Variability in remigial moult chronology and nutrient dynamics of Surf Scoters *Melanita perspicillata*

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Abstract

Little is known of the moulting ecology of the Surf Scoter *Melanita perspicillata*. In this study, we quantify the age and sex composition of moulting flocks, determine moulting chronology and consistency between years, and assess the body condition of scoters moulting along the coast of Labrador, Canada, during 2004–2007. Flocks of moulting scoters were comprised mainly of adult male Surf Scoters and the proportion of adults and sub-adults varied among years. Adult and sub-adult males had similar structural size and body mass but differed in bill morphology. The forecrown patch was a good indicator of age in males during moult, being fully developed in adult males and partially developed in sub-adults. Female Surf Scoters moulted later than males and adult males moulted slightly earlier than sub-adult males. We estimated that Surf Scoters were able to fly when their primaries reached 80% of their full growth, which yielded a flightless period of at least 35 days. We did not find any changes in leg, breast and liver lipid and proteins, but did observe a slight increase in total lipid levels as moult progressed.

Key words: Labrador, *Melanita perspicillata,* moult chronology, nutrient dynamics, Surf Scoter.

Each year, following breeding, most waterfowl species congregate in their hundreds or thousands at moulting sites (Salomonsen 1968; Fox *et al*. 2014; Savard & Petersen 2015), where they become flightless for 3–5 weeks (Hohman *et al*. 1992) whilst growing new flight feathers. For sea ducks, this period of their life cycle is not well known, due in part to the remoteness of most moulting areas (Lamb *et al*. 2020) and to a general lack of research interest until a few decades ago (Savard 1988). Moulting waterfowl typically seek habitats with few predators and abundant food resources (Hohman *et al*. 1992; Derksen *et al*. 2015). During their flightless period, they become more vulnerable to predation (Smith 2006), especially as their diving abilities are impaired because of the lack of wing feathers (Comeau 1923).

Scoters have one of the most extensive moult migrations among North American waterfowl and fly hundreds to thousands of kilometres each year to reach their moulting areas (Bordage & Savard 2020; Anderson *et al.* 2020; Brown & Fredrikson 2020). In eastern North America, Surf Scoters *Melanita perspicillata* moult in a variety of coastal locations ranging from the Hudson Bay to the Labrador coast (Anderson *et al.* 2020) and the estuary of the St. Lawrence River (Savard *et al.* 1998, 1999). In western North America, they also moult across several latitudes, from arctic Canada to southern British Columbia (Anderson *et al.* 2020).

Sea ducks segregate in winter according to their feeding preferences (Stott & Olson 1973; Vermeer & Bourne 1982; Derksen *et al.* 2015) and such segregation may persist at moulting locations. Little is known about the age, sex and species composition of moulting sea duck flocks. Banding drives of moulting waterfowl found that sometimes several species moult in similar habitats (King 1963, 1973).

In Surf Scoters, adult males and sub-adults are the first to reach moulting areas followed by females (Savard *et al.* 2007) and this results in differences in moult chronologies among ages and sexes (Dickson *et al.* 2012). Recently, efforts have been made to determine whether recruitment indices could be obtained from plumage patterns observed during winter surveys (Iverson *et al.* 2003) but differential use of habitats by age and sex classes, and possibly different age-related latitudinal distribution, complicated the interpretation of results (Iverson *et al.* 2004). Because sub-adult and adult males appear to moult at the same locations (Dickson 2011), more reliable recruitment data could potentially be obtained from these sites.

The moult period has been perceived as a stressful time of year for individual birds because of the energy demands of feather growth (King 1981; Hohman *et al.* 1992; Murphy 1996; Guillemette *et al.* 2007). However, some studies of waterfowl have suggested that the flightless period is not nutritionally stressful (Ankney 1979; Hohman 1993; Fox & Kahlert 2005), and few studies have examined this for sea duck species (Fox *et al.* 2008). Dickson (2011) showed that both Surf Scoters and White-winged Scoters *Melanitta deglandii* increased in body mass during moult, suggesting that moult may not be an overly nutritionally stressful period. Moulting sea ducks select highly productive areas to moult (Savard & Petersen 2015; Derksen *et al.* 2015), optimising feeding opportunities while minimising energy expenditures (O'Connor 2008). In Surf Scoters, as in most other sea ducks, moulting sites are used every year, suggesting that there are specific habitat features required for moulting (Bordage & Savard 2020; Anderson *et al.* 2020).

Existing information on moulting scoters in eastern North America is largely anecdotal, having been collected incidentally during the course of other studies. Todd (1963) reported large numbers of moulting Surf Scoters, and lesser numbers of White-winged Scoters and Black Scoters *M. nigra* along the Labrador coast. Savard *et al.* (1999) reported similar dominance of Surf Scoters in the St. Lawrence River estuary and the Gulf of St. Lawrence. Thousands of moulting scoters have been observed on the Hudson Bay (Todd 1963; Reed *et al.* 1996; Savard *et al.* 1998) and nearly half a million Black Scoters moult in James Bay (Ross 1983). Although all three species have been observed, their relative abundance at these sites has yet to be quantified. Notwithstanding the contributions of these investigations, systematic and extensive surveys of moulting scoters have not been conducted resulting in large, unexplored areas where the moulting distribution of these species are not well known, especially in Ungava Bay, Québec and Labrador, Newfoundland and Labrador (Savard *et al.* 1998).

Exploratory surveys conducted in the late 1990s suggested that 50,000–65,000 scoters moulted on the coast of Labrador (SGG unpbl. data), with large aggregations occurring in Backway Bay (56°20' N, 62°05' W) in Lake Melville and at the mouth of Voisey's Bay (56°20' N, 62°05' W) just south of Nain, in Newfoundland and Labrador. Following the discovery of mineral reserves at Voisey's Bay in 1993, a mine and concentrator were established at the Voisey's Bay site, and port facilities in nearby Anaktalak Bay (56°25' N, 62°03' W) to ship the ore. Mining operations began in 2005 and shipping in 2006. The shipping route follows a 90 km channel from the loading terminal, which passes through a maze of islands. In 2004, we initiated a field programme to provide a better understanding of how the area was used by scoters, and potentially to mitigate the impacts of shipping on use of these sites.

Our objectives in this manuscript therefore were to: 1) characterise the species composition of sea duck flocks moulting along the Labrador coast; 2) quantify the age and sex composition of moulting flocks; 3) determine Surf Scoter moulting chronology and consistency among years; and 4) assess the condition of Surf Scoters moulting in the region.

Methods

Study area

Our study area was located around the archipelagos of Iglosiatik, Nukasusutok and David Island near Nain, Newfoundland and Labrador, Canada (Fig. 1). These archipelagos are part of an extensive network of islands that form a classical skerry coast along a deep fjord system that extends seaward for about 80 km (Gilbert *et al.* 1984). Protected coastlines consist of broad areas of intertidal flats strewn with large boulders whereas more exposed outer coasts consist of mostly steeply sloped bedrock. Water temperatures are cold with maximum values of about 4.7°C in August (Gustajtis 1979) but they may reach as high 6.5–7.0°C in shallow waters (Gilbert *et al.* 1984). The mean tidal amplitude is of *c.* 1.7 m.

