC	F	150	125.3 (83%)	139 (93%)	7.4 ± 2.3	39.3	42.7	38.2	45.6
	M	160	138.0 (86%)	158 (98%)	7.4 ± 2.3	42.5	47.6	40.8	48.2
WWSC	F	170	151.8 (89%)	164 (97%)	7.4 ± 2.3	43.0	45.9	39.8	47.2
	M	181	158.3 (88%)	179 (99%)	7.4 ± 2.3	44.5	49.4	42.4	49.8

[a] *Values in parentheses are the percentages of final 9th primary length.*

[b] *Including the pre-emergence interval but excluding the flightless period prior to shedding old primaries; lower and upper estimates are based on the 97.5th and 100th percentiles for the length required for flight, respectively.*

[c] *Final 9th primary lengths are averages based on measurements taken on after-hatch-year scoters caught during winter (D. Esler, SFU, unpublished data)*

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3: Body mass dynamics and foraging effort of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) during remigial moult

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3.1 Abstract

We investigated strategies used by Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) to meet nutritional and energetic costs of remigial moult by assessing body mass dynamics and foraging effort. Scoters were captured at two major moulting locations on the Pacific coast of North America, in southeast Alaska and the Salish Sea (British Columbia and Washington). All age and sex classes of both species (n=3310) exhibited increases in body mass during primary feather growth and body mass was high relative to other annual stages, indicating that endogenous nutrient stores were not catabolised to provide nutrients or energy for remigial moult. Also, foraging effort of radio-marked Surf Scoters (n=91 individuals, 454 1-hr observation periods) and White-winged Scoters (n=48 individuals, 222 1-hr observation periods) was similar to that during winter and, suggesting that energetic and nutritional costs were readily met through moderate foraging effort. Furthermore, we found no evidence of nocturnal foraging. Scoters on the Pacific coast apparently employ strategies and select habitats that preclude nutritional or energetic constraints during the remigial moult phase of the annual cycle.

3.2 Introduction

Growth of new feathers is a major productive event in the annual cycle of birds (Walsberg 1983), yet moult remains poorly understood for most species (Bridge 2011). Accurate quantification of energetic and nutritional requirements associated with moult is difficult, and much debate remains as to the extent and impact of these costs (Murphy 1996). If moult requires substantial increases in energy and/or nutrient use relative to maintenance levels, birds have several, non-exclusive options for meeting those costs: they can reduce other nutrient-demanding functions, increase daily food intake, or catabolise body tissue (Ankney 1979). If one or more of these strategies are not adequate for meeting nutritional and energetic costs of moult, then moult could be considered a constraint resulting in sub-optimal condition, which in turn could reduce subsequent demographic performance.

Growth of remiges represents a major component of moult, both in terms of the amount of feather material replaced and the time required (Murphy 1996; Hedenstrom et al. 2007; Rohwer et al. 2009). In waterfowl, remigial moult is simultaneous – individuals lose all of their flight feathers over a period of few days (or less) and then grow new remiges synchronously over several weeks (Hohman, Ankney and Gordon 1992). In addition to a potential increase in energetic and nutritional demands associated with remigial moult, waterfowl may have decreased ability to find and/or obtain food during this time. If local food supplies are depleted, they are unable to fly to other areas in search of new sources. Even if food is readily available, reduced wing area may affect efficiency of some foraging techniques, including diving (Bridge 2004). Conversely, flapping flight is an energetically expensive mode of locomotion and thus flightlessness may reduce daily energetic costs (Guillemette et al. 2007). Flightless moulting waterfowl also may be more vulnerable to predators (Pomeroy 1990; Guillemette and Ouellet 2005). Dopfner, Quillfeldt and Bauer (2009) suggested that remigial moult is “probably the most critical [period] in a waterbird’s annual cycle,” although empirical data supporting that statement are generally lacking.

Early studies of Canada Geese (*Branta canadensis*) led Hanson (1962) to conclude that moult is the most stressful period in the annual cycle of waterfowl. He found that geese were catabolising pectoral muscle and leg bone to meet demands of remigial moult and were unable to obtain sufficient nutrients by increasing their feeding activity. However, Ankney (1979) found that moulting Lesser Snow Geese (*Chen caerulescens caerulescens*) required little or no catabolism of body tissues, as birds were able to meet their needs through exogenous resources, and he predicted that similar results would be found in other waterfowl. Although Hanson (1962) did not explicitly define the term stressful in his assessment of condition in moulting geese, Ankney (1979) took it to mean "a situation in which a bird's nutrient demands exceed its nutrient ingestion, resulting in catabolism of body tissue". King and Murphy (1985) added the caveat that stress occurs only when net catabolism of body tissue causes "one or more vital physiological functions [to be] impaired".

Body mass dynamics in moulting waterfowl vary considerably, with some species showing declining mass during moult (Douthwaite 1976; van de Wetering and Cooke 2000; Fox and Kahlert 2005; Fox and King 2011), others stability (Young and Boag 1982; Hohman 1993; Fox, Hartmann and Petersen 2008), and a few indicating mass increases (Ankney 1984; Earnst 1992). Variability within species also has been documented – in one study Blue-winged Teal (*Anas discors*) showed an 18% reduction in body mass relative to pre-moult values, with about half of the reduction attributed to loss of flight muscle mass (Brown and Saunders 1998), while in another study Blue-winged Teal increased body mass and fat stores during the flightless period (Dubowy 1985).

When evaluating body mass dynamics, it is often incorrectly assumed that more reserves are better (King and Murphy 1985). While birds with abundant fat and muscle tissue sometimes may be at an advantage (e.g., during migration and breeding) this is not always the case (Lima 1986; McNamara and Houston 1990). Observed declines in mass during wing moult may serve an adaptive function, rather than being a response to nutritional or energetic stress. A reduction in body mass results in lower wing-loading and may allow a bird to regain flight with a smaller wing surface area (i.e. at an earlier stage of feather re-growth) (Sjoberg 1988; Brown and Saunders 1998). If food sources are stable and abundant and the cost of carrying reserves is high (as may be the case for birds attempting to regain flight capability), then building and maintaining large nutrient stores may not be the best strategy (Ankney 1979; Witter and Cuthill 1993).

The concept of capital versus income strategies of nutrient and energy management was originally proposed by Drent and Daan (1980) as a hypothesized mechanism by which females could decide whether to produce an additional egg. Subsequently, the meaning has shifted to refer to the timing of resource acquisition relative to when those resources are used to meet costs of reproduction, with the recognition that most species likely fall somewhere on a continuum between extremes of entirely capital or entirely income strategies (sensu Thomas 1983, 1988; Jonsson 1997). It may be useful to adapt this terminology to characterise moult strategies: individuals can use previously accumulated nutrient stores (capital moulting) or rely on food acquisition (income moulting) to fuel energetic and nutritional costs of remigial moult. The trade-offs associated with these contrasting breeding strategies would be similar during moult, and the preferred strategy depends on food availability relative to requirements (Thomas 1988). Capital strategies provide a buffer against insufficient or unpredictable food availability, but require additional time and energy for acquisition and mobilisation of endogenous stores (Thomas 1988). Additionally, reduced foraging activity during the moult period may help minimize damage to growing feathers (Murphy 1996). Income strategies likely allow for a more direct, efficient use of resources and therefore are favoured when food resources are predictable, abundant and easily accessible (Thomas 1988). Carrying endogenous stores may increase predation danger by reducing flight speed or manoeuvrability (Jonsson 1997) but could also mitigate risks by allowing birds to reduce activity and/or increase vigilance during the remigial moult period (Hohman et al. 1992; Murphy 1996; Adams et al. 2000).

Consideration of activity levels and foraging effort has the potential to expand our understanding of moult mass dynamics. As might be expected, different species of waterfowl show varying activity patterns during remigial moult. Several species appear to reduce activity levels in general and feeding activity in particular (Austin 1987; Dopfner, Quillfeldt and Bauer 2009), while others show increases (Dopfner, Quillfeldt and Bauer 2009) or no change (Guillemette et al. 2007).

Low foraging effort and use of endogenous stores during moult may be adaptations to reduce predation danger during this potentially vulnerable phase of the annual cycle (Owen and Ogilvie 1979; Fox and King 2011). These responses may be less beneficial for waterfowl that moult in areas with low predation danger and abundant food sources, especially if they arrive at moulting areas with low endogenous reserves after having migrated long distances (Fox and King 2011). Given the complexity of factors involved, it is difficult to interpret the meaning of changes in either body mass or foraging effort independently. However, when these metrics are considered in combination, our ability to draw inferences about the possible trade-offs being negotiated during this phase is greatly increased. If decreases in body mass are observed, it is difficult to distinguish whether an animal is relying on endogenous reserves or if mass loss is an adaptive response to environmental conditions. Also, body mass may be an insensitive measure of energetic or nutritional constraint unless conditions are extreme, as animals often will adjust foraging effort to maintain optimal body mass (Hario and Ost 2002; Jakubas et al. 2011). Thus, quantification of foraging effort gives us a context in which to evaluate changes in body mass.

We studied body mass dynamics and foraging effort in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) (hereafter, “scoters”) moulting in southeast Alaska and the Salish Sea of British Columbia and Washington to examine how they met the energetic and nutritional costs of remigial moult. If remigial moult presented nutritional or energetic challenges for moulting scoters, we would expect to see declining body mass and/or increased foraging effort during the moult period. If scoters were able to meet the nutritional and energetic requirements of moult, we would expect body mass to remain constant or increase during feather growth. However, if body mass declines during moult were an adaptive response allowing an early return to flight, then we would predict decreased foraging effort and use of endogenous stores, particularly in later stages of feather growth. Given their differing investments in migration and breeding activities in the months directly preceding remigial moult, we thought that we might see differences among adult males and females and subadults. Subadults and males would have more opportunity than breeding females to build endogenous stores prior to moult, and so would be more likely to exhibit decreases in body mass along with lower foraging effort (i.e. ‘capital moulting’). Adult females arriving from breeding grounds may not have large stores and are also generally moulting later in the season, so higher foraging rates and stable or increasing body mass might be expected (i.e. ‘income moulting’).

3.3 Methods

3.3.1 Field methods

We measured body mass and foraging effort of moulting scoters to assess whether they were catabolising endogenous reserves and/or increasing their foraging effort to meet nutritional and energetic requirements of remigial growth. These separate measures allowed us to explore whether moulting scoters incurred energetic or nutritional stress that might influence their performance during this, or subsequent, stages of the annual cycle. Our study included adults and subadults of both sexes and species at our two study sites.

