# Phenology and duration of remigial moult in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) on the Pacific coast of North America

**R.D. Dickson, D. Esler, J.W. Hupp, E.M. Anderson, J.R. Evenson, and J. Barrett**

**Abstract:** By quantifying phenology and duration of remigial moult in Surf Scoters (*Melanitta perspicillata* (L., 1758)) and White-winged Scoters (*Melanitta fusca* (L., 1758)), we tested whether timing of moult is dictated by temporal optima or constraints. Scoters ($n = 3481$) were captured during moult in Alaska, British Columbia, and Washington, and remigial emergence dates were determined. We provide evidence for a pre-emergence interval of 7.3 days that occurs after old primaries are shed and before new ones become visible. 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 typical remigial growth rates (Surf Scoters: 3.9 mm·day$^{-1}$; White-winged Scoters: 4.3 mm·day$^{-1}$) but a long flightless period (34–49 days), in part because their relatively high wing-loading requires a greater proportion of feather regrowth to regain flight. Our data suggest that moulting scoters are not under strong selective pressure to complete moult quickly.

*Key words: Melanitta perspicillata*, Surf Scoter, *Melanitta fusca*, White-winged Scoter, sea duck, remigial moult, phenology, duration, primary feather.

**Résumé :** La quantification de la phénologie et de la durée de la mue des rémiges chez les macreuses à front blanc (*Melanitta perspicillata* (L., 1758)) et les macreuses brunes (*Melanitta fusca* (L., 1758)) nous a permis de vérifier si le moment de la mue est dicté ou non par des optima ou autres contraintes temporels. Des macreuses ($n = 3481$) ont été capturées durant la mue en Alaska, en Colombie-Britannique et dans l'État de Washington, et les dates d'apparition des rémiges ont été déterminées. Nous présentons des données indiquant qu'un intervalle de 7,3 jours précédant cette apparition s'écoule après la perte des vieilles ailes primaires et avant que les nouvelles ne deviennent visibles. Toutes les classes de sexe et d'âge des deux espèces de macreuses présentent une large fourchette de dates d'apparition (macreuse à front blanc : du 26 juin au 22 septembre; macreuse brune : du 6 juillet au 21 septembre), ce qui laisse croire à l'absence de forts optima temporels de mue des rémiges. Pour les deux espèces, le moment de la mue était influencé par le site, l'année, l'âge et le sexe. Comparativement à d'autres espèces de sauvagines, les macreuses présentent des taux de croissance des rémiges typiques (macreuse à front blanc : 3,9 mm·jour$^{-1}$; macreuse brune : 4,3 mm·jour$^{-1}$), mais une période d'incapacité de voler relativement longue (de 34 à 49 jours), en partie due au fait que, en raison de leur charge alaire relativement élevée, une proportion relativement grande de nouveau matériel alaire est nécessaire pour permettre à ces oiseaux de recouvrer la capacité de voler. Nos données suggèrent que les macreuses en mue ne sont pas assujetties à une forte pression sélective les poussant à muer rapidement.

*Mots-clés : Melanitta perspicillata*, macreuse à front blanc, *Melanitta fusca*, macreuse brune, canard de mer, mue des rémiges, phénologie, durée, aile primaire.

[Traduit par la Rédaction]

**R.D. Dickson, E.M. Anderson,* and J. Barrett.** Centre for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.
**D. Esler.** Centre for Wildlife Ecology, Simon Fraser University, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.
**J.W. Hupp.** Alaska Science Center, US Geological Survey, 4210 University Drive, Anchorage, AK 99508, USA.
**J.R. Evenson.** Washington Department of Fish and Wildlife, Puget Sound Assessment and Monitoring Program, 600 Capitol Way North, Olympia, WA 98501, USA.

**Corresponding author:** Rian D. Dickson (e-mail: rdd@sfu.ca).

*Present address: British Columbia Institute of Technology, 3700 Willingdon Avenue, Burnaby, BC V5G 3H2, Canada.

## Introduction

Remigial moult is a distinct phase in the annual cycle of waterfowl during which all flight feathers are lost simultaneously, leaving individuals flightless. Flight feathers are regrown synchronously, with the flightless period estimated to last between 20 and 40 days, depending on species, age, and sex (Hohman, et al. 1992). Remigial moult occurs during the postbreeding 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 et al. 2007; Lok et al. 2008; Bridge et al. 2010; Mazerolle et al. 2011), often resulting in a high degree of synchrony in timing of those events among individuals in a species or population. For example, arrival on breeding grounds and settling date at nest sites is highly synchronous across a large area for Surf Scoters (*Melanitta perspicillata* (L., 1758)) (Takekawa et al. 2011). In many species, timing of wing moult is constrained by breeding or migration phenology (Murphy 1996). If there are neither strong temporal optima nor constraints dictating the timing of moult, then other factors, such as individual life histories or body condition, may play a larger role.

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 et al. 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 events in the annual cycle and whether temporal constraints are more likely to be present for particular cohorts.

The length of time required to complete remigial moult is determined by primary feather growth rates, which may be constrained by physiological limits (Rohwer et al. 2009). In waterfowl, primary feather growth rates range from 3.0 to 8.1 mm·day$^{-1}$ (Hohman et al. 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 20–30 days (Hohman et al. 1992). Another consideration in determining duration of flightlessness is the period of time that 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 and White-winged Scoters (*Melanitta fusca* (L., 1758)) are sea ducks that breed in northern Canada and Alaska, and winter on the Atlantic and Pacific coasts of North America. In spring, scoters generally migrate northwards and move inland to breeding areas, mainly in the boreal forest (Brown and Fredrickson 1997; Savard et al. 1998; De la 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). If their breeding attempt is unsuccessful, females subsequently remain on breeding grounds for a variable amount of time. After leaving breeding areas, most scoters return to the coast and undergo remigial moult. Scoters have a complex age structure in which sec-

ond-year, nonbreeding birds are present in the population, and these subadults may migrate from winter areas directly to moulting areas (Brown and Fredrickson 1997; Savard et al. 2007).

Both Surf and White-winged scoters moult over a large latitudinal range on the Pacific Coast (J.R. Evenson, unpublished data), 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). Evaluating constraints faced by moulting scoters could reveal whether this phase of the annual cycle may constitute a demographic bottleneck for these species. We hypothesized that temporal optima or temporal constraints dictated the timing of remigial moult in Surf and White-winged scoters. Therefore, we quantified phenology and duration of the moult process to (*i*) determine if timing of moult differed among widely separated moulting areas, (*ii*) evaluate differences in onset of moult among birds in different age and sex classes, (*iii*) contrast moult phenology between two scoter species, and (*iv*) examine the total duration of time that flightless scoters were present at moulting areas. We predicted that if temporal optima or constraints strongly influenced moult phenology in scoters, we would observe synchronous moulting, high feather growth rates, and a short duration of remigial moult.