Field methods

We caught flightless moulting sea ducks over 2–4 week periods between 18 July and 20 August, 2004–2007. Drive-trapping techniques used during the study were a modification of those described by Breault and Cheng (1990) for catching moulting waterbirds with gillnets at sea in deep water, and the capture method is described in detail in Gilliland *et al.* (2010). Briefly, we used

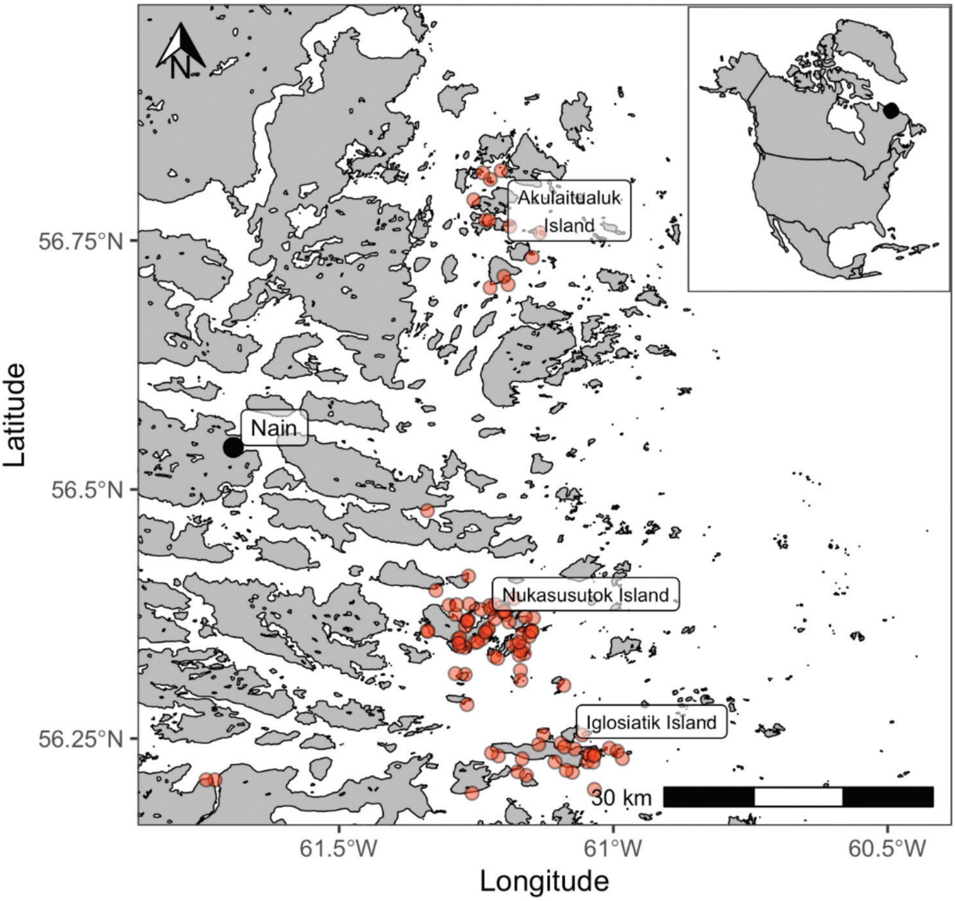

Figure 1. Location of the primary sea duck moult sites near Nain, Newfoundland and Labrador, Canada. Orange circles = capture sites.

three boats to herd birds into a gillnet set in front of the flock. Net sets were made quickly with the lightly-weighted net floating free. Single decoys were used to mark the ends of the net and 8–12 decoys, fixed on two long lines, were attached to the middle of the net. Once the leading edge of the flock reached the net, the birds were enticed to dive by the catch team using cracker shells and air horns. Nets with entangled birds were pulled into the boats and birds removed from the nets. Gillnets were constructed with 0.03 mm nylon monofilament, 90 mm mesh size, were 4 m deep and ranged in length from 150–450 m.

Each bird was aged and sexed using plumage characteristics. To reduce handling time, ninth primary length and body mass were recorded only for the first third of the birds caught, as they were removed from the net. Males with one or more juvenile contour feathers on the belly or breast, or with incomplete development of the bill ornamentation were classified as sub-adults (just one year old). Males with no juvenile feathers and complete development of the bill ornamentation were classified as adults (> 2 years old); all females were combined in one age class (1 year or older) as we could not separate subadults from adults based on their plumage. The ninth primary was flattened and measured to the nearest mm from the insertion of the remiges at the skin surface to the distal end of the ninth primary, and body mass was measured to the nearest 10 g using a spring balance.

In 2005, between 22 July and 21 August we also collected (under Canadian Wildlife Service permit) a total of 16 sub-adult and 28 adult male Surf Scoters, which were weighed and frozen within 6 h of collection. The birds sampled were from three cohorts, based on plumage characteristics: 1) sub-adult males that retained one or more juvenile contour feathers on the belly, 2) sub-adults with no juvenile contour feathers, and 3) adult birds. To ensure that the entire development period of the ninth primary was represented, birds collected were distributed across seven 20 mm size classes of the ninth primary (ranging from 0–140 mm), with a maximum of one bird per plumage cohort collected per capture event. We also compiled data on body mass and ninth primary lengths from adult male Surf Scoters caught as part of other studies at spring staging areas in (i) the Bay of Chaleur, New Brunswick (SGG, unpubl. data), (ii) along the North Shore of the Gulf of St. Lawrence, Québec (JPLS & J. Bédard, unpubl. data), (iii) from autumn staging areas in the Bay of Fundy, New Brunswick (H.S. Makepeace, New Brunswick Department of Natural Resources, unpubl. data), and (iv) in the Gulf of St. Lawrence, Québec (SGG & C. Lepage, Canadian Wildlife Service, unpubl. data). We also collected data on ninth primary and calamus lengths from adult male and female Surf Scoter wings collected as part of the US and Canadian Harvest Surveys during the 2016/17 hunting season.

Laboratory analyses

Ducks were thawed and the lengths of the ninth primary, head, culmen mid-line, culmen width, keel, tarsus (tarbone: Dzubin & Cooch 1992) and *bursa of Fabricius* (hereafter bursa) were measured. Head length was measured from the external occipital ridge of the skull to the tip of the bill nail, culmen mid-line was measured from the feathered edge to the tip of the bill nail, culmen width was the maximum width at the nostrils, and body mass was measured to the nearest g with a digital scale. Bursal depth was measured by first probing the bursa externally (Mather & Esler 1999). Following the scoring criteria developed by Iverson *et al.* (2003), we also recorded the stage of development of the white forecrown and nape patches. Birds were plucked and re-weighed, then the left breast and pectoral muscles were removed and weighed. The keel was exposed and measured from the distal to proximal end of the de-fleshed sternum; the left leg muscle, liver and heart were removed and weighed. The oesophagus, gizzard, and large and small intestines were removed, stripped of any fat, separated, weighed, emptied of contents and reweighed; the fat was weighed and discarded. The bursa was removed, and its length measured to the nearest 0.1 mm. Any abdominal and mesenteric fat was removed, weighed and discarded. Small samples of liver, kidney, breast muscle and fat were collected, weighed and archived. Plucked carcasses, left breasts and leg muscles and livers were sent to the Bird Studies Canada Avian Energetic Laboratory, where body composition (mass of water, protein, lipid and ash) was determined, as described by Ankney & Afton (1988). On determining the lipid and protein content for each of the organs or muscles, we included an estimated value for the tissue samples taken. Any fat that was removed from the bird was likewise included in the total lipid estimates.

Data analyses

Ninth Primary Growth. To estimate the age of the developing ninth primary, we modelled growth from the sample of known age feather measurements taken from Surf Scoters that moulted in captivity (see Viain *et al.* 2014). A detailed description of the care of captive sea ducks is described in Viain *et al.* (2014). Briefly, Surf Scoter eggs collected from Lac Malbaie, Québec, Canada were hatched and raised at the Patuxent Wildlife Research Center, Laurel, Maryland, USA and were fed with Mazuri Sea Duck Diet (#5681; 21.5% protein) *ad libitum* on a daily basis. At weekly intervals from 8 July–8 October 2008, all birds were caught with a landing net and the ninth primary length was measured to the nearest millimetre.