In North America, scoters breed mainly in the northern boreal regions of the continent and winter along both the Atlantic and Pacific coasts. Most scoters leave the breeding areas and migrate to the coast prior to initiating remigial moult. Relative to many other species of ducks, scoters are long-lived with delayed sexual maturity. Non-breeding subadults generally remain in the marine environment and do not migrate to breeding areas until they are at least two years old (Brown and Fredrickson 1997; Savard, Reed and Lesage 2007).

We captured White-winged and Surf scoters that were undergoing wing moult in late July to September of 2008 and 2009 in nearshore marine waters of southeast Alaska and the Salish Sea. Capture locations in southeast Alaska were in upper Seymour Canal, on Admiralty Island (58.0°N, 134.3°W). Seymour Canal is a sheltered inlet, about 65 km long and 8 km wide and is oriented with the long axis running roughly north to south. It has a diversity of shoreline types with a mix of soft- and hard-bottom habitats. The Salish Sea study area was much larger, and included the Fraser River Delta (49.2°N, 123.3°W) and Boundary Bay (49.0°N, 123.0°W) in British Columbia, and Padilla Bay (48.5°N, 122.5°W) and Oak Harbor (48.3°N, 122.6°W) in Washington. The Fraser River Delta and Boundary Bay are composed of intertidal mudflats, eelgrass beds, and occasional rocky outcrops. Padilla Bay is almost entirely intertidal and contains one of the largest contiguous eelgrass (*Zostera* spp.) beds on the Pacific coast of North America (Bulthuis 1995). Oak Harbour is largely unvegetated with intertidal substrates ranging from coarse sand to cobble, and subtidal substrates comprised mainly of fine sands.

To capture scoters, we used a floating gill net method, adapted from a submerged mist net technique (Breault and Cheng 1990). This method was a type of drive-trapping in which we used two to three boats to move flocks of scoters toward a free-floating gill net. When the scoters reached the net, we fired a cracker shell to elicit a dive response. We then retrieved the net and any entangled birds. We removed the birds from the net, placed them in small kennels, and then processed them either at a nearby shore station or on the boats. All birds were handled in accordance with protocols approved by the Animal Care Committee at Simon Fraser University (project number 868B).

We marked all captured scoters with a uniquely numbered stainless steel U.S. Geological Survey tarsal band. They were identified to species, sex was determined by plumage and cloacal characteristics, and age class (second-year [SY] or after-second-year [ASY]) by bursal depth (Mather and Esler 1999). For the purposes of this study, second-year birds refer to those that hatched during the previous summer and are beginning their second year, while after-second-year individuals were two or more years old. We also recorded body mass (± 1 g) and 9th primary length (± 0.1 mm). The length of the 9th primary was used as a metric of the stage of wing moult. In the case of individuals with fully-grown primaries, we examined feather wear to determine if the feathers had been moulted in the current season or if the feathers were from the previous year.

To monitor foraging effort, we deployed VHF radio transmitters (Advanced Telemetry Systems Model 4450, 13g) on 168 scoters. Radio transmitters were distributed among species, sexes, and age classes (Table 3-1), and we marked individuals in early stages of wing moult to maximize the number of foraging observations collected during the period of primary feather growth. Transmitters were mounted dorsally and anchored subcutaneously with single or double stainless steel prongs as described by Pietz et al. (1995) and Lewis and Flint (2008), respectively. Transmitter attachments were performed within two hours of capture to minimize stress and thermoregulatory problems associated with confinement and handling. Iverson et al. (2006) found subcutaneously anchored transmitters to be suitable for short-term studies of free-living scoters.

Scoters forage almost exclusively by diving for benthic invertebrates (Brown and Fredrickson 1997; Savard, Bordage and Reed 1998), so the amount of time spent underwater is a simple measurement of foraging effort. We monitored diving activity remotely, either from boat or from shore, using handheld or boat-mounted four-element Yagi antennas and ATS R4000 receivers. When a scoter, with its attached transmitter, was underwater, the signal was attenuated and undetectable, and then returned when the bird surfaced (Custer, Custer and Sparks 1996). We considered a dive as any loss of signal that was greater than four seconds (Jodice and Collopy 1999). We monitored foraging during one-hour time periods, following protocols of previous studies of scoter foraging behaviour in winter and spring (Lewis et al. 2005; Kirk, Esler and Boyd 2007b; Lewis, Esler and Boyd 2008). We spread observations across both the diurnal period (between sunrise and sunset) and the tidal cycle. We also monitored diving behaviour during dawn (nautical twilight to sunrise), dusk (sunset to nautical twilight), and night (end of dusk to beginning of dawn). The dawn, dusk, and nocturnal observation periods ranged from 30-60 minutes, due to logistical constraints. We only collected foraging data during the period a marked scoter was growing primary feathers.

3.3.2 Data analysis

Body mass dynamics

We used multiple linear regression models to evaluate variation in body mass of moulting scoters. Candidate model sets were analyzed separately for each species and sex combination, under the simplifying and well-supported assumption that body masses differed among these groups, but model sets included the same combinations of explanatory variables. Explanatory variables were 9th primary length, primary emergence date, site (Salish Sea or southeast Alaska), year (2008 or 2009), and age class (ASY or SY). We calculated primary emergence date for each individual as described in Chapter 2 of this thesis. Site, age, and year were included as covariates in all models except the null model, because we felt that they could influence mass but they were not the primary variables of interest. We used 9th primary length as a metric of moult progression, to assess trends in body mass throughout the period of feather growth. Primary emergence date was included in the models to test whether relationships with body mass changed during the moult season (i.e. whether patterns differed for early versus late moulters). Models with additive combinations of primary length and emergence date, as well as each one of all possible two-way interactions were included. The global model included main effects of all five variables and all two-way interactions (Table 3-2 and Table 3-3)

We employed an information-theoretic approach to model selection (Burnham and Anderson 2002). Akaike's information criterion corrected for finite sample sizes (AIC_C) was calculated for each candidate model. Candidate models were ranked by their ΔAIC_C values, calculated as the difference between the AIC_C scores of each model and that of the best-supported model in the candidate set. The relative support for each model in a candidate set was determined by its Akaike weight (w_i), which is a normalized measure of the likelihood of a given model relative to the likelihood of all other models in the candidate set. Parameter likelihood values and weighted parameter estimates based on multi-model inference (Burnham and Anderson 2002) were used to assess the importance of individual variables in the candidate models. Relationships between mass and 9th primary length or emergence date were based on model-averaged parameter estimates.

Foraging effort

We quantified hourly foraging effort as the number of minutes underwater per one-hour observation period. Based on each one-hour observation period, we extrapolated daily foraging effort by using the length of the day during which the hourly observation was taken. We found that diving was very infrequent during crepuscular and nocturnal periods (see Results below), so for estimates of daily foraging effort, day length was calculated as the number of minutes between sunrise and sunset. To analyze variation in foraging effort, we used linear mixed effects models because our data were comprised of repeated measures on individuals. We analyzed foraging effort separately for each species. We used a natural log transformation of the response variable (minutes/hour or minutes/day) to prevent negative predicted values of the response variable and to reduce heteroscedasticity of the residuals. Model results were backtransformed to present more easily interpretable weighted parameter estimates. Both hourly and daily foraging effort data were analyzed but as results were similar, results for daily foraging effort will be presented in this paper (for hourly foraging effort, see Appendix).

Identical candidate model sets were used for all analyses, and predictor variables included primary length (observation time, sea state [calm, moderate, rough], tide height, and tidal state [rising, falling, slack]). We also included squared terms for the continuous variables (primary length, emergence date, observation time) to allow for non-linear relationships. For each radio-marked individual, we used species-specific 9th primary growth rates and primary length at capture to estimate primary emergence date and primary length on dates of foraging observations (see Chapter 2). Primary length and emergence date were included in the models to test for changes in foraging effort during the moult period, while inclusion of the cohort term allowed us to evaluate differences between sex and age classes. The environmental parameters as well as site and year terms were included to account for possible variation due to these factors, but were not of primary interest. Males and females were included in analyses together, but as they have different final primary lengths, we converted primary length to percentage of final length for each species/sex combination.

Using the most highly parameterized model from the candidate model sets, we selected an appropriate random effects structure for each analysis. We ran models with no random effects, random intercept (by individual scoter), and random slopes and intercept (each of the predictor variables in addition to a random intercept term for individuals) and used AIC values (obtained by restricted maximum likelihood estimation) to select the most parsimonious model. We used AIC values, rather than AIC_C, because for mixed models there is no standard method of determining the appropriate value of the sample size (n) which is required to calculate AIC_C (Burnham and Anderson 2002). A conservative method of calculating the AIC_C is to use the number of individuals as the sample size. In these analyses, model selection results based on AIC and AIC_C (with n = number of individuals) were generally in concordance, indicating that our models were not overfitted.

Plots of residuals versus fitted values from global models suggested a relationship between the variance and the response variable, so we included a variance weighting term and again used AIC values to determine whether it should be retained in the models. Because we were using repeated observations of individual over time, we also tested several correlation structures.

Of the random effects models that we examined, the model that included a random intercept term (for individuals) received the most support. Therefore we included a random intercept term in all subsequent candidate models. In the analysis of White-winged Scoter hourly foraging effort, the AIC values of the various random effects structures tested indicated that a random effect of tide height also should be included in the model. All models had a variance weighting term (allowing a relationship between the variance and the response variable) and a temporal correlation structure.

After selecting the appropriate random effects, variance weighting and correlation structure, we evaluated our *a priori* candidate model sets. The candidate set included models testing the effects of primary length, emergence date and cohort separately, as well as in combination. The environmental parameters, as well as site and year, were always added as a group (Table 3-5). The model set included a null model and all models had the same random effects structure as chosen above. We used maximum likelihood estimation to obtain AIC values for models with differing fixed effects.

Candidate models were ranked by their ΔAIC values and the relative support for each model in the candidate set was determined by its Akaike weight (w_i). To obtain parameter estimates for each model, we again used restricted maximum likelihood estimation. Parameter likelihood values and weighted parameter estimates based on all candidate models were used in multi-model inference to assess importance of individual variables (Burnham and Anderson 2002). Model-averaged estimates were used to produce regression lines showing relationships between daily foraging effort and primary length or emergence date.