## Materials and methods

### Field methods

We captured White-winged and Surf scoters during wing moult in late July to September of 2008 and 2009 in southeast Alaska and the Salish Sea (Fig. 1). 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 × 8 km wide. 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 Forbes Point (48.3°N, 122.6°W) in Washington. The Fraser River Delta and Boundary Bay are composed of intertidal mudflats, seagrass beds, and occasional rocky outcrops. Padilla Bay is almost entirely intertidal and contains one of the largest contiguous beds of eelgrass (genus *Zostera* L.) on the Pacific coast of North America (Bulthuis 1995). Forbes Point is largely unvegetated with intertidal substrates ranging from coarse sand to cobble, and subtidal substrates composed mainly of fine sands. 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 (Hodges et al. 2008). Some of the highest concentrations of scoters were observed around eastern Admiralty Island and surveys in 2008 and 2009 indicated that at least 16 000 scoters were in the northern half of Seymour Canal (R.D. Dickson, unpublished data). The Salish Sea contains one of the main moulting sites for

**Fig. 1.** Locations of study sites of moulting Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) in southeast Alaska (SC, Seymour Canal) and the Salish Sea (FR, Fraser River Delta; BB, Boundary Bay; PB, Padilla Bay; FP, Forbes Point).
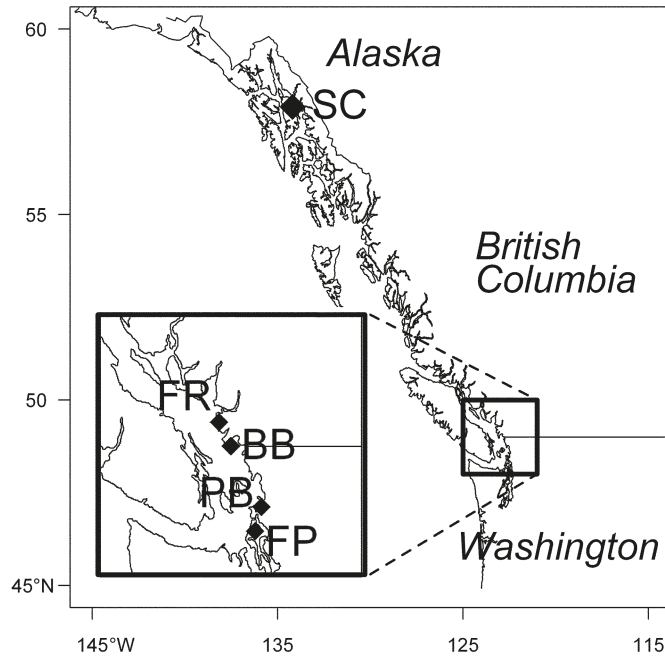


scoters south of Alaska, with upwards of 20 000 scoters (E.M. Anderson and J.R. Evenson, unpublished data).

To capture scoters, we used a floating gill-net method, adapted from a submerged mist-net technique (Breault and Cheng 1990). We used two to three boats to move flocks of scoters toward a free-floating gill net, using cracker shells to elicit a dive response at the net. 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.

We marked all captured scoters with a uniquely numbered stainless steel US 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 (±1 mm). The length of the 9th primary was used as a metric of the stage of wing moult. The 9th primary is the longest primary feather in scoters, and 9th primary length is commonly used in waterfowl morphometrics. We examined feather wear to determine whether fully grown primaries had been moulted in the current season or if the feathers were from the previous year. All birds were handled in accordance with protocols approved by the Animal Care Committee at Simon Fraser University (project No. 868B).

### Statistical analyses

Lengths of primary feathers 1–10 were measured on 14 ASY male Surf Scoters (Table 1). 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 the 9th primary length was used as the metric for remigial moult stage in all analyses.

We defined emergence date as the first day on which new primary feathers became visible. While this is often called the moult initiation date, active feather generation almost certainly begins earlier, before new 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 growing primaries were visible.

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, Environment Canada, unpublished data) and female White-winged Scoters held at Dry Creek Waterfowl in Washington (E.M. Anderson, 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 mean of the estimates across individuals to obtain a single estimate of feather growth rate for each species, as there was no evidence that rates differed between sexes or age classes (J.-P. Savard, personal communication 2010).

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). We estimated the duration of the pre-emergence interval using 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.C. Palm, Simon Fraser University, 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.

The pre-emergence interval 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 captured scoter, we used multiple linear regression models to

**Table 1.** Lengths of primary (P) feathers of after-hatch-year (AHY) male Surf Scoters (*Melanitta perspicillata*), measured during remigial moult in southeast Alaska.

| Bird ID | Primary feather length (mm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | P9 | P10 |
| 09-02 | 37 | 35 | 39 | 39 | 41 | 40 | 39 | 35 | 34 | 35 |
| 09-06 | 103 | 109 | 119 | 124 | 129 | 129 | 149 | 156 | 159 | 160 |
| 09-08 | 100 | 105 | 113 | 121 | 126 | 129 | 131 | 135 | 136 | 120 |
| 09-09 | 108 | 107 | 111 | 124 | 132 | 140 | 148 | 153 | 151 | 129 |
| 09-10 | 106 | 105 | 112 | 122 | 128 | 137 | 134 | 144 | 141 | 131 |
| 09-11 | 103 | 101 | 113 | 123 | 131 | 140 | 144 | 150 | 145 | 139 |
| 09-12 | 108 | 108 | 117 | 124 | 134 | 144 | 152 | 159 | 161 | 152 |
| 09-13 | 97 | 106 | 113 | 129 | 133 | 140 | 130 | 159 | 158 | 149 |
| 09-14 | 107 | 108 | 116 | 115 | 127 | 137 | 144 | 145 | 133 | 127 |
| 09-15 | 105 | 108 | 113 | 126 | 134 | 140 | 149 | 150 | 146 | 138 |
| 09-16 | 102 | 111 | 119 | 130 | 137 | 145 | 152 | 153 | 156 | 156 |
| 09-17 | 101 | 105 | 114 | 125 | 134 | 142 | 151 | 157 | 156 | 147 |
| 09-18 | 99 | 105 | 113 | 122 | 131 | 138 | 148 | 157 | 160 | 149 |
| 09-19 | 100 | 106 | 113 | 122 | 131 | 139 | 149 | 157 | 160 | 150 |
| 09-20 | 110 | 110 | 115 | 124 | 132 | 142 | 150 | 155 | 152 | 144 |

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 (Tables 2 and 3). To run regression models, we used the *lm* function in R (R Development Core Team 2011).

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 $\Delta AIC_c$ values, calculated as the difference between the $AIC_c$ score of each model and that 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 multimodel inference (Burnham and Anderson 2002) to assess the importance of individual variables in the candidate models.

To investigate interannual variation in timing of moult for individuals, we used scoters that were captured in both 2008 and 2009. We calculated the difference between their emergence dates in the 2 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 mean random difference in initiation dates between the 2 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 recaptures 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. To do so, 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 regrowth 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 the length of fully grown 9th primaries for each species and sex (D. Esler, unpublished data). The time required to grow primaries to their full length was calculated by dividing the 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.