We described the relationship between the length of the ninth primary and date using the Gompertz (G.3, G.4), logistic (L.3, L.4) and Weibull (W1.3, W1.4) models from the R package drc (v.3.0-1; Ritz 2015). Estimation of age can be biased high when the growing primary is near emergence from the calamus (see Gilliland & Ankney 1992), because the length of the primary is not zero at emergence as it does not include the developing feather within the calamus. The 3-parameter models, typically used for modelling growth, fix the lower asymptote at zero which results in poor fit as the primary has undergone some growth by the time it emerges from the sheath (Fig. 2a). The parameter c, from the 4-parameter model estimates the lower asymptotes, which in this case corresponds to the length of the calamus. Estimates for the calamus from initial fits of the 4-parameter model were similar for males and females ($\bar{x}$ ± s.d.: males = –13.9 ± 8.3, n = 5; females = –13.7 ± 5.4, n = 3), but were shorter than calamus lengths measured from the sample of adult Surf Scoters wings collected during the US and Canadian Harvest Surveys (males = 26.9 ± 1.9, n = 28; females = 26.5 ± 0.9, n = 13). We re-fitted the 4-parameter logistic model with the lower asymptote fixed at the overall mean calamus length of −26.8 mm (s.d. = 1.7, n = 41). We estimated the day of emergence when the new feather was 0 mm from each growth curve. The length of the feather at the date of emergence was calculated as a proportion of the feathers' asymptotic size with the following formula:

$$\hat{P}_i = \frac{(\bar{c} + 9\text{th } P_i)}{c + \hat{d}_i} \times 100$$

where $\hat{P}$ is the estimate of the length of the ninth primary as a proportion of its asymptotic size, $\bar{c}$ is mean length of the

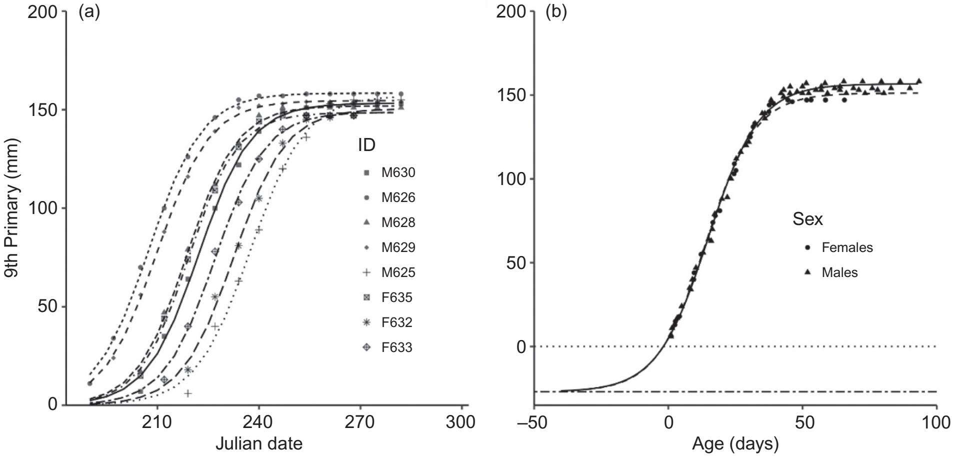

Figure 2. Ninth primary growth rates during Surf Scoters' remigial moult. Panel a = individual fits of the 3-parameter logistic model, for three adult females and five adult males. Panel b = fit of the same data to the 4-parameter logistic model, with the parameters combined by sex, the x-axis set to zero at the estimated emergence date and the lower asymptote (lower dot-dash line) fixed at a mean calamus length of –26.8 mm.

calamus (from the Canadian and US Harvest Surveys; above), 9th P is the length of the primary when measured and $\hat{d}$ is the estimate of the upper asymptote the ith bird. We took the function used to estimate effective doses from the 'drc' package (function ed; Ritz 2015) in order to estimate the emergence date for each curve with the ninth primary length set to 0 mm. We calculated the feather's age by subtracting the estimate of emergence date from date of the measurement. We used the two-stage meta-analysis procedure to fit hierarchical non-linear mixed models from the "medrc" package (function metadrm, v.1.1-0; Gerhard & Ritz 2018), using age as the independent variable and gender as a group to estimate parameters combined across individual fits (Fig. 2b, Table 1). We used the fitted age model and the ed function to make three estimates for each wild Surf Scoter: 1) age of the ninth primary at date of capture, by substituting the length of the primary for the ninth primary in the equation above; 2) date of emergence, by subtracting the estimated age from the date; and 3) date when the ninth primary reached 80% of asymptotic size.

Energetics and chronology. Morphometric measurements from sub-adult and adult males were compared using t-tests and linear regressions to describe relationships between organ sizes, and lipid and protein levels, with the stage of development of the ninth primary. We examined the relationship between body mass and the age of the ninth primary for males caught between 2004 and 2007. For this analysis, we used a 2-way ANOVA with Year and Age included as effects. We also compared body mass of adult males from moulting areas, spring staging areas in Chaleur Bay (New

Table 1. Model averaged parameters fitted to the 4-parameter logistic growth model with the lower asymptote fixed at −26.8 mm, estimated emergence date and estimated age of the ninth primary (in days) when flight capability was regained for three adult female and five adult male Surf Scoters that moulted in captivity at the Patuxent Wildlife Research Center, Maryland, USA (see Viain *et al.* 2014; mean ± s.d.).

Sex	**b**[a]	**d**[b]	$\mathbf{e_{date}}$[c]	**Emergence date**[d]	**Feather age at 80% growth**[e] **(days)**
Females	–0.108 ± 0.003	151.1 ± 1.2	11 Aug ± 3.9	28 Jul ± 3.7	29 ± 0.7
Males	–0.105 ± 0.002	156.6 ± 1.5	4 Aug ± 5.3	20 Jul ± 5.2	30 ± 0.7

[a]Slope; [b]Upper asymptote (mm); [c]Estimated date at inflection point; [d]Estimated date of emergence from calamus; [e]Estimated age at 80% of upper asymptote.

Brunswick) and along the north shore of the Gulf of St. Lawrence (Québec), and from autumn staging areas in the Bay of Fundy (New Brunswick) and the Gulf of St. Lawrence (Québec) using 1-way ANOVA. We examined relationships between estimated ninth primary emergence dates with Age and Year for males, and the relationships with Gender and Year using 2-way ANOVAs.

All analyses were performed using R (v.3.4.4; R Development Core Team 2018) and individual effects were tested using "Type III" tests in the "car" package (v.3.0-2; Fox & Weisberg 2019). All *post-hoc* pair-wise comparisons were conducted using Tukey HSD adjusted *P* values.

Results

Ninth primary growth

The asymptotic size of the ninth primary estimated by the 4-parameter logistic model (parameter b; Table 1) was similar to a sample of adult birds captured in early autumn in Forestville, Québec, in 2012 ($\bar{x}$ ± s.d.: males = 159.5 ± 10.0 mm, $n = 47$; females = 150.7 ± 8.4 mm, $n = 50$; Sea Duck Joint Venture 2015), suggesting that the model may be a reasonable representation of primary growth in wild birds.

Using the fitted models, we estimated that the lower asymptote occurred about 27 days before emergence of the primary and the upper asymptote occurred about 59 days after emergence resulting in period of growth for the ninth primary of about 86 days. In American Black Ducks *Anas rubripes*, Bowman (1987) estimated that there was a period of 2–3 days of flightlessness before the birds shed their primaries and a period of 2–4 days following shedding before the new feather emerged from the sheath, resulting in a flightless period of *c.* 6 days prior to emergence. Several authors have suggested that waterfowl regain flight when the primary reaches 80–90% of the terminal length (Savard & Petersen 2015).

We estimated that the ninth primary reached 80% of asymptotic size at 29–30 days after emergence from the sheath (Table 1) and estimated the flightless period for Surf Scoters at 34–36 days.

Species, age and sex composition

We captured 1,919 sea ducks during 2004–2007 (Table 2). Surf Scoters comprised *c.* 95% of the captures, and only a small number of White-winged Scoters, Black Scoters, Long-tailed Ducks *Clangula hyemalis* and Common Eiders *Somateria mollissima* moulted in the area. Of the Common Eiders, fourteen were classified as *S. m. borealis*, two as *S. m. borealis-dresseri* intergrades and one as a *S. m. dresseri* (following Mendall 1986).

In all four years, female Surf Scoters comprised only a small portion of the catch (4–8%; Table 2). Most sub-adult male Surf Scoters still had one or more juvenile contour feathers on the breast or belly; however, the number of juvenile feathers varied from complete coverage of the belly to no juvenile feathers. The distribution of the depths of the internal bursal for males

Table 2. Number of flightless waterfowl (with number of sub-adults in parentheses) caught in moult drives near Nain, Newfoundland and Labrador, Canada during 2004–2007. Female Surf Scoters were not aged.