As there was a very low incidence of diving observed during crepuscular and nocturnal periods, we did not use the mixed modelling approach described above to analyze those data. Instead, we simply calculated the minutes underwater per hour observed during nocturnal and crepuscular periods, as well as the proportion of observation periods with any diving activity recorded.

All statistical analyses were conducted and graphs produced using the program R (R Development Core Team 2011). We used the *lm* function for multiple regression analyses and the *lme* function in the nlme package (Pinheiro et al. 2011) for linear mixed modelling analyses.

3.4 Results

Body mass dynamics

For all categories of species, sex, age, site and year, moulting scoters exhibited a positive relationship between primary length and body mass. There was also a general trend of increasing body mass with primary emergence date, except for male White-winged Scoters. Model-averaged parameter estimates were used to plot relationships between body mass and 9th primary length (Figure 3-1) and body mass and emergence date (Figure 3-2). Model selection results indicated that the best-supported model for Surf Scoter female body mass during primary moult was the mostly highly parameterized model, including all main effects and all two-way interactions of the predictor variables with a model weight of >0.99 (Table 3-2). For male Surf Scoters, the three best supported models (with combined model weights of >0.63) included all the main effects and the following two-way interactions: year × emergence date (w_i = 0.299), primary length × emergence date (w_i = 0.210), and age × primary length (w_i = 0.124) (

		Surf Scoter		White-winged Scoter	
Site	Year	Female	Male	Female	Male
SEAK	2008	15	18	6	13
	2009	21	12	7	13
SALS	2008	14	8	0	0
	2009	10	12	7	12

). In the analysis of female White-winged Scoter body mass variation, the most highly supported model included all five main effects and the interaction between primary length and emergence date (w_i = 0.204) (Table 3-3). However, support was very spread out amongst the model set and for 24 of the 31 candidate models $0.01 < w_i < 0.08$. For male White-winged Scoters, the best-supported model contained all five main effects and the interaction between primary length and emergence date (w_i = 0.67) (Table 3-3). Parameter likelihoods and model averaged parameter estimates obtained from these analyses are shown in Table 3-4.

Surf Scoters of both sexes and female White-winged Scoters were heavier in 2009 than in 2008, while male White-winged Scoters had lower initial mass in 2009 but were heavier by the end of primary feather growth. In most cases, ASY scoters weighed more than SY birds. However, for some site/year combinations, ASY female Surf Scoters weighed less than their SY counterparts, but due to a faster rate of mass gain achieved higher masses by the end of remigial moult. Female White-winged Scoters were heavier in the Salish Sea than in southeast Alaska while the opposite was true for all other groups. Interactions between the effect of primary length and site/age were not large for male Surf Scoters and female White-winged Scoters, but were more important for female Surf Scoters and male White-winged Scoters.

Relationships between primary emergence date and body mass, at the beginning of moult when 9th primary length equals zero (Figure 3-2) exhibit some similarities to the relationship with primary length. In general, mass was higher in 2009 than 2008 and birds were heavier in southeast Alaska than the Salish Sea (except female White-winged Scoters). Male White-winged Scoters showed a marked decrease in body mass at later emergence dates, while male Surf Scoters and female White-winged Scoters had increasing body mass at later emergence dates. Interactions between emergence date and site/year for female Surf Scoters make it more difficult to generalize. Female Surf Scoters had higher masses in 2008 than 2009 at early emergence dates, but mass increased more rapidly with emergence date in 2009, resulting in higher body masses for late moulters. In 2008 in southeast Alaska, female Surf Scoter body mass increased with emergence date, while in the Salish Sea it decreased for SY female Surf Scoters and remained stable for ASY birds.

Foraging effort

In the mixed modelling analysis of Surf Scoter foraging effort the top two best-supported models for daily foraging effort contained the environmental condition parameters (time, sea state, tide height and state), site, and year. Additionally, the top supported model also included effects of emergence date and 9th primary length, while the second most parsimonious model included cohort in addition to emergence date and primary length (Table 3-5). For White-winged Scoters daily foraging effort, the model with just emergence date had the most support (w_i = 0.85) (Table 3-5).

Daily foraging effort in Surf Scoters increased with primary length until 9th primaries reached about 80% of their final length, and then effort decreased slightly (Figure 3-3). Daily foraging effort was higher in 2009 than in 2008 and was higher in the Salish Sea than in southeast Alaska. In southeast Alaska, foraging effort increased from about 100 minutes/day to 130 minutes/day, while in the Salish Sea it was from 135 to 180 minutes/day. For White-winged Scoters, daily foraging effort remained almost constant throughout primary moult at about 170 minutes/day. White-winged Scoters in southeast Alaska spent slightly more time foraging than in the Salish Sea but there was very little difference between years.

Relationships between daily foraging effort and 9th primary emergence date also were quite different between the two species (Figure 3-4). Surf Scoters that initiated primary moult earlier in the summer foraged at relatively high rates. Foraging effort decreased with primary emergence date until mid-August and then increased again for individuals that moulted later. Consistent with previous results, Surf Scoters spent more time foraging in the Salish Sea than in southeast Alaska and more time in 2009 than 2008. For White-winged Scoters, daily foraging effort decreased in a nearly linear relationship with emergence date and there was very little difference between years or sites.

In Figure 3-3 and Figure 3-4, regression lines are simplified representations of models of daily foraging effort. Model-averaged parameter estimates were used to plot lines (Table 3-6). However, only the adult female cohort is presented, as differences among cohorts were small. Median values for observation time and tide height were used and these variables had very little effect for either species. Regression lines presented are for calm sea conditions (rather than moderate or rough) and a falling tide (rather than rising or slack). The parameter estimates for these variables were close to zero, except that Surf Scoters spent less time foraging when conditions were rough or when the tide was slack.

For all species and sexes combined, during nocturnal observations in the Salish Sea we recorded at least one dive during 16% of the observation periods, but dives were short and infrequent, and only 0.2% of the total observation time was spent underwater (1.3 minutes underwater of 750 minutes total observation time). In southeast Alaska, scoters dove during 12% of the observation periods, but only 0.6% of the time was spent underwater (14.5 minutes of 2343 minutes). In southeast Alaska, no diving activity was recorded during the dawn crepuscular period in 877 minutes of observation, while during dusk 7% of the observation periods had at least one dive, but just 1.7% of the time was spent underwater (23.9 minutes out of 1434 minutes). In comparison, during diurnal observations we recorded dives during 80% of the observation periods and scoters spent about 10-25% of the time underwater, depending on location and date.

3.5 Discussion

Our results indicated that neither Surf nor White-winged scoters were nutritionally or energetically stressed during remigial moult across a broad latitudinal extent of their coastal moulting range. Across species, locations, years, and cohorts, body mass increased through the process of remigial moult (Figure 3-1), indicating that scoters met costs of remigial feather growth without catabolising nutrient reserves. Similarly, high body mass during remigial moult, relative to other stages of the annual cycle (Figure 3-5), was consistent with the conclusion that endogenous reserves were not required to fuel costs of remigial moult. Thus, it seems that on the Pacific coast of North America scoters employ an income strategy during remigial moult. Increases in body mass or nutrient reserves during remigial moult have been recorded for only a few other species of waterfowl, specifically, Blue-winged Teal (Dubowy 1985), female Tundra Swans

(Earnst 1992), Brant (Ankney 1984), and Canvasbacks (Thompson and Drobney 1996). Most waterfowl species that have been studied have shown decreasing or constant body mass during remigial moult (Hohman, Ankney and Gordon 1992).). While mass loss does not necessarily imply nutritional or energetic stress, increasing body mass is a clear indication of lack of energetic or nutritional stress or constraints.

Consistent with body mass results, we found that scoters did not expend high foraging effort during remigial moult, suggesting that they were able to meet their dietary requirements without drastically increasing effort. Based on the model-averaged parameter estimates, Surf Scoters spent 92 to 320 minutes/day underwater during the moult period. For White-winged Scoters with median emergence dates, predicted foraging effort ranged from 160-175 minutes/day, but varied from 242 minutes/day for birds that initiated moult early to 81 minutes/day late in the season. Accounting for latitudinal differences and changing day length throughout the study period, Surf Scoters spent 11-41% of daylight time underwater, while the range for White-winged Scoters was 10-27%. During winter in southern British Columbia, Surf Scoters and White-winged Scoters spent an average of 20% and 22% of their time foraging, respectively, in high quality habitat (Lewis, Esler and Boyd 2008). Based on the time period of that study (mid-November to mid-March), they would have foraged for just over 100 minutes/day on average. Other studies have shown that during the winter Surf Scoter daily foraging effort can range from 64-154 minutes/day in southern British Columbia (Kirk, Esler and Boyd 2007b), 41-128 minutes/day in southeast Alaska, and was around 206 minutes/day in Baja California (VanStratt 2011). For scoters wintering in Haida Gwaii, BC, time spent underwater ranged from about 100-200 min/day for Surf Scoters and 150-220min/day for White-winged Scoters (Goudie 1999). Foraging effort varied during the moult period, but in general was comparable to winter foraging effort, suggesting that forage demands during moult were no greater than in winter.

In other species of waterfowl, varying shifts in foraging behaviour have been observed during the remigial moult period. Flightless male and female Lesser Scaup (*Aythya affinis*) spent less time feeding than during fall migration (Austin 1987). Gadwall (*Anas strepera*) and Tufted Ducks foraged less during remigial moult than in the weeks immediately before and after (Dopfner, Quillfeldt and Bauer 2009). In the same study, an increase in foraging effort during moult was observed in Mute Swans (*Cygnus olor*) and Red-crested Pochard (*Netta ruffina*) (Dopfner, Quillfeldt and Bauer 2009). Female Common Eider (*Somateria mollissima*) did not show any changes in daily diving time (a measure of foraging activity) in the four weeks prior to or following the flightless period (Guillemette et al. 2007). Captive Barnacle Geese exhibited a 25% decline in body mass during remigial moult and foraging effort was very low relative to the rest of the annual cycle (Portugal, Green and Butler 2007). Given that access to food was unlimited, predation risk was nil, and metabolic rates were high (oxygen consumption increased by 80% compared to non-moulting periods), the authors surmised that these behavioural and physiological changes are innate responses to the challenges typically faced during moult by this species.