All values reported in Results are means ± SE, unless otherwise noted. All statistical analyses were conducted using R (R Development Core Team 2011).

## Results

### Feather growth rates

Estimated 9th primary growth rates based on combined mean values for captive and wild scoters were 3.9 ± 0.2 mm·day$^{-1}$ for Surf Scoters and 4.3 ± 0.2 mm·day$^{-1}$ for White-winged Scoters. These growth rates are equivalent to a daily percent change in length of 2.5% and 2.4% (relative to fully grown 9th primaries) for Surf Scoters and White-winged Scoters, respectively. For wild-caught scoters, primary growth rates were 3.8 ± 0.2 mm·day$^{-1}$ for Surf Scoters

**Table 2.** Multiple linear regression model results assessing variation in 9th primary feather emergence dates in Surf Scoters (*Melanitta perspicillata*) in southeast Alaska and the Salish Sea.

| Model | $k$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|
| Cohort[a] + site[b] + year[c] + cohort × site + cohort × year + site × year | 14 | 0.0 | 0.99 |
| Cohort + site + year + cohort × year + site × year | 11 | 8.4 | 0.01 |
| Cohort + site + year + cohort × site + site × year | 11 | 22.9 | 0.00 |
| Cohort + site + year + site × year | 8 | 31.7 | 0.00 |
| Cohort + site + year + cohort × year | 10 | 53.1 | 0.00 |
| Cohort + site + year + cohort × site + cohort × year | 13 | 54.3 | 0.00 |
| Cohort + site + year | 7 | 101.5 | 0.00 |
| Cohort + site + year + cohort × site | 10 | 104.1 | 0.00 |
| Cohort + site | 6 | 109.4 | 0.00 |
| Cohort + site + cohort × site | 9 | 111.2 | 0.00 |
| Cohort + year + cohort × year | 9 | 174.3 | 0.00 |
| Cohort + year | 6 | 231.1 | 0.00 |
| Cohort | 5 | 242.2 | 0.00 |
| Site + year + site × year | 5 | 2091.9 | 0.00 |
| Site + year | 4 | 2215.4 | 0.00 |
| Site | 3 | 2235.8 | 0.00 |
| Year | 3 | 2515.9 | 0.00 |
| Null | 2 | 2551.0 | 0.00 |

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

[a]Cohort is either femaleASY, femaleSY, maleASY, or maleSY, where ASY is after second year and SY is second year.

[b]Site is either southeast Alaska or Salish Sea.

[c]Year is either 2008 or 2009.

**Table 3.** Multiple linear regression model results assessing variation in 9th primary feather emergence dates in White-winged Scoters (*Melanitta fusca*) in southeast Alaska and the Salish Sea.

| Model | $k$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|
| Cohort[a] + site[b] + year[c] + cohort × year + site × year | 11 | 0.0 | 0.46 |
| Cohort + site + year + cohort × year | 10 | 0.3 | 0.40 |
| Cohort + site + year + cohort × site + cohort × year + site × year | 14 | 3.8 | 0.07 |
| Cohort + site + year + cohort × site + cohort × year | 13 | 3.8 | 0.07 |
| Cohort + site + year | 7 | 17.1 | 0.00 |
| Cohort + site + year + cohort × site | 10 | 17.7 | 0.00 |
| Cohort + site + year + site × year | 8 | 18.8 | 0.00 |
| Cohort + site + year + cohort × site + site × year | 11 | 19.5 | 0.00 |
| Cohort + site | 6 | 31.9 | 0.00 |
| Cohort + site + cohort × site | 9 | 32.2 | 0.00 |
| Cohort + year + cohort × year | 9 | 98.5 | 0.00 |
| Cohort + year | 6 | 109.9 | 0.00 |
| Cohort | 5 | 141.7 | 0.00 |
| Site + year | 4 | 258.2 | 0.00 |
| Site + year + site × year | 5 | 260.3 | 0.00 |
| Site | 3 | 276.1 | 0.00 |
| Year | 3 | 388.8 | 0.00 |
| Null | 2 | 431.1 | 0.00 |

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

[a]Cohort is either femaleASY, femaleSY, maleASY, or maleSY, where ASY is after second year and SY is second year.

[b]Site is either southeast Alaska or Salish Sea.

[c]Year is either 2008 or 2009.

($n$ = 9) and 4.7 ± 0.1 mm·day$^{-1}$ for White-winged Scoters ($n$ = 8). For captive scoters at Patuxent Wildlife Research Center, primary growth rates were 4.0 ± 0.1 mm·day$^{-1}$ for Surf Scoters ($n$ = 5) and 4.4 ± 0.04 mm·day$^{-1}$ for White-winged Scoters ($n$ = 14) (J.-P. Savard, Environment Canada, unpublished data). Captive White-winged Scoters ($n$ = 12) at Dry Creek Waterfowl had a primary growth rate of 3.8 ± 0.4 mm·day$^{-1}$. Estimated growth rates based on the combined mean values for each species were used in further analyses.

### Pre-emergence interval

We estimated the pre-emergence interval for male AHY White-winged Scoters ($n$ = 30) to be 7.3 ± 0.04 days. Two other methods of estimating the pre-emergence interval, which included male and female Surf Scoters, gave similar mean values (Dickson 2011), so 7.3 days was used for both species and sexes in further analyses.

### Variation in emergence date

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 ($w_i$ = 0.99) (Table 2). For White-winged Scoters, the two top-supported models included all three main effects and either the cohort × year and site × year interactions ($w_i$ = 0.46) or just the cohort × year interaction ($w_i$ = 0.40) (Table 3). All top-supported models had good explanatory power; $r^2$ = 0.62 for Surf Scoters and $r^2$ = 0.43 and 0.42 for the two top-supported models for White-winged Scoters, respectively. Model-averaged parameter estimates from both models are given in Table 4.

Mean remigial emergence dates for each species, cohort, site, and year are given in Table 5. For both scoter species, SY individuals of both sexes began remigial moult earlier than ASY birds, and males started earlier than females (Figs. 2 and 3). 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. ASY females began moult 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 4). 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 5).