		Species				
Year	**Sex**	**Common Eider**	**Surf Scoter**	**White-winged Scoter**	**Black Scoter**	**Long-tailed Duck**
2004	Female	2	37	2	0	0
	Male	3 (1)	595 (61)	18 (7)	0	0
2005	Female	1	39	0	1	0
	Male	6 (2)	623 (35)	1	0	0
2006	Female	0	15	0	0	0
	Male	1	415 (26)	5	2	0
2007	Female	0	8	1	0	22
	Male	5 (4)	103 (10)	11 (1)	3	0
Total	Female	3	99	3	1	22
	Male	15 (7)	1,736 (132)	35 (8)	5	0
Total		**18**	**1,835**	**38**	**6**	**22**

was bimodal with modes at zero (adult) and 36 mm (second-year), although one individual had a bursa depth of 15.2 mm, which we suspect was a third-year male. A Welch Two Sample t-test suggested there was no difference in internal bursa depth between the immature males that had juvenile feathers on the breast or belly (37.8 ± 8.0 mm, n = 8) and those without (35.5 ± 11.5 mm, n = 5; $t = -0.80$, $P = 0.46$, d.f. = 5.1, n.s.). However, bursa depth differed between adults and sub-adults (Table 3). Adult and sub-adult males had similar structural size and body mass but differed in bill morphology (Table 3). The incomplete formation of the rhamphotheca in sub-adult males resulted in slightly narrower bills than in adults, and adults had slightly shorter culmen-midline lengths than sub-adults (Table 3) which resulted from the black feathering extending further down the bill of adult males.

The development of the white forecrown patch was a good indicator of age during moult (Fig. 3). With the exception of the third-year male (15.2 mm bursa), only adults had completely developed forecrown patches, and only second-year birds completely lacked the forecrown patch. The nape patch is not a good indicator of age as its development varied across age classes and was moulted simultaneously with the primaries. The ratio of sub-adult to adult males varied among years ($\chi^2_3 = 11.1$, $P \leq 0.01$; Table 2), with relatively high ratios of sub-adults occurring in 2004 and 2007 (*c.* 10% in both), and lower ratios in 2005 and 2006 (*c.* 6% in both years).

Table 3. Comparisons of morphometric measurements (mean ± s.d.) between sub-adult and adult male Surf Scoters captured during remigial moult near Nain, Newfoundland and Labrador, Canada in 2005.

	Age				
Measurement	**Sub-adult (n = 13)**	**Adult (n = 23)**	t	**d.f.**	P
Bursa probed[a] (mm)	18.2 ± 7.7	0	–14.65	12.0	≤ 0.001
Bursa interior[b] (mm)	36.9 ± 9.9	0	–8.49	12.0	≤ 0.001
Head (mm)	109.9 ± 3.4	111.1 ± 2.7	1.01	19.7	0.33
Culmen mid-line (mm)	39.3 ± 3.0	37.0 ± 2.0	–2.44	18.0	0.025
Culmen width (mm)	28.0 ± 2.0	31.7 ± 1.3	5.85	17.9	≤ 0.001
Tarsus (mm)	44.0 ± 1.3	44.5 ± 1.7	0.99	20.3	0.34
Body mass (g)	1,045.7 ± 59.6	1,041.7 ± 64.8	–0.19	26.8	0.85
Keel (mm)	93.4 ± 3.7	91.8 ± 2.5	–1.42	18.5	0.17

[a]*Bursa of Fabricius* probed depth; [b]*Bursa of Fabricius* dissected and measured.

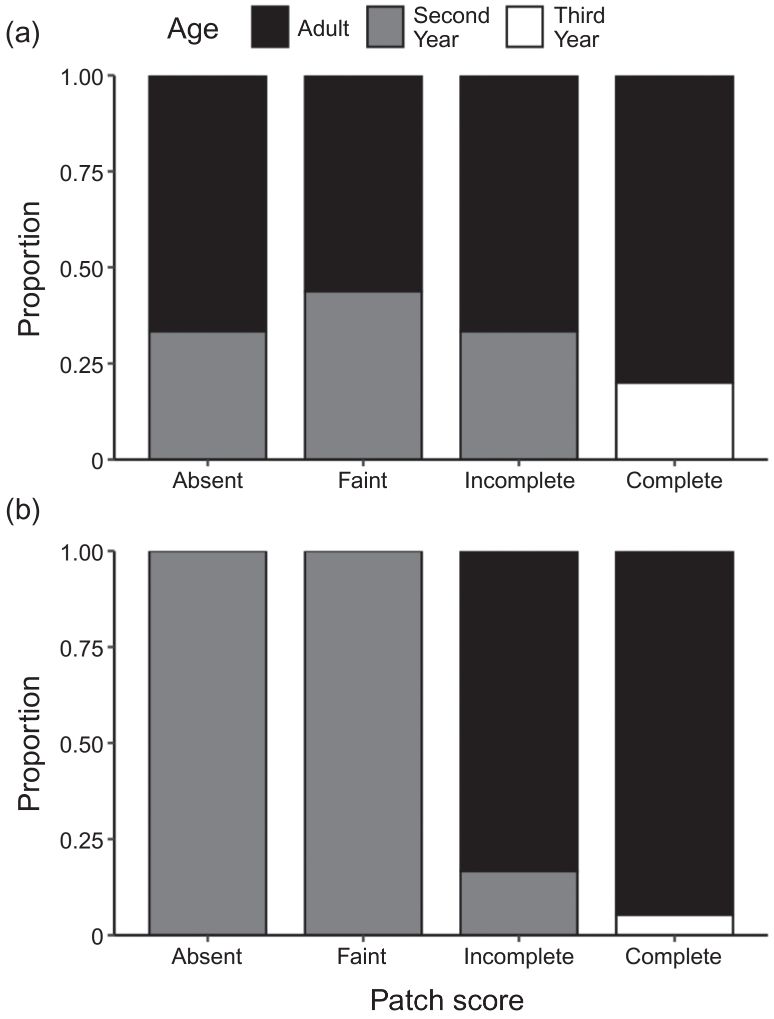

Figure 3. Stages of development of (a) the nape, and (b) the white forecrown patches, for male Surf Scoters collected during remigial moult near Nain, Newfoundland and Labrador (*n* = 36 individuals), in relation to the age of the birds. For description of patch scores see Iverson *et al.* (2003).

Chronology of moult

None of the Surf Scoters observed in the study area appeared capable of flight at our arrival on the study area between 18–25 July. Only two of the 1,835 Surf Scoters handled had one or more of their old primary flight feathers intact when captured, and almost all birds had shed their old primaries and were re-growing new remigial feathers. It was not until the middle of August that the first birds were observed avoiding trap nets by flying, indicating that some birds had regained flight capacity. We caught few birds with ninth primaries between 125–140 mm long (78% and 88% of final growth, respectively; Fig. 4), suggesting that the scoters had regained some level of flight capability before the ninth primary was completely re-grown.

The interaction between the effects of Age and Year on primary emergence date was significant ($F_{3,679} = 3.2$, $P = 0.023$). There was no difference in the emergence dates for sub-adults across years (Fig. 5a). A Tukey *post-hoc* test revealed that, within years, emergence dates for adult males differed from those for sub-adults in all years ($P \leq 0.001$) except 2004. This test also showed that there were differences ($P \leq 0.001$) in the timing of emergence for adults among all years except between 2005 and 2007, and between 2006 and 2007. Emergence dates for sub-adults were similar to adults in 2004, but occurred 5.8 days, 7.8 days and 11 days later than adults in 2005, 2006 and 2007, respectively. Emergence dates for adults in 2004 occurred 3.9 days, 7.9 days and 5.1 days later than in 2005, 2006 and 2007, respectively.

The interaction between the effects of Year and Gender was significant ($F_{3,735} = 8.7$, $P \leq 0.001$). A Tukey *post-hoc* test revealed that for each of the four years sampled, emergence dates of primaries differed between females and males ($P \leq 0.001$ in each case), with females averaging 8.8, 18.2, 14.3 and 15.8 days later than males in 2004, 2005, 2006 and 2007, respectively (Fig. 5b).