If the costs of moult were driving foraging behaviour, we would expect to see high but consistent foraging effort throughout the feather growth period, rather than the gradually increasing foraging effort observed for Surf Scoters (Figure 3-3). Because body mass also was increasing, increased foraging effort may have been related to accumulation of stores for fall migration and/or winter. It is also possible that increasing foraging effort was a response to decreasing food availability as the density of scoters on moulting areas was high, and scoters are capable of depleting standing stocks of bivalves (Guillemette, Reed and Himmelman 1996; Kirk, Esler and Boyd 2007a; Lewis, Esler and Boyd 2007). Foraging effort by White-winged Scoters remained constant throughout feather growth, and decreased with emergence date, suggesting that prey depletion was not occurring. However, Surf Scoters may have been limited to consuming smaller bivalves than those eaten by White-winged Scoters and thus depletion of size classes preferred by Surf Scoters may not have affected the larger-bodied White-winged Scoters. During winter, larger increases in seasonal foraging effort have been observed for Surf Scoters than for White-winged Scoters and have generally been attributed to decreasing bivalve availability (Lewis, Esler and Boyd 2008; Anderson and Lovvorn 2011).

We also observed an increase in foraging effort for Surf Scoters that initiated moult later in the season and this could be linked to decreased food availability or to the need to build reserves before fall. Surf Scoters also showed high foraging effort for individuals that initiated moult early in the season, and early-moulting individuals also tended to have lower body mass, possibly because their reserves were depleted from breeding activity and migration. If they begin moult soon after arrival at moulting areas, they may have to forage more than individuals that arrived at the same time but delayed moult initiation. For Surf Scoters, foraging effort was consistently higher in the Salish Sea than in southeast Alaska, perhaps due to richer or more abundant food sources in Alaska. As well, anthropogenic disturbance is likely higher in the Salish Sea, and could lead to higher daily energetic costs. However, foraging effort in White-winged Scoters was slightly higher in southeast Alaska.

White-winged Scoters spent a consistent amount of time foraging throughout the primary feather growth period, but foraging effort declined dramatically with primary emergence date. Despite a constant foraging effort during remigial moult, both male and female White-winged Scoters had increasing body mass. On the other hand, later moulting female White-winged Scoters had higher body masses, while mass decreased with emergence date for males, but both sexes exhibited decreasing foraging effort at later primary emergence dates.

Many studies of activity budgets and foraging effort rely on visual estimation methods, so data on nocturnal behaviour are lacking. The telemetry-based data that do exist suggest that scoters are generally diurnal foragers but nocturnal foraging has been observed (Lewis et al. 2005; C.VanStratt, SFU, unpublished data). Although diurnal foraging appears to be the norm for many sea ducks species (Nilsson 1970; Goudie and Ankney 1986; McNeil, Drapeau and Goss-Custard 1992), waterfowl are capable of extending foraging behaviour into the nocturnal period if day length is short or food is limiting (Lane and Hassall 1996; Systad, Bustnes and Erikstad 2000; Systad and Bustnes 2001). Increases in nocturnal foraging activity during remigial moult have been observed in several species of waterfowl (Hohman, Ankney and Gordon 1992). We found very little evidence of diving activity during either the nocturnal or crepuscular periods, suggesting that during remigial moult scoters are able to meet their nutritional and energetic needs without having to forage outside of the diurnal period.

For Surf and White-winged Scoters undergoing remigial moult, body mass is relatively high and even increasing, daily foraging effort falls within the range of values observed during winter, and foraging occurs almost entirely during daylight hours. Although feather production and associated physiological processes may be costly, scoters apparently meet the nutritional and energetic costs of wing moult through an income-based moulting strategy. Energetic costs of moult may be partially offset by lower thermoregulatory costs than would be incurred during winter and reductions in energy use associated with flightlessness. Furthermore, abundant, easily accessible and/or rich food sources may allow efficient nutrient and energy acquisition. Surf and White-winged scoters moulting on the Pacific coast seem to employ a moult strategy that successfully avoids nutritional or energetic constraints. In addition, like in other sea ducks in similar environments (Iverson and Esler 2007), moulting scoters have high survival (B. Uher-Koch, SFU, unpublished data), further indicating that they use safe and productive sites to accomplish wing moult. Waterfowl species may select moulting sites based on a suite of requirements, which may involve trade-offs between predation danger, protein resources, and energetic profitability (Fox and Kahlert 2005). Scoters appear able to choose moulting sites that allow them to avoid the need to make trade-offs between safety and foraging opportunity. The generality of these conclusions to other sea ducks warrants additional study. Furthermore, recent evidence from satellite telemetry (J. Evenson, WDFW, unpublished data) and stable isotope analysis of primary feathers (R. Dickson, unpublished data) indicates that a significant proportion of adult female White-winged Scoters undergo remigial moult on inland lakes and the trade-offs between safety and nutritional and energetic needs could be very different in these environments.

3.6 Figures

Figure 3-1. Regressions of body mass on 9th primary length (at median primary emergence date for each cohort) are based on model-averaged parameter estimates for Surf and White-winged scoters in southeast Alaska and the Salish Sea.

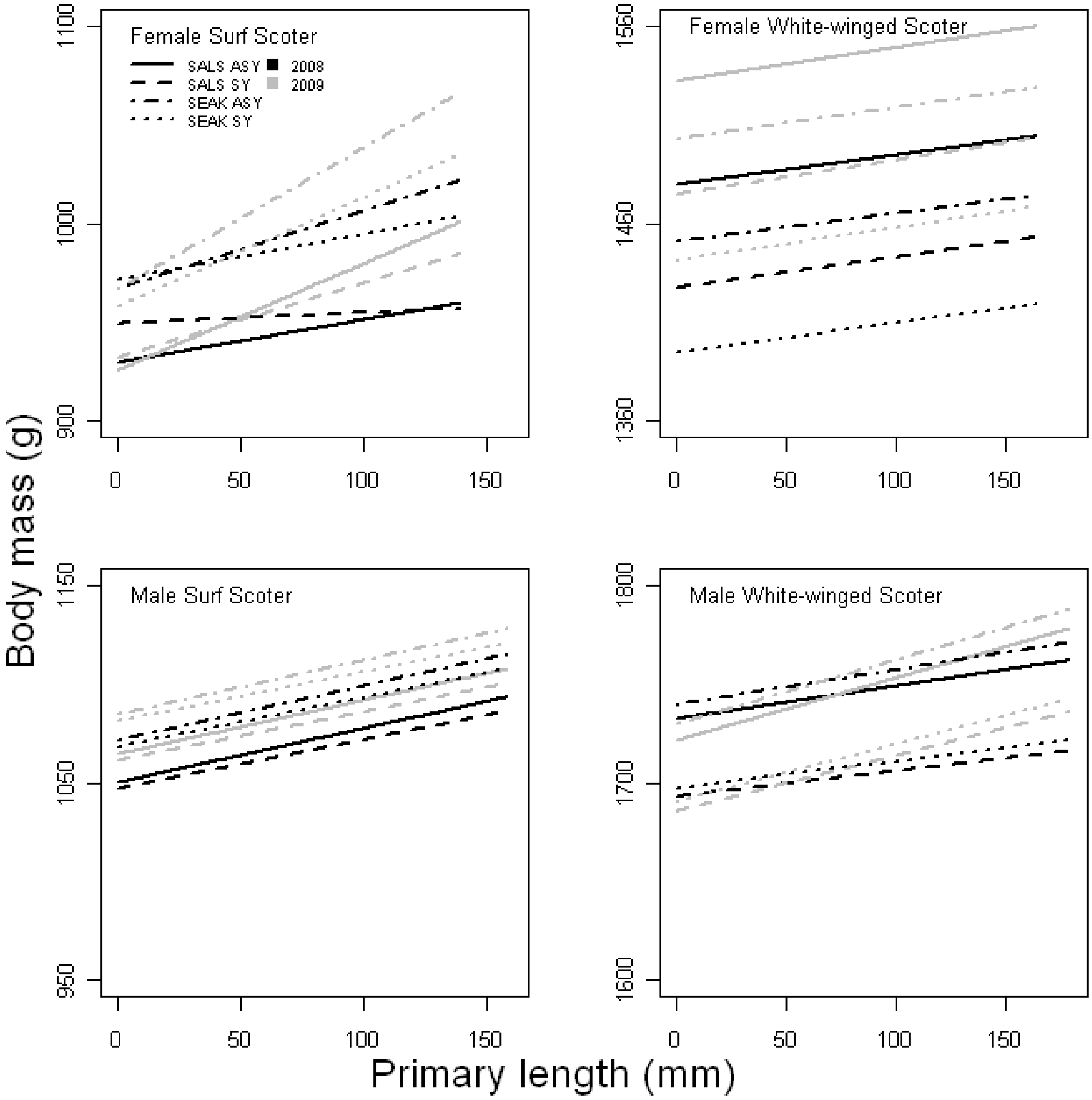


Figure 3-2. Regressions of body mass on primary emergence date (at the beginning of the remigial growth period) are based on model-averaged parameter estimates for Surf and White-winged scoters in southeast Alaska and the Salish Sea.