Mean emergence dates for both species were earlier 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 4). 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 had low parameter likelihoods (and small parameter estimates) in the White-winged Scoter analysis, but higher support in the Surf Scoter analysis. They indicated that for Surf Scoters, although SY males and females initiated 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 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 difference was 12.0 ± 0.1 days (range 4.4–26.0 days), indicating that 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 6). 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 with the mean values of 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 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

**Table 4.** Parameter likelihoods and weighted parameter estimates ± unconditional standard error (SE) from multiple linear regression models evaluating variation in remigial emergence dates in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) in southeast Alaska (SEAK) and the Salish Sea (SALS) (dates based on 25 June = 0).

| | Surf Scoter | | White-winged Scoter | |
|---|---|---|---|---|
| Explanatory variable | Parameter likelihood | Parameter estimate ± SE | Parameter likelihood | Parameter estimate ± SE |
| Intercept | 1.00 | 62.0±0.4 | 1.00 | 48.9±2.0 |
| Cohort(FSY) | 1.00 | −23.3±1.2 | 1.00 | −8.5±3.0 |
| Cohort(MASY) | 1.00 | −22.2±1.0 | 1.00 | −9.9±2.1 |
| Cohort(MSY) | 1.00 | −36.7±1.2 | 1.00 | −14.4±2.6 |
| Site(SEAK) | 1.00 | −15.2±1.7 | 1.00 | −10.4±2.4 |
| Year(2009) | 1.00 | −3.6±0.6 | 1.00 | 13.3±2.4 |
| Cohort(FSY) × site(SEAK) | 0.99 | 5.6±2.6 | 0.14 | 1±2.1 |
| Cohort(MASY) × site(SEAK) | 0.99 | 0.4±1.5 | 0.14 | 0.9±1.9 |
| Cohort(MSY) × site(SEAK) | 0.99 | 6.1±2.2 | 0.14 | 1.2±2.4 |
| Cohort(FSY) × year(2009) | 1.00 | −6.4±1.7 | 1.00 | −12.9±3.6 |
| Cohort(MASY) × year(2009) | 1.00 | 2.0±1.2 | 1.00 | −11.5±2.5 |
| Cohort(MSY) × year(2009) | 1.00 | 3.9±1.4 | 1.00 | −13.4±3.2 |
| Site(SEAK) × year(2009) | 1.00 | 10.2±1.4 | 0.53 | 1.4±1.8 |

**Note:** Parameter likelihoods closest to 1 have the greatest relative support. FSY, female second year; MASY, male after second year; MSY, male second year. All variables are categorical; references cases are cohort(FASY), site(SALS), and year(2008).

**Table 5.** Remigial emergence dates (mean ± SE) for Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) moulting in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009 (SY, second year; ASY, after second year; NA, not available).

| | | | Surf Scoter | | | White-winged Scoter | | |
|---|---|---|---|---|---|---|---|---|
| Cohort | Site | Year | *n* | Mean ± SE | Range | *n* | Mean ± SE | Range |
| Male SY | SEAK | 2008 | 43 | 11 July ± 0.9 | 30 June – 28 July | 30 | 20 July ± 1.1 | 8 July – 7 Aug. |
| | SEAK | 2009 | 27 | 21 July ± 1.1 | 9 July – 6 Aug. | 18 | 23 July ± 1.2 | 15 July – 1 Aug. |
| | SALS | 2008 | 107 | 20 July ± 1.2 | 27 June – 8 Sept. | 18 | 29 July ± 1.9 | 18 July – 16 Aug. |
| | SALS | 2009 | 174 | 20 July ± 0.7 | 27 June – 5 Sept. | 24 | 27 July ± 1.5 | 12 July – 13 Aug. |
| Male ASY | SEAK | 2008 | 108 | 19 July ± 1.0 | 26 June – 21 Aug. | 63 | 24 July ± 1.2 | 6 July – 17 Aug. |
| | SEAK | 2009 | 198 | 29 July ± 0.7 | 5 July – 23 Aug. | 42 | 27 July ± 1.2 | 11 July – 11 Aug. |
| | SALS | 2008 | 159 | 4 Aug. ± 1.1 | 3 July – 12 Sept. | 174 | 3 Aug. ± 0.7 | 12 July – 30 Aug. |
| | SALS | 2009 | 284 | 1 Aug. ± 0.7 | 29 June – 7 Sept. | 306 | 4 Aug. ± 0.6 | 17 July – 13 Sept. |
| Female SY | SEAK | 2008 | 20 | 23 July ± 3.9 | 5 July – 4 Sept. | 20 | 26 July ± 1.5 | 16 July – 5 Aug. |
| | SEAK | 2009 | 13 | 25 July ± 2.9 | 17 July – 18 Aug. | 13 | 27 July ± 2.1 | 15 July – 10 Aug. |
| | SALS | 2008 | 101 | 2 Aug. ± 1.9 | 7 July – 13 Sept. | 6 | 1 Aug. ± 1.9 | 27 July – 9 Aug. |
| | SALS | 2009 | 83 | 23 July ± 1.6 | 3 July – 12 Sept. | 17 | 5 Aug. ± 2.7 | 19 July – 30 Aug. |
| Female ASY | SEAK | 2008 | 13 | 18 Aug. ± 5.3 | 13 July – 12 Sept. | 2 | 20 July ± 1.0 | 19–21 July |
| | SEAK | 2009 | 83 | 16 Aug. ± 0.7 | 23 July – 1 Sept. | 1 | 28 Aug. | NA |
| | SALS | 2008 | 683 | 25 Aug. ± 0.4 | 5 July – 22 Sept. | 20 | 14 Aug. ± 2.5 | 27 July – 6 Sept. |
| | SALS | 2009 | 575 | 22 Aug. ± 0.5 | 6 July – 21 Sept. | 56 | 26 Aug. ± 1.5 | 4 Aug – 21 Sept. |

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 mean final length of 9th primary feathers (measured on winter-captured scoters). The time required to complete growth of the 9th primaries was 45.6 and 48.2 days for female and male Surf Scoters, respectively, and 47.2 and 49.8 days for female and male White-winged Scoters, respectively. See Table 6 for estimates of the length of the growth period excluding the pre-emergence interval. The population-level duration of remigial moult for each species is depicted in Figs. 4 and 5. 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 et al. 1992).

## Discussion

Our data indicate that there is a not a strong temporal optimum for the timing of remigial moult in Surf Scoters and White-winged Scoters, as emergence dates were highly variable among and within cohorts in southeast Alaska and the Salish Sea in both years of this study. Although individual scoters may be constrained in the timing of their moult by factors such as recent breeding activity, migration timing, or body condition, there is a wide temporal window during