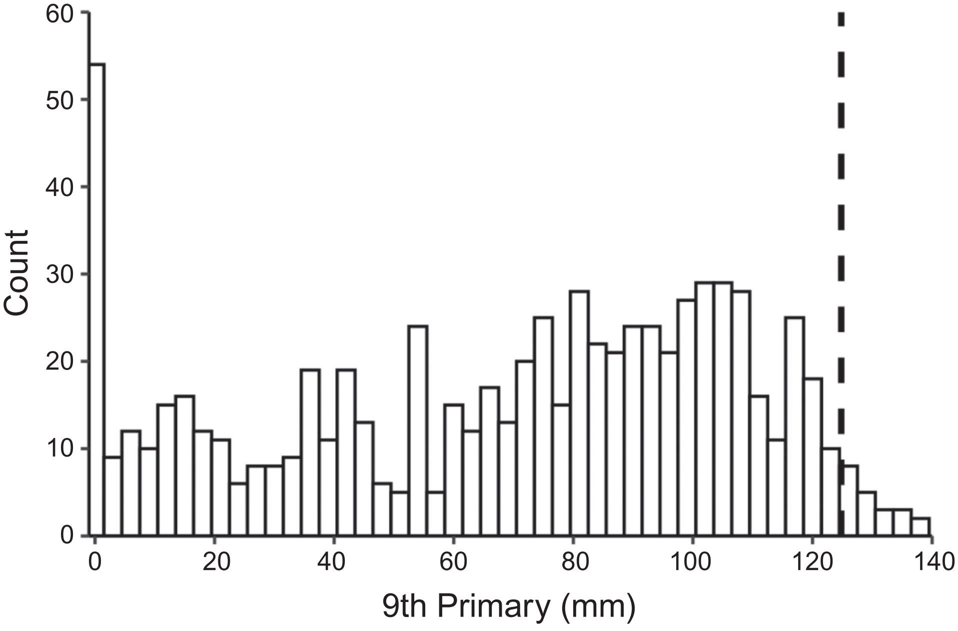

Figure 4. Frequency distribution of ninth primary lengths for Surf Scoters captured near Nain, Newfoundland and Labrador during remigial from 2004–2007 ($n = 743$). Vertical dashed line represents the length of the ninth primary at 80% of asymptotic size.

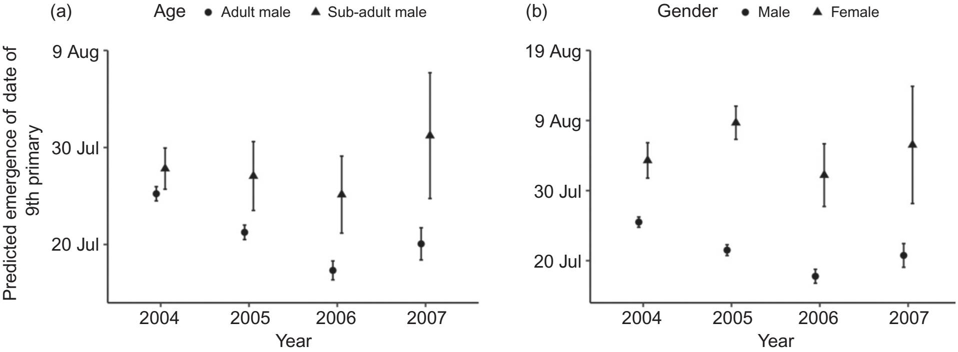

Figure 5. Plots of marginal means (± 95% CIs) showing the interaction between: (a) Age and Year on ninth primary emergence dates for male Surf Scoters (*n* = 687), and (b) the effects of the interaction between Gender and Year on ninth primary emergence dates for adult male (*n* = 638) and female Surf Scoters (*n* = 56) caught during remigial moult near Nain, Newfoundland and Labrador, in 2004–2007.

Estimated moult initiation dates and a flightless period of 35 days (above), were used to estimate the period when flightless birds used moult sites (Fig. 6). The first flightless birds occurred as early as 1 July, and the peak flightless period was between 1–15 August, when > 90% of birds were flightless. Most of the flightless birds using the site in September were females (Fig. 6).

Nutrient dynamics

There was no change in body mass, heart mass, or the lipid and protein content of various organs with the age of the ninth primary (Table 4). Although there was an increase in the mass of the plumage with the age of the primary, the relationship was not linear, and was best described by the 4-parameter logistic model (Fig. 7). At emergence of the ninth primary, the mass of the plumage was 59.6 g (lower asymptote) and increased rapidly (growth rate = –0.57) to 93.4 g (upper asymptote) by primary age 14 days. The inflection point occurred at primary age 6.9 days.

An ANCOVA was carried out on the body mass of males by Year and Age (of the bird) with the age of the ninth primary included as a covariate. None of the interactions were significant and with the interactions dropped from the model, only the main effect of Year was significant (Fig 8a; $P \leq 0.001$). A Tukey *post-hoc* test showed that males were 27 g heavier in 2004 than 2005 ($P \leq 0.001$) and 37 g heavier in 2004 than 2006 ($P \leq 0.001$; Fig. 9). Adult male body mass varied with season ($F_{2,825} = 44.6$, $P \leq 0.0001$), with the Tukey *post-hoc* test revealing that adult males were about 50 g lighter during moult than birds collected at spring staging areas ($P \leq 0.001$) and 113 g lighter than birds collected at autumn staging areas (Fig. 8b, $P \leq 0.001$).

Discussion

Moulting flocks of sea ducks in our coastal Labrador study area were species-specific, and were mostly composed of Surf Scoters. Sea ducks generally moult in single species flocks (Hohman *et al.* 1992; Frimer 1995;

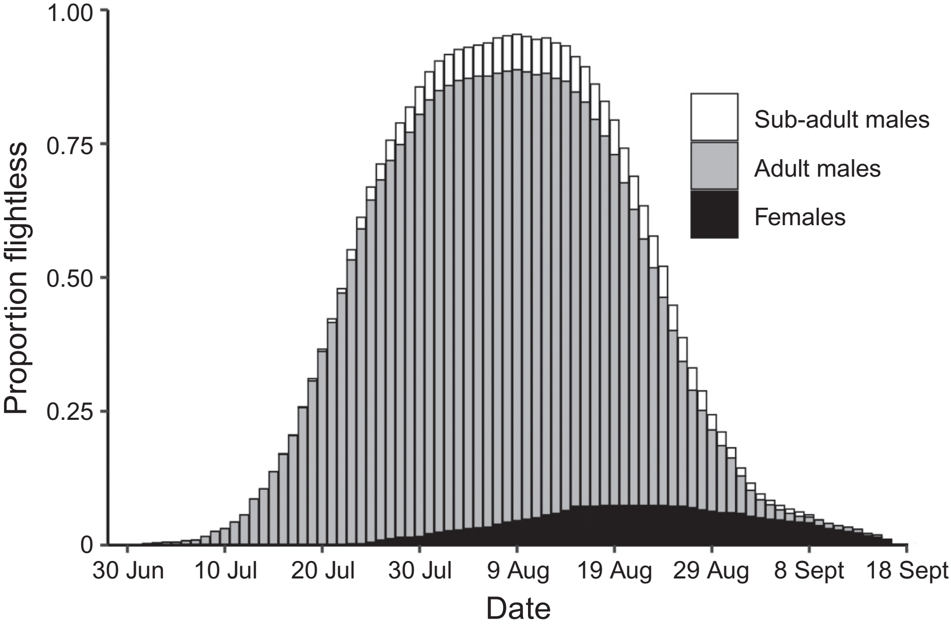

Figure 6. Proportion of moulting Surf Scoters near Nain, Newfoundland and Labrador that were flightless, by age and sex, for each day of the moult period (n = 743).

Gilliland *et al.* 2002), a pattern which is thought to reflect differences in feeding preferences among species. On the St. Lawrence River in Québec, moulting locations of Common Eiders and Surf Scoters are quite distinct with eiders avoiding sandy sub-tidal areas, but Surf and White-winged Scoters sometimes moult at the same location (Rail & Savard 2003), and also in western North America (Dickson *et al.* 2012). Much therefore remains to be learned about the spatial segregation of species on the moulting grounds, especially in the absence of disturbance from potential predators and other sources.