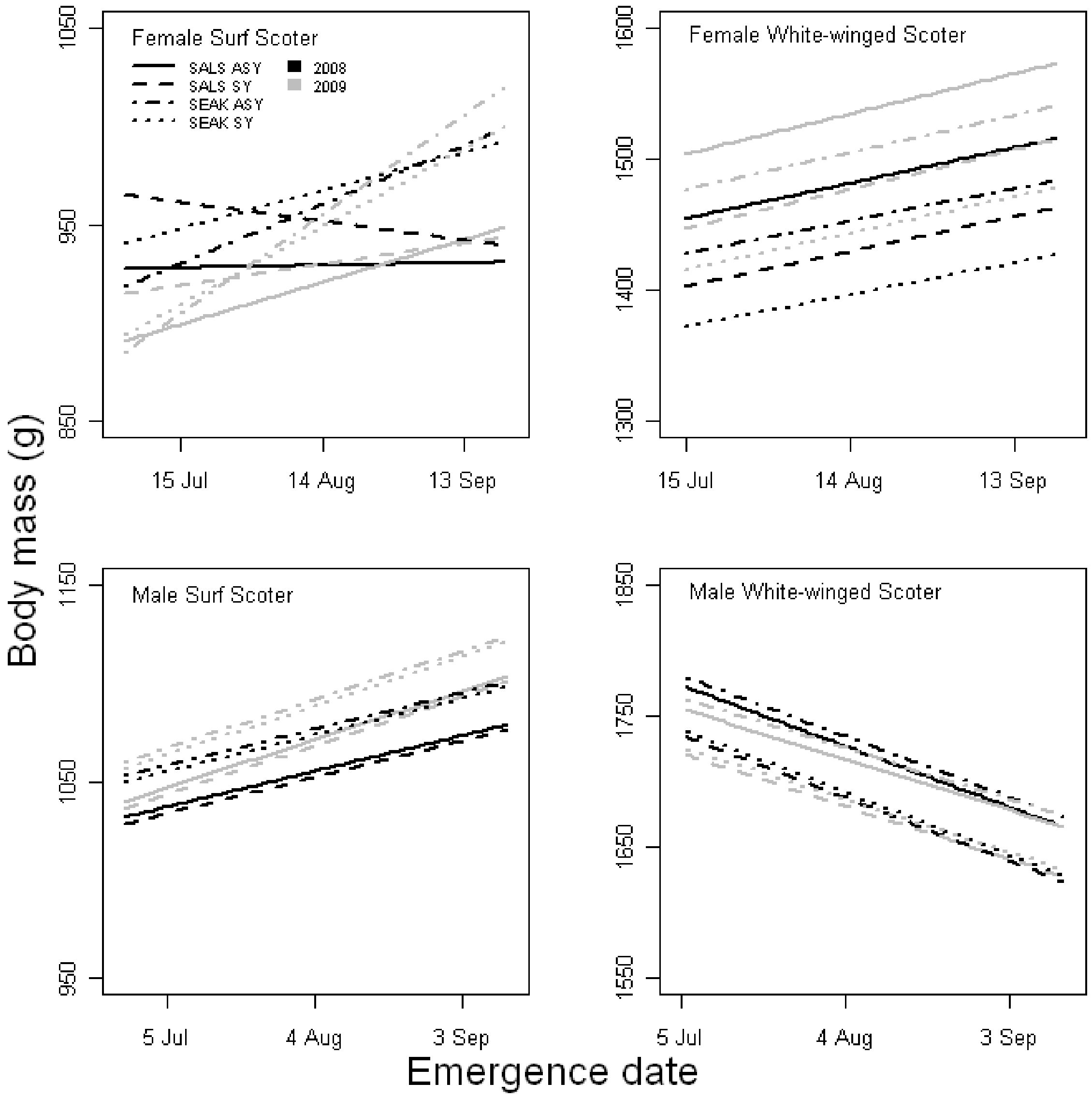


Figure 3-3. Daily foraging effort over the course of remigial growth in Surf and White-winged scoters in southeast Alaska and the Salish Sea. Primary length is expressed as percentage of final 9th primary length to account for differing final primary lengths between species and sexes. Regression lines are based on the ASY female cohort, using the median primary emergence date for each cohort, at the median time of day and median tide height in calm sea conditions on a falling tide.

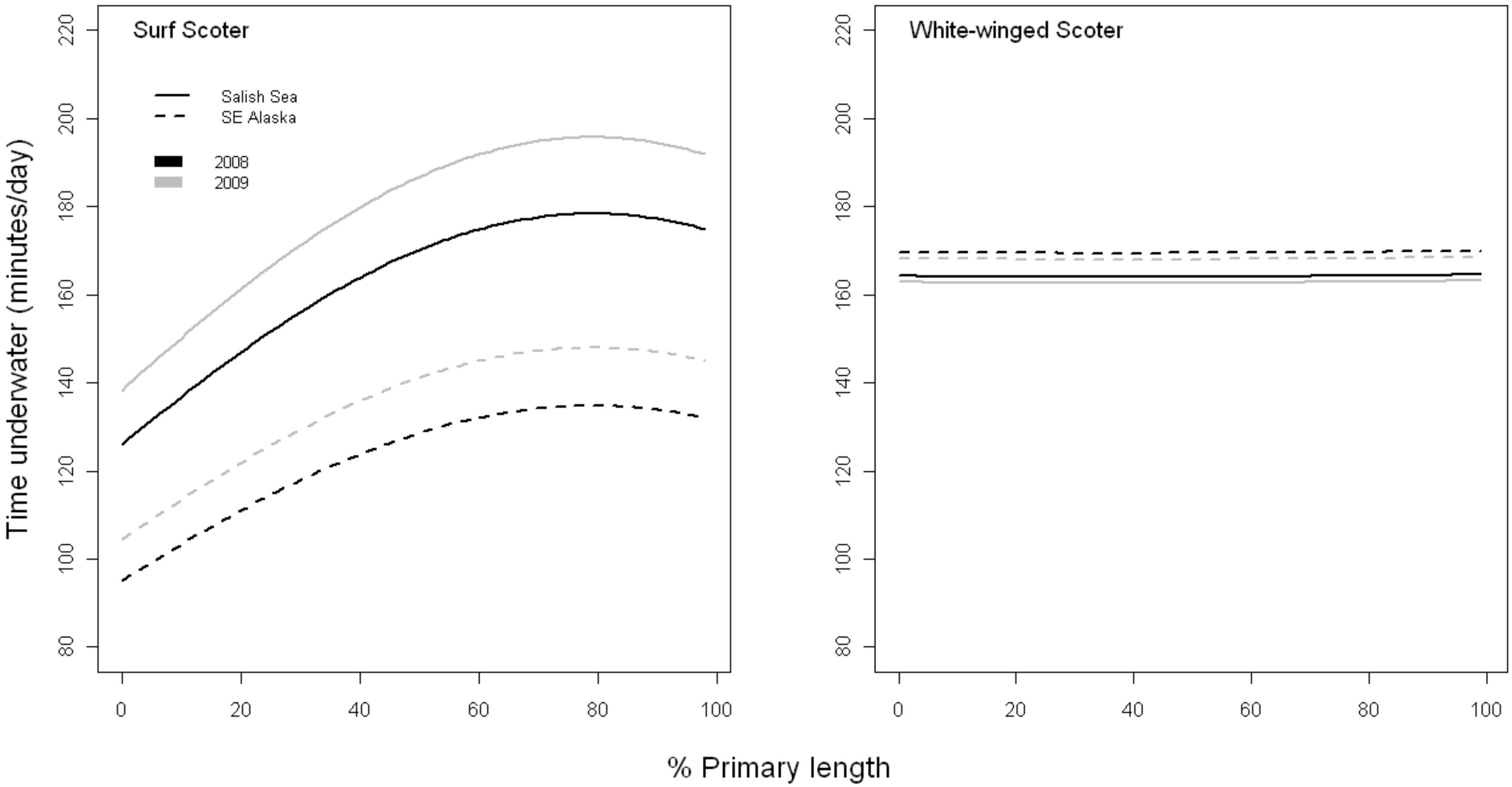


Figure 3-4. Daily foraging effort as a function of primary emergence date for individual Surf and White-winged scoters moulting in southeast Alaska and the Salish Sea. Regression lines are based on the ASY female cohort, at the median time of day and median tide height in calm sea conditions on a falling tide (at the beginning of remigial growth).