**Fig. 2.** Relative frequency of remigial emergence dates for Surf Scoters (*Melanitta perspicillata*) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009 (SY, second year; ASY, after second year).
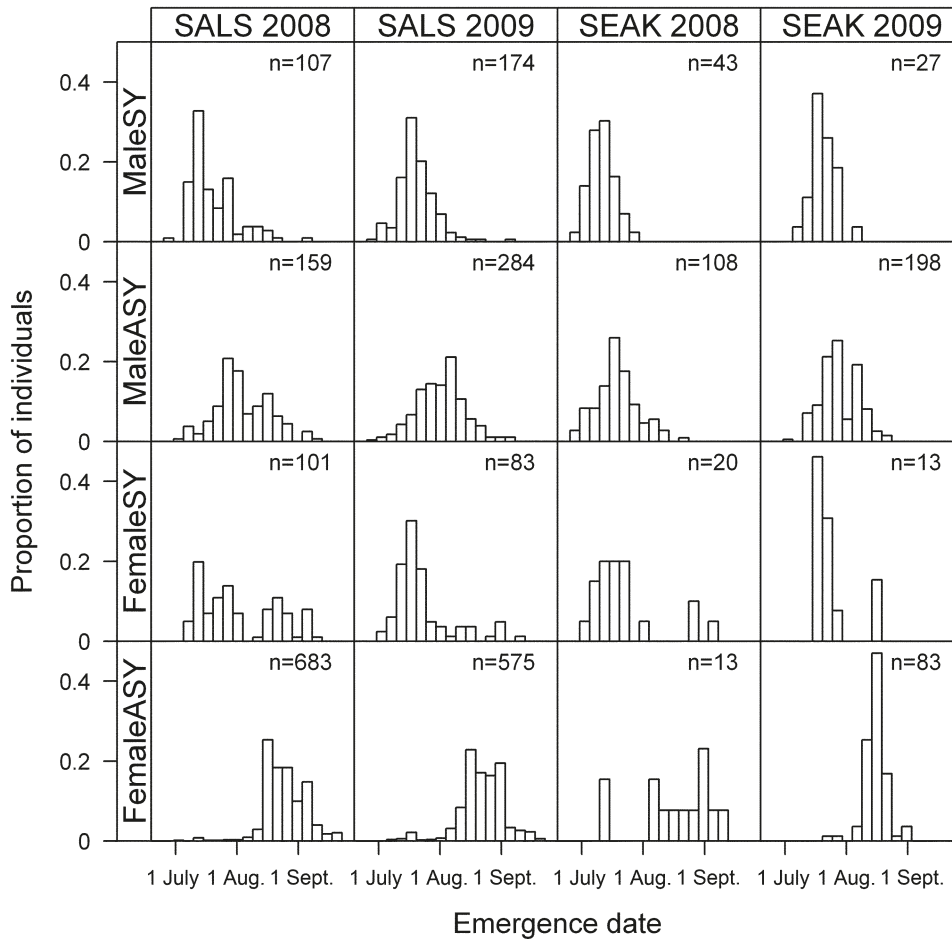
which scoters undergo moult on the Pacific coast. The duration of the flightless period is long relative to other waterfowl, evidence that scoters are not under strong pressure to complete moult rapidly. The earliest remigial emergence dates were in late June (for SY and ASY male Surf Scoters) and the latest emergence dates were 21–22 September (for ASY females of both species). The latest moulting 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 10% of the year for an individual scoter, but at the population level, the process occurs over a period of more than 4 months.

**Remigial moult and breeding phenology**

Moult initiation dates for scoters on the Pacific coast generally corresponded 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 broods before leaving the breeding grounds. Female Surf Scoters in Quebec begin incubation in mid- to late June, at which time most male Surf

Scoters leave the breeding areas (Savard et al. 2007). Females that fail early in reproduction or lose their broods after hatching leave breeding areas after the males (Savard et al. 2007), whereas successful females stay with their broods until late August or September, when they abandon their ducklings (Savard et al. 2007; Lesage et al. 2008).

For White-winged Scoters, timing of breeding activities has been documented at several sites in western North America, including Redberry Lake, Saskatchewan, Cardinal Lake, Northwest Territories, and Yukon Flats, Alaska. Generally, breeding phenology is quite synchronous across a large geographic area and 15° of latitude; most females begin incubation in late June to early July, whereupon males leave breeding areas (Brown and Fredrickson 1997; Safine 2005; S. Slattery, Ducks Unlimited Canada, unpublished data). 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. Mean emergence dates for ASY White-winged Scoter males were 24–28 July in southeast Alaska and 3–5 August in the Salish Sea, 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 did not begin moult until 2 months after the latest incubation initiation dates. There is considerable variation in

**Fig. 3.** Relative frequency of remigial emergence dates for White-winged Scoters (*Melanitta fusca*) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009 (SY, second year; ASY, after second year). Data for ASY females in southeast Alaska are not plotted because of small sample sizes (2008: $n = 2$; 2009: $n = 1$).
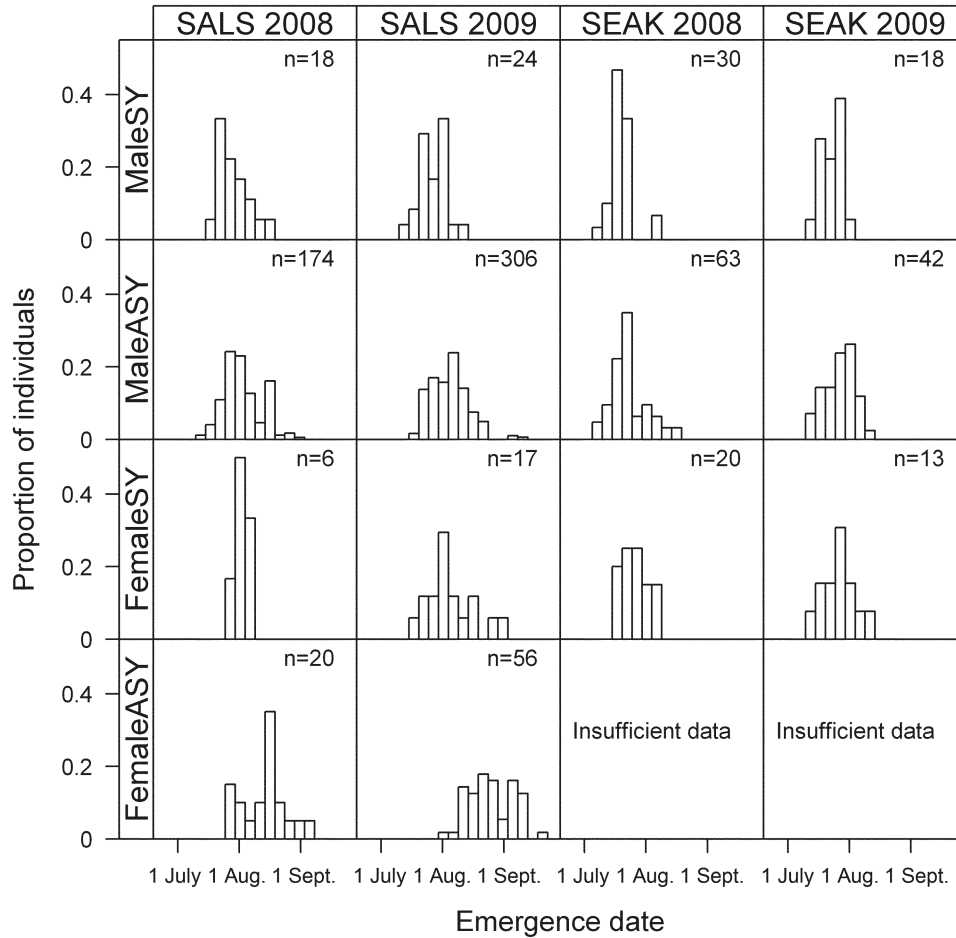


**Table 6.** Estimates of the duration of the flightless period during remigial moult for Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) in southeast Alaska and the Salish Sea.