The preponderance of adult males in moulting flocks was expected given male-biased sex ratios in several of the sea duck populations (Donald 2007; Eadie & Savard 2015; Rodway *et al.* 2015). In Surf Scoters, the timing of moult migration varies with age, sex and pairing and breeding status. Sub-adults of both sexes and unpaired adult males migrate first, followed by paired adult males, unsuccessful breeding females and successful breeding females (Savard *et al.* 2007). Similar segregation by age and sex in the timing of moult migration has been reported in several other sea duck species, and this appears to be the norm (Joensen 1973; Frimer 1994; Phillips *et al.* 2006). The low number of females captured suggests that females may not have reached their moulting sites by the time that we caught the birds (Savard *et al.* 2007), or that the Labrador coast is mainly a male moulting area. Use of different moulting areas by male and females has been documented in

Table 4. Mean lipid and protein content of various organs, and results of linear regression models (*P* values all > 0.05, so not significant) for protein and lipid contents with ninth primary length for male Surf Scoters (*n* = 36) captured during remigial moult near Nain, Newfoundland and Labrador, in 2005.

Organ	**Mean ± s.d.**	$F_{1,35}$	***P***
Leg lipid	0.8 ± 0.2	0.084	0.77
Leg protein	12.1 ± 0.9	0.448	0.51
Breast lipid	1.1 ± 0.3	0.560	0.46
Breast protein	17.2 ± 2.4	0.454	0.51
Liver lipid	0.5 ± 0.2	0.001	0.98
Liver protein	10.4 ± 1.5	0.428	0.52
Total lipid	96.9 ± 24.4	2.502	0.12
Total protein	215.6 ± 10.8	0.232	0.63
Body mass	1,043.1 ± 62.2	0.004	0.95
Heart	13.6 ± 2.1	2.377	0.13

some sea ducks (Joensen 1973; Boyd & Esler 2012) but its extent needs to be better quantified.

There was significant annual variability in the age composition of moulting flocks, with the proportion of sub-adult males in 2004 and 2007 being almost double that observed in 2005 and 2006. The proportion of sub-adults in the population is a function of production in the previous year and first year survival, and therefore may provide a good index of recruitment to the population, with variability in reproductive success perhaps explaining the differences we observed in age ratios among years. Morrier *et al*. (2008) reported large differences in numbers of Surf Scoter ducklings present on Lake Malbaie, Quebec (115 in 1994; 307 in 1995), which they attributed to the cold and wet conditions in 1994 contrasting with warm and dry conditions in 1995. Factors affecting the reproductive success of sea ducks are numerous (Mallory 2015), with their impact varying annually, resulting in fluctuations in the proportion of sub-adults present in the population each year. Moreover, given that Surf Scoters nest in the northern boreal forest near close to the snowline, breeding propensity may vary with the timing of the spring thaw each year (Takekawa *et al.* 2011). Variability in breeding effort also may explain the differences in age ratios observed among years. Although the Eastern Waterfowl Breeding Pair Survey suggests the abundance of Surf Scoters breeding in eastern Canada was stable between 1990 and 2012, the abundance of

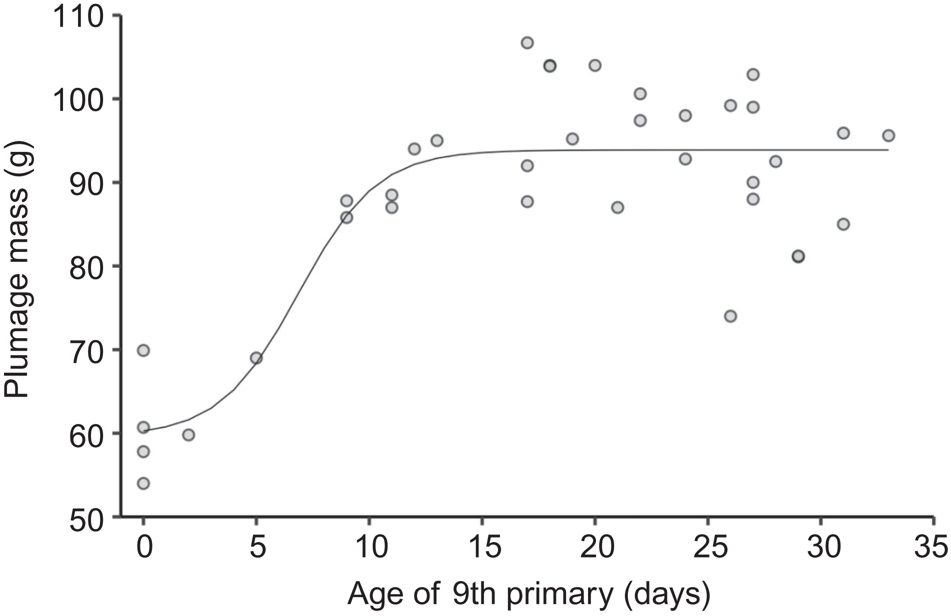

Figure 7. The relationship between plumage mass and stage of development of the ninth primary during remigial moult, described by the 4-parameter logistic model for Surf Scoters collected from sites near Nain, Newfoundland and Labrador, Canada (*n* = 36).

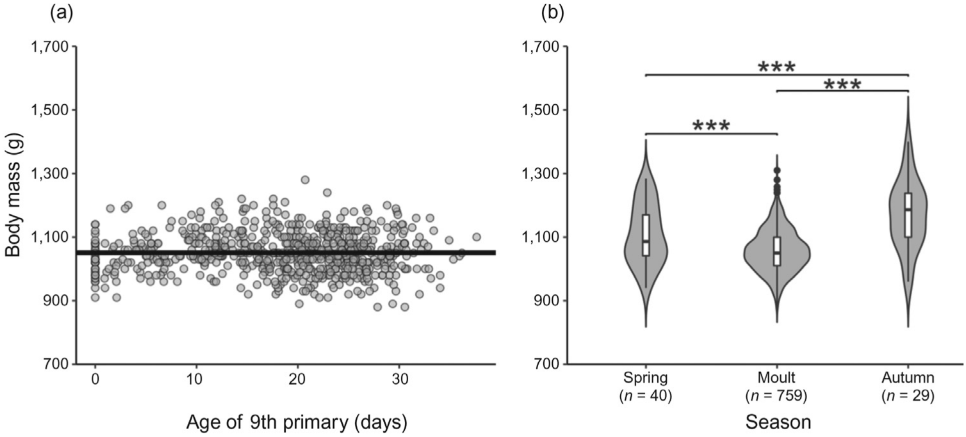

Figure 8. The relationship between (a) development of the ninth primary and body mass for male Surf Scoters caught during remigial near Nain, Newfoundland and Labrador, during 2004–2007 (*n* = 759), and (b) mean body mass (± 95% CI) of adult male Surf Scoters at autumn and spring staging sites and during remigial moult (*** = Tukey multiple comparisons where $P \leq 0.001$).