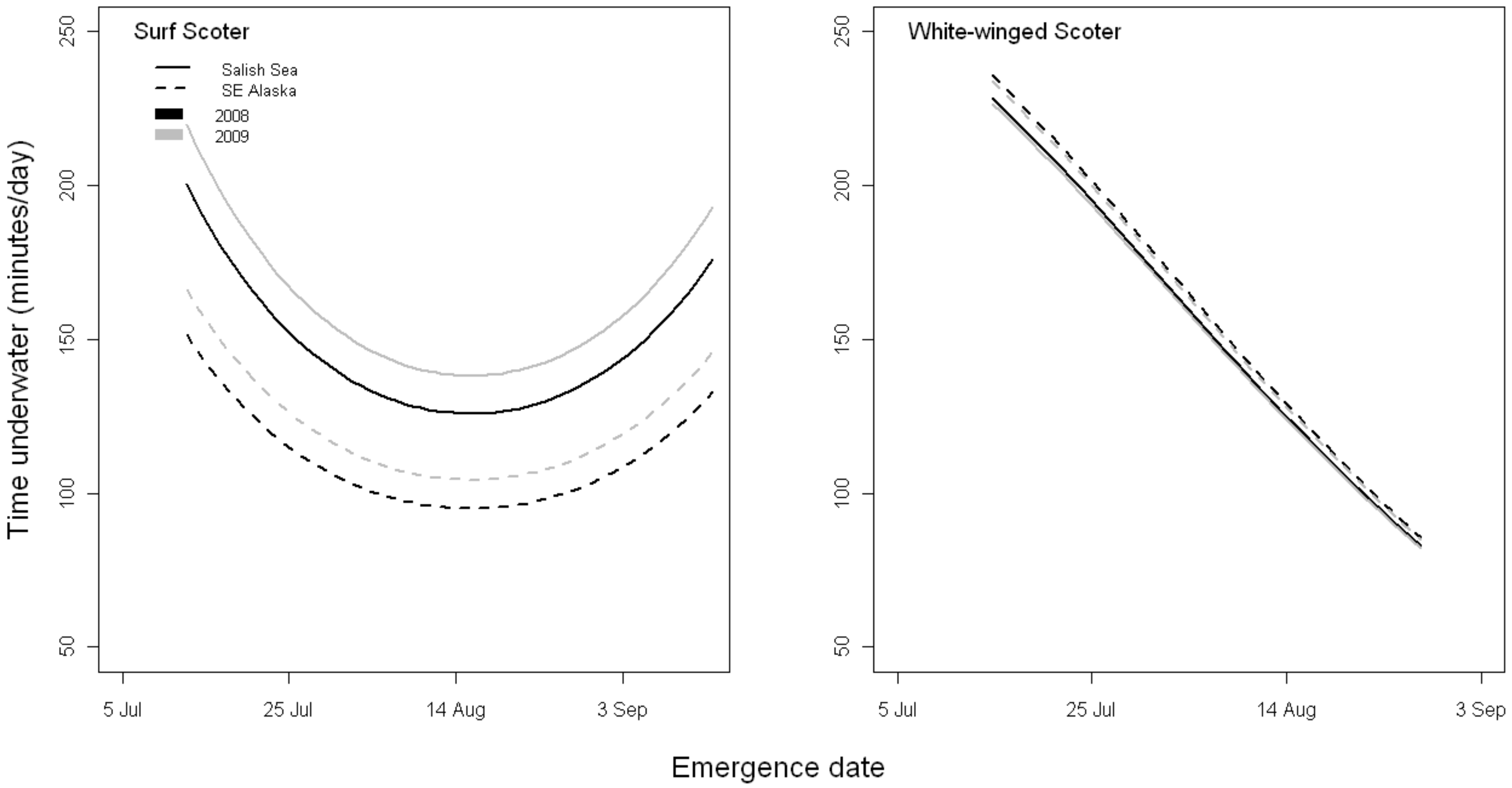
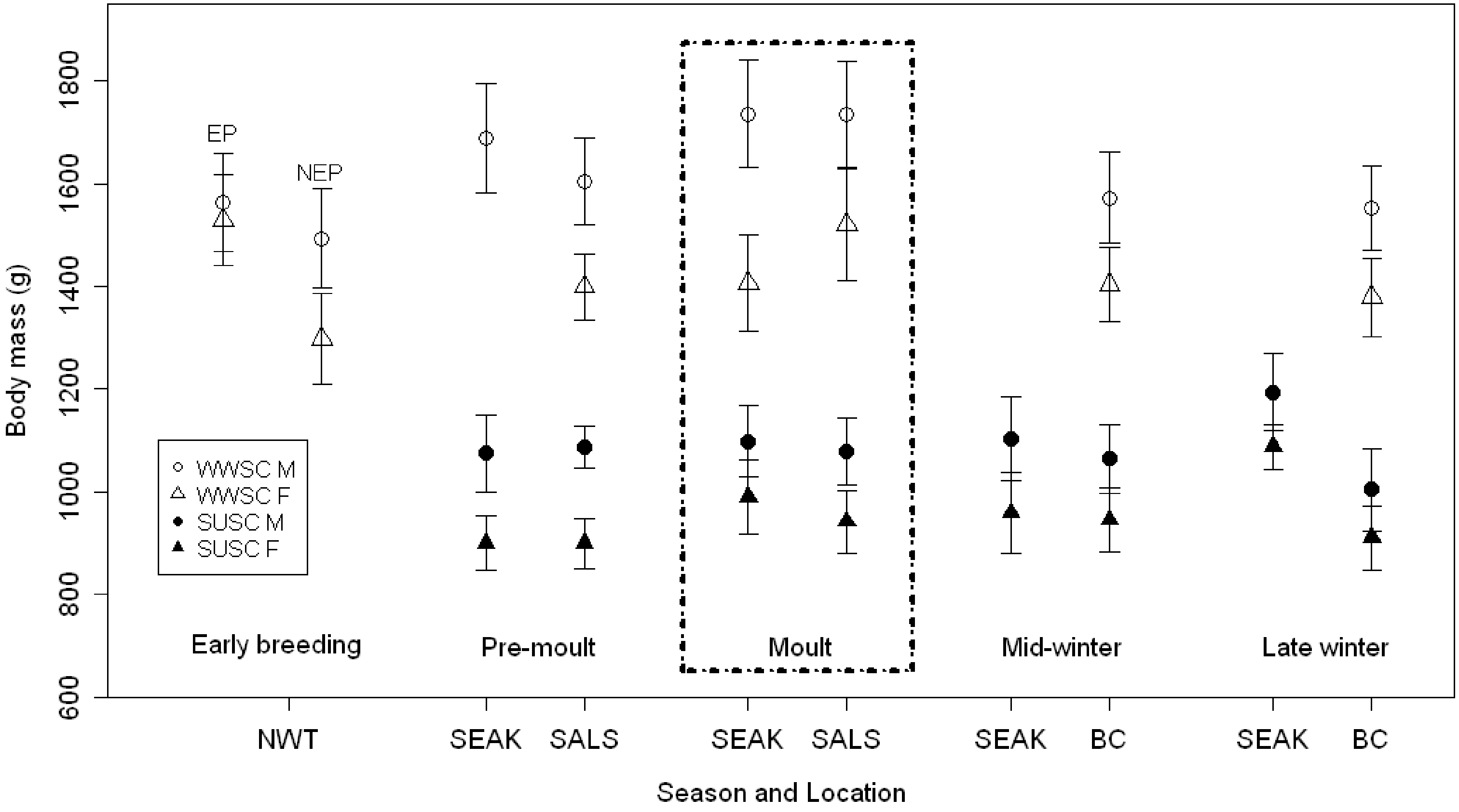


Figure 3-5. Body mass of ASY Surf and White-winged scoters throughout the annual cycle. Error bars are ± one standard deviation. Early breeding data is from White-winged Scoters captured during pre- or early-nesting at Cardinal Lake, Northwest Territories; EP = egg-producing, NEP = non-egg-producing (for males, indicates status of mate) (S. Slattery, DUC, unpublished data). Pre-moult masses were obtained in the present study, from captured scoters bearing old primaries. Mid-winter (November-December) and late-winter (February-March) data were from southeast Alaska and southern British Columbia (C. VanStratt and D. Esler, SFU, unpublished data).



3.7 Tables

Table 3-1. Distribution of VHF radio-transmitters on Surf and White-winged Scoters in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009.

		Surf Scoter		White-winged Scoter	
Site	Year	Female	Male	Female	Male
SEAK	2008	15	18	6	13
	2009	21	12	7	13
SALS	2008	14	8	0	0
	2009	10	12	7	12

Table 3-2. Multiple linear regression model results assessing variation in body mass of male and female Surf Scoters undergoing remigial moult in southeast Alaska and the Salish Sea.

		Female		Male	
Model	**k**	**$\Delta \mathrm{AIC}_c$**	**w_i**	**$\Delta \mathrm{AIC}_c$**	**w_i**
Site[a] + Year[b] + Age[c] + Pri[d] + Emerg[e] + Site × Year + Site × Age + Site × Pri + Site × Emerg + Year × Age + Year × Pri + Year × Emerg + Age × Pri + Age × Emerg + Pri × Emerg	17	0.000	1.000	9.616	0.002
Site + Year + Age + Pri + Emerg + Pri × Emerg	8	19.403	0.000	0.710	0.210
Site + Year + Age + Pri + Emerg + Age × Emerg	8	32.181	0.000	4.213	0.036
Site + Year + Age + Pri + Emerg + Age × Pri	8	27.045	0.000	1.756	0.124
Site + Year + Age + Pri + Emerg + Year × Emerg	8	33.936	0.000	0.000	0.299
Site + Year + Age + Pri + Emerg + Year × Pri	8	25.882	0.000	4.509	0.031
Site + Year + Age + Pri + Emerg + Year × Age	8	31.059	0.000	4.571	0.030
Site + Year + Age + Pri + Emerg + Site × Emerg	8	23.561	0.000	4.480	0.032
Site + Year + Age + Pri + Emerg + Site × Pri	8	34.441	0.000	4.509	0.031
Site + Year + Age + Pri + Emerg + Site × Age	7	24.943	0.000	4.532	0.031
Site + Year + Age + Pri + Emerg + Site × Year	8	32.441	0.000	2.361	0.092
Site + Year + Age + Emerg + Emerg × Age	8	92.033	0.000	30.410	0.000
Site + Year + Age + Emerg + Emerg × Year	7	97.143	0.000	25.873	0.000
Site + Year + Age + Emerg +Emerg × Site	7	82.560	0.000	29.533	0.000
Site + Year + Age + Emerg + Year × Age	7	92.902	0.000	30.014	0.000
Site + Year + Age + Emerg + Site × Age	7	82.131	0.000	30.375	0.000
Site + Year + Age + Emerg + Site × Year	7	90.588	0.000	29.442	0.000
Site + Year + Age + Pri + Age × Pri	6	62.396	0.000	18.413	0.000
Site + Year + Age + Pri + Year × Pri	7	68.417	0.000	22.271	0.000
Site + Year + Age + Pri + Year × Age	7	69.699	0.000	22.037	0.000
Site + Year + Age + Pri + Site × Pri	7	75.441	0.000	21.179	0.000
Site + Year + Age + Pri + Site × Age	7	65.822	0.000	22.278	0.000
Site + Year + Age + Pri + Site × Year	7	72.458	0.000	21.985	0.000
Site + Year + Age + Year × Age	7	104.036	0.000	36.147	0.000
Site + Year + Age + Site × Age	6	95.665	0.000	36.704	0.000
Site + Year + Age + Site × Year	6	103.201	0.000	36.521	0.000
Site + Year + Age + Pri + Emerg	7	33.501	0.000	2.637	0.080
Site + Year + Age + Emerg	6	95.997	0.000	28.507	0.000
Site + Year + Age + Pri	6	74.604	0.000	20.258	0.000
Site + Year + Age	5	108.550	0.000	34.719	0.000
Null	2	195.127	0.000	74.397	0.000

Table 3-3. Multiple linear regression model results assessing variation in body mass of male and female White-winged Scoters undergoing remigial moult in southeast Alaska and the Salish Sea.