| Species | Sex | Final 9th primary length[c] (mm) | Length required for flight[a] (mm) | | Estimate of pre-emergence interval (days; mean ± SE) | Length of flightless period[b] (days) | | Ninth primary growth period (days) | |
| | | | 97.5th percentile | 100th percentile | | Lower estimate | Upper estimate | From emergence date | With pre-emergence interval |
|---|---|---|---|---|---|---|---|---|---|
| SUSC | Female | 150 | 125.3 (83%) | 139 (93%) | 7.3±0.04 | 39.2 | 42.7 | 38.2 | 45.5 |
| | Male | 160 | 138.0 (86%) | 158 (98%) | 7.3±0.04 | 42.4 | 47.5 | 40.8 | 48.1 |
| WWSC | Female | 170 | 151.8 (89%) | 164 (97%) | 7.3±0.04 | 42.9 | 45.8 | 39.8 | 47.1 |
| | Male | 181 | 158.3 (88%) | 179 (99%) | 7.3±0.04 | 44.4 | 49.3 | 42.4 | 49.7 |

**Note:** Estimates are calculated using feather growth rates of 3.9 mm·day$^{-1}$ for Surf Scoters and 4.3 mm·day$^{-1}$ for White-winged Scoters. The length required for flight is based on the distributions of primary lengths of flightless scoters captured during remigial moult.

[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 mean values based on measurements taken on after-hatch-year scoters caught during winter (D. Esler, unpublished data).

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 2 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. For male diving ducks breeding and moulting in Idaho, about 6 weeks elapsed between desertion of their mates and the onset of flightlessness (Oring 1964) and Bar-

**Fig. 4.** Population-level duration of remigial moult in Surf Scoters (*Melanitta perspicillata*) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009. Horizontal lines indicate the maximum range of dates during which a particular cohort undergoes remigial moult (from emergence date to completion of 9th primary growth) and bars indicate when >25%, >50%, and >75% of a cohort is moulting.
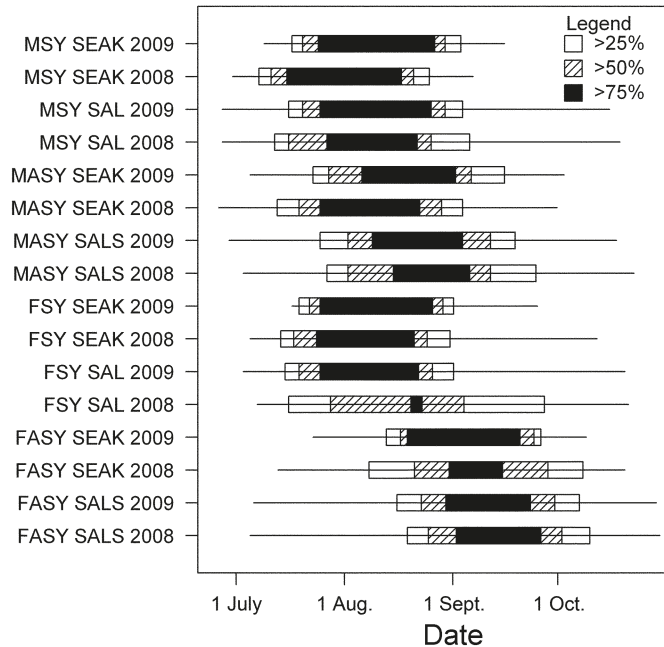


**Fig. 5.** Population-level duration of remigial moult in White-winged Scoters (*Melanitta fusca*) in southeast Alaska (SEAK) and the Salish Sea (SALS) in 2008 and 2009. Horizontal lines indicate the maximum range of dates during which a particular cohort undergoes remigial moult (from emergence date to completion of 9th primary growth) and bars indicate when >25%, >50%, and >75% of a cohort is moulting. *For FASY in southeast Alaska, *n* = 2 and *n* = 1 for 2008 and 2009, respectively.
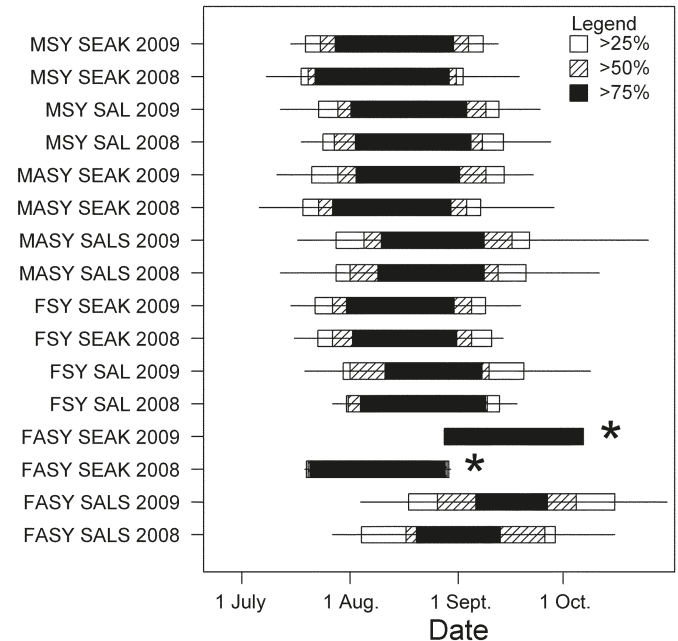


row's Goldeneye (*Bucephala islandica* (Gmelin, 1789)) arrived at moulting areas over a month before shedding primary feathers (Robert et al. 2002).

### Remigial moult and migration

Salomonsen (1968) suggested that adult female waterfowl moulting with males and subadults are likely nonbreeders (in that year). However, our data suggest that many adult females moulting on the coast could have spent the summer on breeding areas, and either did not successfully nest or may have hatched ducklings but not remained with them until fledging. White-winged Scoters begin to fledge in mid-September (Brown and Fredrickson 1997) and the latest emergence dates we recorded for ASY females were mid- to late September (6 September 2008 and 21 September 2009). Those females probably would have arrived on the moulting grounds at least 1 week before remigial growth first became visible and 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 et al. 2008).

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 et al. 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. In the spring and summer, SY scoters generally move northwards on the coast, from wintering to moulting areas. On average, female Surf Scoters winter farther south than do males (D. Esler, unpublished data), so perhaps SY females have farther to migrate and (or) migrate more slowly before beginning remigial moult. There is also evidence that some SY females migrate to breeding grounds (S. Slattery, Ducks Unlimited Canada, unpublished data), which could influence the mean emergence date for that cohort, even though the majority of SY females moult at about the same time as SY males. It appears that there were two "waves" of moult initiation for Surf Scoter SY females in the Salish Sea (Fig. 2). It may be that the earlier group were SY females that remained on the coast, moving directly from wintering to moulting areas, whereas the second group migrated to breeding grounds and then returned to the coast to undergo remigial moult.