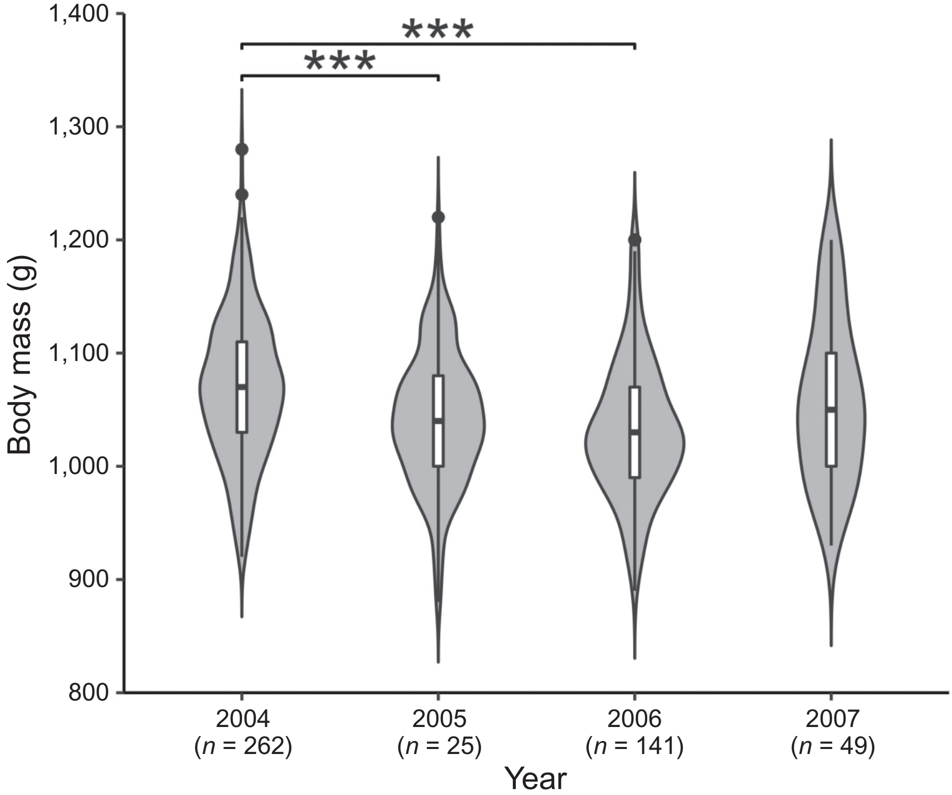

Figure 9. Comparisons of body mass with year for Surf Scoters captured during remigial moult near Nain, Newfoundland and Labrador, 2004–2007 (*** = Tukey multiple comparisons where $P \leq 0.001$).

breeding Surf Scoters was highest in 2004 and 2007 (Fig. 1.10 in Bowman *et al.* 2015). If the high age ratios of sub-adult males observed on the moulting areas in Labrador resulted from higher than average breeding effort in 2004 and 2007, we would have expected to see higher than average sub-adult age ratios on the moult sites in the following year. This did not occur, suggesting that variability in reproductive effort may not be the cause of the relatively high proportion of sub-adult males we observed on the Labrador moulting areas in 2004 and 2007.

Flint (2013) found that size and trends of North American sea ducks were strongly influenced by oceanic conditions. He speculated that changes in ocean conditions affected forage communities, which would influence both survival and productivity for sea ducks feeding on these resources. The peaks in abundance on the breeding areas in eastern Canada and high sub-adult age ratios on the moult sites occurred in the same years, suggesting that foraging conditions in the previous winter may have been favourable for first-year over-winter survival and breeding propensity.

There are few measures of productivity or recruitment for scoters (see Anderson *et al.* 2020; Krementz *et al.* 1997), and the use of plumage characteristics to quantify yearly fluctuations in adult to young ratios of male Surf Scoters measured during winter has been proposed for monitoring sea duck productivity and recruitment (Iverson 2004; Smith *et al.* 2001). Iverson *et al.* (2003) assessed the reliability of plumage as an indicator of age for male Surf Scoters and suggested that nape and forecrown patches were lost in a portion of all male age classes in late summer/early autumn. They concluded that differentiation of second-year and after-second-year males was not possible at that time of year. However, their sample size was small during wing moult. We found that adult male Surf Scoters moult their white nape patch during wing moult but not their white forecrown patch. The forecrown patch, based on our limited sample sizes, appears to be a good indicator of age in males during moult. Adult males are characterised by a fully developed white forecrown patch and sub-adults by an absent or only partially developed patch. More data are needed to determine whether the size of the forecrown patch is related to sub-adult age. This difference could prove useful for obtaining adult to sub-adult ratios from moulting flocks, possibly using aerial photographs.

Remigial growth and moult chronology

In sea ducks, there is much variation in the timing of moult migration within a given year, due to variability in the timing of reproduction among individuals and populations (Petersen 1981; Robertson *et al.* 1997; Robert *et al.* 2002). This is reflected in the annual variability in the length of the ninth primary at a given date. However, we observed significant variation in the initiation of moult among years, indicating that variability in environmental conditions may also influence the timing of moult.

Female Surf Scoters moulted later than males; this is characteristic of most, if not all, of the sea duck species (Frimer 1994; Savard *et al.* 2007; Lepage *et al.* 2020). However, timing of moult in sub-adults has not been well established. In our study, sub-adults moulted slightly later than adult males, but in the St. Lawrence River estuary, and also in British Columbia, sub-adults moulted slightly earlier than adult males (JPLS & C. Lepage, unpubl. data; Dickson 2011). Timing of flight feather moult is under hormonal control (Bluhm 1988), and as such may vary among individuals and with age. The proportion of previously paired to unpaired males at the moulting sites therefore may explain these differences, as unpaired males that do not go to the breeding areas may be expected to moult earlier than paired males (maybe also in comparison with sub-adults), with differences observed between studies (or between years in our study) perhaps reflecting the proportion of previously unpaired and paired males in moulting flocks. If this is the case, it would seem that moulting areas on the Labrador coast are dominated by previously unpaired males. We have observed large flocks of unpaired adult males on the south coast of Labrador in the first week of June, suggesting that there may be movements of non-breeding male Surf

Scoters in the area prior to the breeding season (SGG unpubl. data). Preliminary results of stable carbon isotope analysis however found significant C^{13} enrichment of the breast tissues later in moult for both sub-adult and adult males, and there were also higher levels of C^{13} in the base of the ninth primary (which was synthesised later in the moult) relative to the tip of the feather (Budge & Gilliland 2007). These results are consistent with a shift from a terrestrial-based diet at inland breeding areas to a marine-based diet during moult (Budge & Gilliland 2007), indicating that if the males on the Labrador coast were non-breeders, then they must have spent time in the interior breeding areas prior to moult.

We can only speculate on what may drive the annual variation in the primary feather emergence dates. When we initiated this study, we believed that males had a high fidelity to their moult sites, but this is not necessarily the case as one of the first males which we fitted with a satellite tag at the Labrador moulting site in 2006 subsequently moulted > 1,000 km to the west on the Hudson Bay in 2007 (SGG, unpubl. data). We have since documented movements of individual males among the major Black Scoter moulting areas in eastern North America (Lamb *et al.* 2021), and have additional tracking data for Surf Scoters which suggest that they do the same (Sea Duck Joint Venture 2015). The main information missing from our study was the abundance birds using the site, and it was our impression that numbers varied annually. Foraging range is restricted during the flightless period and we expect that prey were depleted within and among years. The Labrador current is very cold, and recovery of the prey base is likely slow. We speculate that moulting areas in eastern North America are part of a large inter-connected network, and that the birds' use of nodes within the network varies annually. Additionally, Lepage *et al.* (2020) report that White-wing Scoter fidelity to moult sites is influenced by breeding status, with males that migrate to breeding areas having lower fidelity to moulting areas than non-breeders. It is possible that some of the variation in moult chronology we observed may have resulted from differential use of moulting areas among years.

Moulting Surf Scoters, like other moulting waterfowl, are vulnerable while flightless (Comeau 1923) and would reduce risks by minimising the duration of their flightless period. Viain *et al.* (2014) concluded that feather growth rates in sea ducks were lower than for other waterfowl, and that sea ducks do not maximise feather growth rates to minimise the duration of flightlessness. Most waterfowl can fly before their remiges have reached their final length (Sjöberg 1988; Hohman *et al.* 1992), thereby quickly regaining their ability to escape from predators. On the Labrador coast, we estimated that Surf Scoters were able to fly when their primaries reached between 80–90% of their full growth. This is similar to Barrow's Goldeneye *Bucephala islandica* males, which regain their flight capacity when the primaries reached *c.* 80% of their final length (Van de Wetering 1997; Van de Wetering & Cooke 2000; Hogan *et al.* 2013). Dickson *et al.* (2012) estimated that male Surf Scoters moulting in western North

America required 86–98% of the final ninth primary length to fly. However, they do not provide an explanation for how that large range was estimated. Because their study was based on captured birds, it is possible that some of the birds included were able to fly.