		Female		**Male**	
Model	**k**	**$\Delta \mathrm{AIC_C}$**	**w_i**	**$\Delta \mathrm{AIC_C}$**	**w_i**
Site[a] + Year[b] + Age[c] + Pri[d] + Emerg[e] + Site × Year + Site × Age + Site × Pri + Site × Emerg + Year × Age + Year × Pri + Year × Emerg + Age × Pri + Age × Emerg + Pri × Emerg	17	8.514	0.003	3.724	0.104
Site + Year + Age + Pri + Emerg + Pri × Emerg	8	0.000	0.204	0.000	0.670
Site + Year + Age + Pri + Emerg + Age × Emerg	8	4.800	0.018	11.250	0.002
Site + Year + Age + Pri + Emerg + Age × Pri	8	4.806	0.018	9.971	0.005
Site + Year + Age + Pri + Emerg + Year × Emerg	8	3.579	0.034	10.102	0.004
Site + Year + Age + Pri + Emerg + Year × Pri	8	3.756	0.031	5.616	0.040
Site + Year + Age + Pri + Emerg + Year × Age	8	3.860	0.030	11.849	0.002
Site + Year + Age + Pri + Emerg + Site × Emerg	8	4.448	0.022	12.206	0.001
Site + Year + Age + Pri + Emerg + Site × Pri	8	4.500	0.021	10.684	0.003
Site + Year + Age + Pri + Emerg + Site × Age	7	4.141	0.026	10.702	0.003
Site + Year + Age + Pri + Emerg + Site × Year	8	4.660	0.020	11.933	0.002
Site + Year + Age + Emerg + Emerg × Age	8	4.185	0.025	21.839	0.000
Site + Year + Age + Emerg + Emerg × Year	7	3.060	0.044	19.739	0.000
Site + Year + Age + Emerg +Emerg × Site	7	3.745	0.031	22.290	0.000
Site + Year + Age + Emerg + Year × Age	7	3.472	0.036	21.953	0.000
Site + Year + Age + Emerg + Site × Age	7	3.654	0.033	21.142	0.000
Site + Year + Age + Emerg + Site × Year	7	4.175	0.025	22.431	0.000
Site + Year + Age + Pri + Age × Pri	6	6.469	0.008	8.113	0.012
Site + Year + Age + Pri + Year × Pri	7	5.660	0.012	3.567	0.113
Site + Year + Age + Pri + Year × Age	7	4.683	0.020	10.016	0.004
Site + Year + Age + Pri + Site × Pri	7	6.192	0.009	8.892	0.008
Site + Year + Age + Pri + Site × Age	7	6.321	0.009	8.919	0.008
Site + Year + Age + Pri + Site × Year	7	6.342	0.009	10.127	0.004
Site + Year + Age + Year × Age	7	2.980	0.046	20.408	0.000
Site + Year + Age + Site × Age	6	4.305	0.024	19.556	0.000
Site + Year + Age + Site × Year	6	4.420	0.022	20.907	0.000
Site + Year + Age + Pri + Emerg	7	2.549	0.057	10.278	0.004
Site + Year + Age + Emerg	6	1.967	0.076	20.424	0.000
Site + Year + Age + Pri	6	4.315	0.024	8.435	0.010
Site + Year + Age	5	2.338	0.063	18.918	0.000
Null	2	44.003	0.000	24.426	0.000

Note: *For both preceding tables, the number of parameters (k) includes +1 for intercept and +1 for model variance estimated for each model.*

.[a] Site = Southeast Alaska or Salish Sea, [b] Year = 2008 or 2009, [c]Age = SY or ASY, [d]Primary = 9th primary length, [e]Emerg = Primary emergence date

Table 3-4. Parameter likelihoods and weighted parameter estimates ± unconditional standard error (SE) from multiple linear regression models evaluating variation in body mass in Surf and White-winged scoters moulting in southeast Alaska and the Salish Sea.

	Surf Scoter				**White-winged Scoter**			
	Female		**Male**		**Female**		**Male**	
Explanatory variable	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Constant	1.00	927.2 ± 18.52	1.00	1031.2 ± 15.16	1.00	1436.8 ± 60.55	1.00	1789.1 ± 45.5
Site(SEAK)	1.00	-17.2 ± 36.58	1.00	21.3 ± 5.68	1.00	-24.9 ± 36.12	1.00	7.1 ± 15.4
Year(2009)	1.00	-42.4 ± 20.47	1.00	7.8 ± 11.46	1.00	46.7 ± 30.44	1.00	-20.5 ± 31.5
Age(SY)	1.00	40.4 ± 21.89	1.00	-3.4 ± 7.19	1.00	-51.4 ± 31.97	1.00	-37.2 ± 20.8
Primary	1.00	-0.54 ± 0.23	1.00	0.22 ± 0.12	0.57	-0.15 ± 0.46	1.00	-0.72 ± 0.54
Emergence	1.00	0.04 ± 0.29	1.00	0.60 ± 0.35	0.76	0.9 ± 1.08	0.84	-1.5 ± 1.1
Site(SEAK) × Year(2009)	1.00	3.7 ± 14.67	0.09	-1.2 ± 2.52	0.08	-0.68 ± 4.21	0.11	0.88 ± 3.5
Site(SEAK) × Age(SY)	1.00	-15.4 ± 19.63	0.03	-0.12 ± 0.48	0.09	-4.0 ± 10.75	0.12	-3.3 ± 7.2
Site(SEAK) × Primary	1.00	0.18 ± 0.16	0.03	0.00 ± 0.01	0.03	-0.01 ± 0.03	0.12	0.01 ± 0.04
Site(SEAK) × Emergence	1.00	0.97 ± 0.55	0.03	0.01 ± 0.02	0.06	-0.08 ± 0.21	0.11	0.01 ± 0.14
Year(2009) × Age(SY)	1.00	-13.4 ± 12.67	0.03	-0.08 ± 0.38	0.13	-5.3 ± 11.64	0.11	3.6 ± 7.5
Year(2009) × Primary	1.00	0.32 ± 0.09	0.03	-0.00 ± 0.01	0.05	0.02 ± 0.04	0.26	0.15 ± 0.24
Year(2009) × Emergence	1.00	0.68 ± 0.32	0.30	0.21 ± 0.32	0.08	0.12 ± 0.28	0.11	0.26 ± 0.49
Age(SY) × Primary	1.00	-0.16 ± 0.16	0.13	-0.03 ± 0.05	0.03	0.01 ± 0.02	0.12	-0.04 ± 0.08
Age(SY) × Emergence	1.00	-0.36 ± 0.35	0.04	0.01 ± 0.03	0.05	-0.01 ± 0.1	0.11	-0.06 ± 0.27
Primary × Emergence	1.00	0.01 ± 0.00	0.21	0.00 ± 0.00	0.21	0.01 ± 0.01	0.77	0.02 ± 0.01

Table 3-5. Linear mixed model results assessing variation in daily foraging effort during remigial moult in Surf and White-winged scoters in southeast Alaska and the Salish Sea.

Response	**Model**	**k**	**ΔAIC**	***w_i***
Surf Scoter				
Daily foraging effort	Env + Site + Year + Emerg + Pri	18	0	0.574
	Env + Site + Year + Cohort + Emerg + Pri	21	2.23	0.188
	Env + Site + Year + Emerg	16	3.77	0.087
	Env + Site + Year + Pri	16	4.82	0.051
	Env + Site + Year + Cohort + Pri	19	5.43	0.038
	Env + Site + Year + Cohort + Emerg	19	6.33	0.024
	Pri	7	6.85	0.019
	Emerg	7	8.24	0.009
	Env + Site + Year	14	9.93	0.004
	Env + Site + Year + Cohort	17	10.75	0.003
	Null	5	10.80	0.003
	Cohort	8	12.64	0.001
White-winged Scoter				
Daily foraging effort	Emerg	7	0.00	0.853
	Env + Site + Year + Emerg	16	6.04	0.042
	Cohort	8	6.07	0.041
	Env + Site + Year + Cohort + Emerg	19	7.19	0.023
	Env + Site + Year + Emerg + Pri	18	9.06	0.009
	Env + Site + Year	14	9.28	0.008
	Null	5	9.70	0.007
	Env + Site + Year + Cohort	17	9.87	0.006
	Env + Site + Year + Cohort + Emerg + Pri	21	10.47	0.005
	Pri	7	11.63	0.003
	Env + Site + Year + Pri	16	11.66	0.003
	Env + Site + Year + Cohort + Pri	19	12.62	0.002

Note: The number of parameters (k) includes +1 for intercept, random variance of the intercept, + 1 for the covariance structure for repeated measures, +1 for variance weighting and +1 for residual variance. Models are listed in decreasing order of model weighting (w_i).

Env = time + time^2 + sea (calm, moderate, rough) + tide height + tide state (rise, fall, slack)

Site = Salish Sea or southeast Alaska

Year = 2008 or 2009

Cohort = FASY, FSY, MASY or MSY (F=female, M=male, ASY=after second year, SY =second year)

Emerg = emergence + emergence^2 (Day 1 = June26)

Pri = primary + primary^2

Table 3-6. Parameter likelihoods and weighted parameter estimates ± unconditional standard error (SE) from linear mixed models evaluating daily foraging effort by Surf and White-winged scoters moulting in southeast Alaska and the Salish Sea. Response variable was log(min/day+1).

	Surf Scoter		**White-winged Scoter**	
Explanatory variable	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Intercept	1.00	5.88 ± 0.69	1.00	5.61 ± 0.82
Time	0.97	-0.02 ± 0.08	0.10	<0.01 ± 0.01
Time^2	0.97	0 ± <0.01	0.10	<0.01 ± <0.01
Sea(moderate)	0.97	0.06 ± 0.07	0.10	-0.02 ± 0.04
Sea(rough)	0.97	-0.42 ± 0.18	0.10	<0.01 ± 0.02
Tide height	0.97	0.02 ± 0.02	0.10	<0.01 ± 0.01
Tide(rise	0.97	-0.03 ± 0.07	0.10	-0.01 ± 0.02
Tide(slack)	0.97	-0.16 ± 0.09	0.10	-0.02 ± 0.04
Site(SEAK)	0.97	-0.28 ± 0.10	0.10	0.03 ± 0.06
Year(2009)	0.97	0.09 ± 0.10	0.10	-0.01 ± 0.02
Cohort(FSY)	0.25	0.03 ± 0.0	0.08	0.3 ± 0.06
Cohort(MASY)	0.25	-0.03 ± 0.06	0.08	<0.01 ± 0.02
Cohort(MSY)	0.25	-0.01 ± 0.7	0.08	0.01 ± 0.03
Emergence date	0.88	-0.04 ± 0.02	0.93	<0.01 ± 0.04
Emergence date^2	0.88	<0.01 ± 0.06	0.93	<0.01 ± 0.02
Primary length	0.87	0.01 ± 0.01	0.02	<0.01 ± <0.01
Primary length^2	0.87	<0.01 ± <0.01	0.02	<0.01 ± <0.01

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4: General Conclusions

4.1 Thesis Summary

In this thesis, I presented findings pertaining to remigial moult in Surf and White-winged scoters on the Pacific coast of North America. I documented phenology of remigial moult in these species at sites in southeast Alaska and the Salish Sea, with a focus on primary feather growth rates, duration of the flightless period, and variation in timing of moult. Furthermore, by quantifying body mass dynamics and foraging effort, I assessed strategies used by scoters to meet nutritional and energetic costs of moult. By assessing the occurrence of nutritional, energetic, or temporal constraints during remigial moult, I evaluated whether scoter population dynamics could be limited during this stage of the annual cycle.