On the Pacific coast of North America, there is considerable overlap in moulting and wintering areas of scoters, although there is a general southwards shift during winter (Brown and Fredrickson 1997; Savard et al. 1998; J.R. Evenson, unpublished data). By moving from northern and interior breeding areas to the coast prior to moulting, scoters may avoid some of the temporal constraints that would potentially be imposed by declining food availability and inclement weather conditions on breeding areas. Other species of waterfowl with northward and (or) inland moult migrations have more synchronous moult timing than do scoters (e.g.,

Black Brant (*Branta bernicla nigricans* (Lawrence, 1846)): Taylor 1995; Barrow's Goldeneye: Hogan 2012). Generally, we observed a wider range of emergence dates and later emergence dates in the Salish Sea than in southeast Alaska. It could be that individuals migrating from breeding areas to the coast later in the season are more likely to go to southern moulting areas or that individuals moulting in the Salish Sea spend a longer period on the coast before beginning moult.

### Feather growth rates

Our estimates of scoter primary feather growth rates are similar to those obtained for adults of other duck species (4.2–5.2 mm·day$^{-1}$) and fall within the typical range of 2%–3% daily change in length, relative to final primary length (Hohman et al. 1992). However, they are higher than values obtained from allometric equations (Rohwer et al. 2009), which give values of 3.3 and 3.5 mm·day$^{-1}$ 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.

### Pre-emergence interval

Estimates of the pre-emergence period are lacking in most published descriptions of remigial moult. Balat (1970) reported that 2–4 days elapsed between the shedding of old primaries and appearance of the new in captive Mallards (*Anas platyrhynchos* L., 1758) and Bowman (1987) used a value of 3 days of no visible primary growth in American Black Ducks (*Anas rubripes* Brewster, 1902). However, our data indicate that the pre-emergence period may last at least a week. 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 (*Histrionicus histrionicus* (L., 1758)) indicate that the pre-emergence interval for this species is ≥7 days (E.M. Anderson, unpublished data), and for Spectacled Eiders (*Somateria fischeri* (Brandt, 1847)), it may be ≥14 days (T. Hollmén, Alaska SeaLife Center, personal communication 2010) Thus, our estimate of 7.3 days seems reasonable. Furthermore, primary feather growth appears to be slightly slower during the earlier stages (J.-P. Savard, Environment Canada, personal communication 2010), so our estimate of the pre-emergence interval should be conservative, and in reality, this period may be even longer.

The pre-emergence 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 20% 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). Although 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; however, for remiges and rectrices of larger birds, it is likely that several days elapse before new feathers visibly emerge from follicles.

### Individual interannual variation

Timing of remigial moult for individual ASY female Surf Scoters was remarkably consistent between years, based on individuals that were captured in both years of our study. 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; De la Cruz et al. 2009; Regehr 2011). However, we had expected high between-year variation in emergence dates for the ASY female cohort, in particular. If initiation of wing moult occurs shortly after breeding activity ceases, we hypothesized that an adult female'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 only 2–4 days.

### Duration of flightlessness

Although 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 et al. 1992). This resulted from our finding that the percentage of remigial regrowth necessary for flight was higher for scoters (85%–99%) than reported for other waterfowl (Hohman et al. 1992), as well as our inclusion of the pre-emergence interval. Much previous work has focused 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. Furthermore, scoters maintain high body mass during moult relative to other phases of the annual cycle (Dickson 2011), which also would contribute to high wing-loading and a high percentage of remigial growth required to achieve flight. Mass loss has been observed in moulting waterfowl of several species and has been interpreted as an adaptive response to shorten the flightless period (Sjöberg 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 and 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), which also suggests that there are not strong temporal constraints on wing moult in scoters.

## Acknowledgements

J. Reed, V. Richard, B. Uher-Koch, C. VanStratt, and J. Whissel. In British Columbia and Washington, fieldwork was carried out by S. Quinlan, D. Nysewander, B. Murphie, and T. Cyra, with help from dozens of volunteers. A. Schouten of Dry Creek Waterfowl made measurements of captive Scoters possible. This work was supported financially and logistically by the Sea Duck Joint Venture, Environment Canada, Natural Sciences and Engineering Research Council of Canada (Canada Graduate Scholarship to R.D.D.), United States Geological Survey Alaska Science Center, Ducks Unlimited Canada (fellowship to R.D.D.), Simon Fraser University, the Province of British Columbia through the Ministry of Advanced Education (funding for R.D.D.), United States Fish and Wildlife Service, United States Forest Service, and the Washington Department of Fish and Wildlife. We thank J.-P. Savard, R. Ydenberg, T. Williams, and two anonymous reviewers for their comments on earlier versions of the manuscript.

## References

Austin, J.E., and Fredrickson, L.H. 1986. Molt of female Lesser Scaup immediately following breeding. Auk, **103**(2): 293–298.

Balat, F. 1970. On the wing moult in the Mallard, *Anas platyrynchos*, in Czechoslovakia. Zool. Listy, **19**: 135–144.

Bowman, T.D. 1987. Ecology of male Black Ducks molting in Labrador. M.Sc. thesis, Wildlife Management, University of Maine, Orono.

Breault, A.M., and Cheng, K.M. 1990. Use of submerged mist nets to captures diving birds. J. Field Ornithol. **61**(3): 328–330.

Bridge, E.S. 2011. Mind the gaps: what's missing in our understanding of feather molt. Condor, **113**(1): 1–4. doi:10.1525/cond.2011.100228.

Bridge, E.S., Kelly, J.F., Bjornen, P.E., Curry, C.M., Crawford, P.H.C., and Paritte, J.M. 2010. Effects of nutritional condition on spring migration: do migrants use resource availability to keep pace with a changing world? J. Exp. Biol. **213**(14): 2424–2429. doi:10.1242/jeb.041277. PMID:20581272.

Brown, P.W., and Brown, M.A. 1981. Nesting biology of the white-winged scoter. J. Wildl. Manage. **45**(1): 38–45. doi:10.2307/3807871.

Brown, P.W., and Fredrickson, L.H. 1997. White-winged Scoter (*Melanitta fusca*). *In* The birds of North America. No. 274. Cornell Lab of Ornithology, Ithaca, N.Y.

Brown, P.W., and Houston, C.S. 1982. Longevity and age of maturity of White-winged Scoters. J. Field Ornithol. **53**(1): 53–54.

Brown, R.E., and Saunders, D.K. 1998. Regulated changes in body mass and muscle mass in molting Blue-winged Teal for an early return to flight. Can. J. Zool. **76**(1): 26–32. doi:10.1139/z97-164.

Bulthuis, D.A. 1995. Distribution of seagrasses in a north Puget Sound estuary: Padilla Bay, Washington, USA. Aquat. Bot. **50**(1): 99–105. doi:10.1016/0304-3770(94)00443-P.

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

Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C., and Eccleston, L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc. R. Soc. Lond. B Biol. Sci. **267**(1457): 2093–2098. doi:10.1098/rspb.2000.1254. PMID:11416914.