Estimates of feather growth rates have been used to assess the stage of feather development (age), and are useful for comparing moult chronology between sites and across years, but determining feather growth rates in wild birds requires that the birds be recaptured. Our within-year recapture rates were low (< 1%; SGG unpubl. data) and we relied on feather growth rates estimated from captive birds. Previous estimates of primary feather growth rates have treated feather growth as a linear function. For example, on investigating the moult chronology of Surf Scoters in Alaska and British Columbia, Dickson *et al.* (2012) used our preliminary linear growth rate estimate of 3.8 ± 0.2 mm/day for the ninth primary, obtained by measuring the feather growth of captive birds during our study. Earlier, Van de Wetering (1997) and Hogan *et al.* (2013) reported mean ninth primary growth rates of 4.04 ± 0.05 mm and 3.94 ± 0.13 mm per day, respectively, for Barrow's Goldeneye between two recapture periods. Although feather growth is non-linear, treating growth as a linear function may be a reasonable assumption as the shape of the growth curve is nearly linear from emergence up to about 80% of asymptotic size (see Fig. 2b).

Using repeated measurements from captive birds allowed us to model growth of the ninth primary during remigial moult more accurately; however, growth of moulting feathers may be influenced by nutrition, which may differ for captive and free-ranging birds. Pehrsson (1987) found that food quality did not affect the growth rate of the primary feathers for captive birds, but when exposed to low protein food, even after recovering flight capability, birds, especially males, developed shorter wing feathers. The ninth primaries of Surf Scoters caught in the spring and autumn were similar in length to asymptotic lengths for captive-reared Surf Scoters. If anything, the lengths of the ninth primaries of wild caught males were slightly longer than in captive males, suggesting that the nutritional quality of the diet for captive and free-ranging birds was similar or better. We cannot say for sure that there were no differences between free-ranging and captive-reared birds, but if remigial growth rates of captive-reared birds were greater than for free-ranging birds, we would expect that emergence dates may be overestimated and the flightless period to be underestimated.

Nutrient dynamics

It is generally thought that waterfowl may reduce body mass during moult as a strategy to reduce the flightless period (Douthwaite 1976; Brown & Sanders 1998; Sjöberg 1988). Rapid changes in body organs have also been documented in several species of birds during migration and moult (Gaunt *et al.* 1990; Jehl 1997; Fox & Kahlert 2005; Fox *et al.* 2008), which may enhance flight capability (Viain *et al.* 2014). We did not find any significant changes in the parameters we measured despite a hint of increase in total lipid levels as moult progressed. Although we did not detect significant gain in body mass during moult, there was a signal of an increasing trend over the first 10–15 days of moult (Fig. 8). The period and magnitude of the apparent increase in body mass was similar to that observed for plumage mass (Fig. 7), so any increases observed in body mass during the early part of moult may not represent improvements in nutritional status. Adult male Surf Scoters were lighter during moult than in either spring or autumn, and that may help them to regain flight capabilities sooner. This seems to be a common pattern in sea ducks (Hogan *et al.* 2013). Causes underlying between- and within-year differences in moult chronology have yet to be identified, but likely involve climate, reproductive success, and the condition of the individual birds.

Most studies indicate that ducks and geese are not nutritionally stressed during the flightless period (Ankney 1979; Hohman 1993; Thompson & Drobney 1996; Hohman *et al.* 1992; Fox & Kahlert 2005), with varying levels of endogenous nutrient reserves being used to offset the energetic cost of moult (Pehrsson 1987; Panek & Majewski 1990; Moorman *et al.* 1993; Adams *et al.* 2000; Van de Wetering & Cooke 2000). However, Guillemette *et al.* (2007) suggest that the energetic costs of moult are high for Common Eiders, perhaps higher than during any other part of the annual cycle. Surf Scoters entered into the flightless period with most of their endogenous nutrient reserves spent and had to rely on local food resources to fuel the metabolic costs of daily activities, thermoregulation and feather growth. A concurrent behavioural study of Surf Scoters during wing-moult reported that the portion of time spent foraging during wing-moult was high, with foraging effort increasing with the progression of the moult (O'Connor 2008). We are not certain if the increase in foraging effort resulted from higher energetic costs or prey depletion. Faeces from scoters caught in the early and middle stages of the moult was comprised primarily of cockles (possibly *Clinocardium ciliatum*), molluscs of *Astare* sp. and clams *Macoma* sp., but were dominated by Blue Mussels *Mytilus edulis* and Green Sea Urchins *Strongylocentrotus drobachiensis* towards the end of the moult, suggesting possible depletion of food resources (SGG pers. obs.). Reduced foraging efforts early in the moult may however simply be a strategy to protect fragile, newly-emerging primaries (O'Connor 2008; Savard & Petersen 2015). Regardless, we expect that one of the primary characteristics affecting the selection of a moulting site is an abundance of high-quality food resources, because the nutrients required to cover the energetic costs of moult had to be acquired locally.

Energetic costs during the flightless period must be high, and we find it intriguing that male Surf Scoters enter the flightless period with almost no endogenous nutrient reserves. Males depart their breeding sites in mid-June (Savard *et al.* 2007) and initiate remigial moult just over a month later (Fig. 5), which should provide adequate time to build ample nutrient reserves to fuel the moult. Satellite tracking studies (O'Connor 2008; Sea Duck Joint Ventire 2015) show that male Surf Scoters may remain in coastal Labrador for just over a month following moult (SGG unpubl. data), and they must build significant reserves during this period as they have gained body mass by the time that they arrive at staging sites along the north shore of the Gulf of St. Lawrence (Fig. 8). That they do not do so prior to moult suggests there must be some disadvantage to initiating remigial moult with large nutrient reserves.

In addition to shortening the flightless period, we suggest that minimising body mass during moult benefits dive performance, which may be important for escape dives, with diving being the main means of evading predators at this time. White-winged Scoters and Common Eiders have a relatively high buoyancy (Lovvorn & Jones 1991a), which has a negative effect on dive performance during descent (Lovvorn & Jones 1991b), but both species use foot and wing propulsion during dives particularly in the initial phase of descent when respiratory air and also air trapped in the plumage makes them more buoyant (Richman & Lovvorn 2008). The scoters' wings enable them to be especially manoeuvrable underwater (S. Richman, pers. comm.), which is important during the shallow phase of escape dives. Minimising lipids, and possibly plumage volume (Fig. 7), as they enter the flightless period also may be advantageous for improving dive performance during the initial phase of descent. Moulting to a less dense and lighter eclipse plumage in late spring (Hohman *et al.* 1992; Savard & Petersen 2015) may further reduce buoyancy during the summer as a mechanism to improve dive performance while they are flightless.

Management implications

Sea ducks congregate by thousands to undergo their wing-moult (Savard & Petersen 2015; Petersen & Savard 2015). Aerial surveys conducted in the late 1990s indicated that 50,000–60,000 scoters moulted along the Labrador coast (SGG unpubl. data) and 30,000 moulted along the Gulf of St. Lawrence in Quebec (Rail & Savard 2003). Assuming the relative chronology of moult is the same across moult sites we would expect that 90% of these birds would be simultaneously flightless for about a fifteen-day period. At this time, birds are highly concentrated, and their daily movements are restricted to a few kilometres (5–7 km; O'Connor 2008) and home ranges are small (95% home range = 25.37 ± 2.82 km^2; O'Connor 2008). Clearly these moulting areas are critically important in the life cycle of continental populations of Surf Scoters.

Frimer (1994) and O'Connor (2008) suggest that the foraging behaviour of flightless sea ducks is affected by disturbances. Because of their strong response to disturbance (O'Connor 2008), and potentially high energetic requirements, disturbance should be minimised during wing-moult, and marine area protective status afforded to foraging habitats and moulting areas should be identified in marine planning. At least during the moulting season, modifications to shipping lanes should be considered to minimise the potential impacts of these activities on moulting scoters. The earlier moulting by adult males and later moulting by females is also important and should be taken into account, because their vulnerabilities will differ. In some areas, opening of the hunting season in or near moulting areas should be delayed, to reduce the risk of taking flightless females.

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