In Chapter 2, I described phenology of moult in Surf and White-winged scoters on the Pacific coast of North America. Species-specific 9th primary feather growth rates, based on a combination of measurements from wild and captive scoters, were 3.9mm/day for Surf Scoters and 4.3mm/day for White-winged Scoters. These values lie within the range of remigial growth rates documented for adults of other duck species (4.2 – 5.2mm/day) (Hohman, Ankney and Gordon 1992). I also documented occurrence of a pre-emergence interval – the time elapsed from when old primaries are shed and new ones first become visible. This phenomenon is infrequently mentioned in the moult literature and the few existing estimates are 2-4 days (Balat 1970; Bowman 1987); my best estimate was 7.4 days. Neglecting to account for this period could lead to underestimation of the flightless period in waterfowl by roughly 20%. Based on my estimates for the pre-emergence interval and feather growth rates, I estimated duration of the flightless period at 34-48 days for Surf Scoters and 37-49 days for White-winged Scoters. Although there was a large degree of inter-individual variation in timing of initiation of moult, individuals appeared to be quite consistent from one year to the next, based on data from adult female Surf Scoters in the Salish Sea. For both species, timing of moult in individuals was influenced by site, cohort (age and sex), and year. The largest, most consistent differences were between cohorts; average primary emergence dates were earliest for second-year males, then second-year females and after-second-year males around the same time, with after-second-year females moulting later. However, because of the large range in emergence dates within each cohort, there was overlap in the moult period among all cohorts. Remigial emergence dates for Surf Scoters ranged from 26 June – 22 September and for White-winged Scoters from 6 July – 21 September. Thus, at both sites (southeast Alaska and the Salish Sea) there were moulting scoters of both species present for at least four months of the year, from late June to late October or early November.

It has been postulated that non-breeding female waterfowl may undergo moult migrations and moult with males and subadults, but that breeding females moult elsewhere (Salomonsen 1968). However, based on timing of breeding activities and moult for both Surf and White-winged scoters, it is plausible that many adult females moulting on the coast had time to nest, incubate, and hatch ducklings before returning to the coast to moult. This was congruent with data from satellite telemetry studies of Surf Scoter migration, which indicated that almost all females that travel to the breeding grounds return to the coast to moult (J. Evenson, WDFW, unpublished data). In White-winged Scoters, breeding females may be more likely to remain on inland lakes during remigial moult (J. Evenson, WDFW, unpublished data; R. Dickson, unpublished data)

Despite many claims that moult is nutritionally and/or energetically costly and that it is a stressful phase in the annual cycle of birds, few studies have explicitly and thoroughly evaluated this in wild waterfowl. In Chapter 3, I presented data on body mass dynamics and foraging effort of Surf and White-winged scoters. I used this combination of metrics to evaluate whether scoters were able to meet costs of remigial moult without relying on endogenous stores. I found that for all cohorts, sites, and years, body mass increased during remigial growth, indicating that scoters were not nutritionally or energetically constrained during this time. This finding was corroborated by the fact that body mass during remigial moult was not reduced relative to other phases of the annual cycle. Foraging rates during moult were not markedly higher than other annual cycle stages, indicating that moulting scoters were able to meet nutritional and energetic costs without increasing foraging effort. Surf Scoters showed increases in foraging effort in later stages of remigial moult and later in the season (independent of moult stage), which could have several explanations. Depletion of preferred prey may have occurred or scoters may have been building reserves in anticipation of fall migration and winter.

Overall, it appears that moulting scoters on the Pacific coast of North America have a wide temporal window during which they can moult and they do not rely on endogenous stores to meet the nutritional and energetic costs of moult. As survival also was very high during this time (B. Uher-Koch, SFU, unpublished data), it appears that scoters select safe and productive environments during moult. They apparently avoid having to make trade-offs between safety and food availability, which confront many species of waterfowl during remigial moult.

4.2 Future Directions

To expand our understanding of moult ecology of scoters, studies of phenology, body mass dynamics and behavioural patterns could be conducted at other locations, particularly where there are smaller aggregations of scoters moulting in coastal areas and/or on inland lakes. Additionally, similar research on other sea ducks would enable us to understand how broadly we can generalize these findings across species. Elucidating broader trends in constraints and population limitation is key to effective conservation planning.

Quantification of prey availability and profitability at moulting sites could refine our interpretation of foraging effort comparisons. Depletion of prey by wintering scoters has been documented, and given the high numbers of scoters at some moult sites, it is possible that prey availability changes significantly over the course of the moulting period.

More in-depth studies of moult in captive sea ducks would be highly informative. While one must always be cautious about applying generalizations based on data from captive birds to wild populations, much could be learned by investigating the effects of factors such as diet and photoperiod on the timing and duration of moult and the subsequent quality of primary feathers. Measurements on captive Barnacle Geese have indicated endogenous control of changes in body mass, metabolic rate, and behaviour in relation to moult (Portugal, Green and Butler 2007).

4.3 Management implications and recommendations

Based on findings presented in this thesis, I suggest that factors causing current declines in scoter populations are likely not occurring during moult on the Pacific coast. Continued efforts are required to determine why North American scoter populations are decreasing. Although the moult period does not appear to constitute a demographic bottleneck for scoters, areas used during moult are likely important habitat for these species. About 20% of the North American population of scoters may be found in southeast Alaska during the late summer, with many of those birds concentrated around eastern Admiralty Island (Hodges, Groves and Conant 2008). It is thus important to identify key features of the habitats used by moulting scoters and determine how best to protect them. This raises questions of fidelity to moult sites and temporal variability: if current moulting habitat becomes unsuitable, how quickly can scoters adapt and move to new areas?

Sea ducks are vulnerable to marine oil pollution (Piatt et al. 1990; Dickson and Gilchrist 2002), and perhaps particularly so during remigial moult when flightless. During this time there is also potential for large numbers of scoters to be impacted simultaneously because of large aggregations. In light of proposed development and increases in oil tanker traffic on the central and north coast of British Columbia, impacts on moulting scoters and other sea ducks should be considered.

As mentioned earlier, there is evidence that some scoters, particularly adult female White-winged Scoters, moult their remiges on inland lakes, rather than on the coast. Given the importance of this cohort to population dynamics, efforts should be made to determine the location of inland moult sites, evaluate their importance, and identify and mitigate potential risks to these sites.

4.4 References

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5: Appendix

Table A-1. Linear mixed model results assessing variation in hourly foraging effort during remigial moult in Surf and White-winged scoters in southeast Alaska and the Salish Sea.

Response	Model	k	ΔAIC	w_i
Surf Scoter				
Hourly foraging effort	Env + Site + Year + Emerg + Pri	18	0	0.581
	Env + Site + Year + Cohort + Emerg + Pri	21	2.59	0.159
	Env + Site + Year + Pri	16	2.82	0.142
	Env + Site + Year + Cohort + Pri	19	3.60	0.096
	Pri	7	6.82	0.019
	Env + Site + Year + Emerg	16	12.39	0.001
	Env + Site + Year	14	13.39	0.001
	Env + Site + Year + Cohort	17	15.38	0.000
	Env + Site + Year + Cohort + Emerg	19	15.46	0.000
	Null	5	16.92	0.000
	Emerg	7	18.87	0.000
	Cohort	8	19.48	0.000
White-winged Scoter				
Hourly foraging effort	Pri	9	0.00	0.438
	Emerg	9	0.14	0.409
	Cohort	10	3.59	0.073
	Null	7	4.30	0.051
	Env + Site + Year + Pri	18	7.99	0.008
	Env + Site + Year + Emerg + Pri	20	8.09	0.008
	Env + Site + Year + Emerg	18	9.73	0.003
	Env + Site + Year + Cohort + Pri	21	10.06	0.003
	Env + Site + Year + Cohort + Emerg + Pri	23	10.46	0.002
	Env + Site + Year	16	10.69	0.002
	Env + Site + Year + Cohort + Emerg	21	10.91	0.002
	Env + Site + Year + Cohort	19	11.75	0.001

Note: The number of parameters (k) includes +1 for intercept, random variance of the intercept, + 1 for the covariance structure for repeated measures, +1 for variance weighting and +1 for residual variance. Models are listed in decreasing order of model weighting (w_i).

Env = time + time^2 + sea (calm, moderate, rough) + tide height + tide state (rise, fall, slack)

Site = Salish Sea or southeast Alaska

Year = 2008 or 2009

Cohort = FASY, FSY, MASY or MSY (F=female, M=male, ASY=after second year, SY =second year)

Emerg = emergence + emergence^2 (Day 1 = June26

Pri = primary + primary^2

Table A-2. Parameter likelihoods and weighted parameter estimates ± unconditional standard error (SE) from linear mixed models evaluating hourly foraging effort by Surf and White-winged scoters moulting in southeast Alaska and the Salish Sea. Response variable was log(min/hour+1).

	Surf Scoter		**White-winged Scoter**	
Explanatory variable	Parameter likelihood	Parameter estimate ± SE	Parameter likelihood	Parameter estimate ± SE
Intercept	1.00	2.87 ± 0.61	1.00	2.62 ± 0.54
Time	0.98	-0.01 ± 0.07	0.03	<0.01 ± <0.01
Time^2	0.98	<0.01 ± <0.01	0.03	<0.01 ± <0.01
Sea(moderate)	0.98	0.04 ± 0.06	0.03	<0.01 ± 0.01
Sea(rough)	0.98	-0.38 ± 0.16	0.03	<0.01 ± 0.01
Tide height	0.98	0.02 ± 0.02	0.03	<0.01 ± <0.01
Tide(rise)	0.98	-0.03 ± 0.06	0.03	<0.01 ± 0.01
Tide(slack)	0.98	-0.16 ± 0.08	0.03	<0.01 ± 0.01
Site(SEAK)	0.98	-0.27 ± 0.09	0.03	0.01 ± 0.02
Year(2009)	0.98	0.11 ± 0.10	0.03	<0.01 ± 0.01
Cohort(FSY)	0.26	0.02 ± 0.06	0.08	0.03 ± 0.06
Cohort(MASY)	0.26	-0.04 ± 0.07	0.08	<0.01 ± 0.02
Cohort(MSY)	0.26	-0.01 ± 0.06	0.08	0.01 ± 0.03
Emergence date	0.74	-0.03 ± 0.02	0.42	<0.01 ± 0.02
Emergence date^2	0.74	<0.01 ± 0.06	0.42	<0.01 ± 0.02
Primary length	1.00	0.01 ± <0.01	0.46	<0.01 ± <0.01
Primary length^2	1.00	<0.01 ± <0.01	0.46	<0.01 ± <0.01