De la Cruz, D.L., Takekawa, J.Y., Wilson, M.T., Nysewander, D.R., Evenson, J.R., Esler, D., Boyd, W.S., and Ward, D.H. 2009. Spring migration routes and chronology of Surf Scoters (*Melanitta*

*perspicillata*): a synthesis of Pacific coast studies. Can. J. Zool. **87**(11): 1069–1086. doi:10.1139/Z09-099.

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

Dickson, D.L., and Gilchrist, H.G. 2002. Status of marine birds of the southeastern Beaufort Sea. Arctic, **55**: 46–58.

Goudie, R.I., Brault, S., Conant, B., Kondratyev, A.V., Petersen, M.R., and Vermeer, K. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *In* Transactions of the 59th North American Wildlife and Natural Resources Conference, Anchorage, Alaska, 18–23 March 1994. *Edited by* the Wildlife Management Institute Publications Department, Gardners, Pa. pp. 27–49.

Hodges, J.I., King, J.G., Conant, B.P., and Hanson, H.A. 1996. Aerial surveys of waterbirds in Alaska 1957–94: population trends and observer variability. National Biological Service Information and Technology Report 4. US Fish and Wildlife Service, Anchorage, Alaska.

Hodges, J.I., Groves, D.J., and Conant, B.P. 2008. Distribution and abundance of waterbirds near shore in southeast Alaska, 1997–2007. Northwest. Nat. **89**(2): 85–96. doi:10.1898/1051-1733(2008)89[85:DAAOWN]2.0.CO;2.

Hogan, D. 2012. Postbreeding ecology of Barrow's Goldeneyes in northwestern Alberta. M.Sc. thesis, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.

Hohman, W.L., Ankney, C.D., and Gordon, D.H. 1992. Ecology and management of postbreeding waterfowl. *In* Ecology and management of breeding waterfowl. *Edited by* B.D.J. Batt, A.D. Afton, and M.G. Anderson. University of Minnesota Press, Minneapolis. pp. 128–189.

Lesage, L., Reed, A., and Savard, J.-P.L. 2008. Duckling survival and use of space by Surf Scoter (*Melanitta perspicillata*) broods. Ecoscience, **15**(1): 81–88. doi:10.2980/1195-6860(2008)15[81:DSAUOS]2.0.CO;2.

Lok, E.K., Kirk, M., Esler, D., and Boyd, W.S. 2008. Movements of pre-migratory Surf and White-winged scoters in response to Pacific herring spawn. Waterbirds, **31**(3): 385–393. doi:10.1675/1524-4695-31.3.385.

Mather, D.D., and Esler, D. 1999. Evaluation of bursal depth as an indicator of age class of Harlequin Ducks. J. Field Ornithol. **70**(2): 200–205.

Mazerolle, D.F., Sealy, S.G., and Hobson, K.A. 2011. Interannual flexibility in breeding phenology of a Neotropical migrant songbird in response to weather conditions at breeding and wintering areas. Ecoscience, **18**(1): 18–25. doi:10.2980/18-1-3345.

Murphy, M. 1996. Energetics and nutrition of moult. *In* Avian energetics and nutritional ecology. *Edited by* C. Carey. Chapman and Hall, New York. pp. 158–198.

Nysewander, D.R., Evenson, J.R., Murphie, B.L., and Cyra, T.A. 2005. Report of marine bird and marine mammal component, Puget Sound Ambient Monitoring Program, for July 1992 to December 1999 period. Washington Department of Fish and Wildlife, Olympia.

Oring, L.W. 1964. Behaviour and ecology of certain ducks during the postbreeding period. J. Wildl. Manage. **28**(2): 223–233. doi:10.2307/3798081.

Phillips, L.M., and Powell, A.N. 2006. Evidence for wing molt and breeding site fidelity in King Eiders. Waterbirds, **29**(2): 148–153. doi:10.1675/1524-4695(2006)29[148:EFWMAB]2.0.CO;2.

R Development Core Team. 2011. R: a language and environment for

statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Regehr, H.M. 2011. Movement rates and distances of wintering Harlequin Ducks: implications for population structure. Waterbirds, **34**(1): 19–31. doi:10.1675/063.034.0103.

Robert, M., Benoit, R., and Savard, J.-P.L. 2002. Relationship among breeding, molting, and wintering areas of male Barrow's Goldeneyes (*Bucephala islandica*) in eastern North America. Auk, **119**(3): 676–684. doi:10.1642/0004-8038(2002)119[0676: RABMAW]2.0.CO;2.

Robertson, G., and Cooke, F. 1999. Winter philopatry in migratory waterfowl. Auk, **116**(1): 20–34.

Rohwer, S., Ricklefs, R.E., Rohwer, V.G., and Copple, M.M. 2009. Allometry of the duration of flight feather molt in birds. PLoS Biol. **7**(6): e1000132. doi:10.1371/journal.pbio.1000132. PMID: 19529759.

Safine, D.E. 2005. Breeding ecology of White-winged Scoters on the Yukon Flats, Alaska. M.Sc. thesis, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks.

Salomonsen, F. 1968. The moult migration. Wildfowl, **19**: 5–24.

Savard, J.-P.L., Bordage, D., and Reed, A. 1998. Surf Scoter (*Melanitta perspicillata*). *In* The birds of North America. No. 363. Cornell Lab of Ornithology, Ithaca, N.Y.

Savard, J.-P.L., Reed, A., and Lesage, L. 2007. Chronology of breeding and molt migration in Surf Scoters (*Melanitta perspi-

cillata*). Waterbirds, **30**(2): 223–229. doi:10.1675/1524-4695 (2007)30[223:COBAMM]2.0.CO;2.

Savile, D.B.O. 1957. Adaptive evolution in the avian wing. Evolution, **11**(2): 212–224. doi:10.2307/2406051.

Sjöberg, K. 1988. The flightless period of free-living male Teal *Anas crecca* in northern Sweden. Ibis, **130**(2): 164–171. doi:10.1111/j. 1474-919X.1988.tb00968.x.

Takekawa, J.Y., De La Cruz, S.W., Wilson, M.T., Palm, E.C., Yee, J., Nysewander, D.R., Evenson, J.R., Eadie, J.M., Esler, D., Boyd, W.S., and Ward, D.H. 2011. Breeding distribution and ecology of Pacific coast Surf Scoters. *In* Boreal birds of North America: a hemispheric view of their conservation links and significance. Stud. Avian Biol. **41**: 41–64.

Taylor, E.J. 1995. Molt of Black Brant (*Branta bernicla nigricans*) on the Arctic Coastal Plain, Alaska. Auk, **112**(4): 904–919.

Traylor, J.J., Alisauskas, R.T., and Kehoe, F.P. 2008. Ecological correlates of duckling adoption among White-winged Scoters *Melanitta fusca*: strategy, epiphenomenon, or combination? Behav. Ecol. Sociobiol. **62**(7): 1085–1097. doi:10.1007/s00265-007-0536-6.

Voitkevich, A.A. 1966. The feathers and plumage of birds. October House, New York.

Ydenberg, R.C., Butler, R.W., and Lank, D.B. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. J. Avian Biol. **38**(5): 523–529.