

AGE AND SEX DISTRIBUTIONS OF WINTERING SURF SCOTERS: IMPLICATIONS FOR THE USE OF AGE RATIOS AS AN INDEX OF RECRUITMENT

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Abstract. We assessed age- and sex-specific distribution patterns of Surf Scoters (*Melanitta perspicillata*) wintering in southern coastal British Columbia, Canada, and evaluated potential biases associated with the use of male age ratios as an index of their recruitment. For surveys conducted during 2000 through 2002, annual variations in male age ratios were evident, with estimates ranging from 0.07 ± 0.02 to 0.13 ± 0.03 (SE; first-year males:total males). Flock composition patterns indicated first-year males did not distribute independently, but tended to associate with other first-year males. With respect to habitat, male age-class proportions did not vary among shoreline substrate types, but higher proportions of first-year males were found in sites with low exposure to wind and waves (<50 km fetch). To determine the efficacy of male age ratios for indexing recruitment, we used a power analysis, which incorporated overdispersion in age-class segregation and determined the sample sizes required for precise estimates of the proportion of first-year male Surf Scoters. Samples of approximately 600–1000 total males were required to obtain 95% confidence limits within 5% of the estimated mean, with sampling accuracy leveling off at about 2% when 6000 or more males were aged. Recruitment among waterfowl species is typically modeled using the ratio of female recruits to breeding-age females. Based on the sex and male age-ratio estimates obtained in this study, we calculated a female age ratio of 0.23 (first-year females:adult females).

Key words: age-ratio estimation, flock, *Melanitta perspicillata*, overdispersion, recruitment, seabird, Surf Scoter.

Distribuciones Invernales de Edad y Sexo en *Melanitta perspicillata*: Implicancias del Uso de Cocientes de Edad como un Índice de Reclutamiento

Resumen. Estimamos los patrones de distribución específicos de edad y sexo de *Melanitta perspicillata* invernando en la zona costera sur de la Columbia Británica, Canadá, y evaluamos los sesgos potenciales asociados con el uso de cocientes de edad de machos como un índice de su reclutamiento. Durante los muestreos realizados entre el 2000 y el 2002 las variaciones anuales en el cociente de edad de los machos fueron evidentes, con estimaciones que variaron entre 0.07 ± 0.02 (EE) y 0.13 ± 0.03 (machos del primer año: total de machos). Los patrones de composición de las bandadas indicaron que los machos del primer año no se distribuyeron independientemente, sino que tendieron a asociarse con otros machos del primer año. Con relación al hábitat, las proporciones de clases de edad de los machos no variaron entre los tipos de sustrato de la línea de costa, pero se encontraron mayores proporciones de machos del primer año en sitios con baja exposición al viento y a las olas (sitios de mar abierto <50 km de ancho). Para determinar la eficacia de los cocientes de edad de los machos como índice de reclutamiento, usamos un análisis de poder, el cual incorporó sobre-dispersión en la segregación de las clases de edad y determinó los tamaños de muestreo necesarios para estimaciones precisas de la proporción de machos del primer año de *M. perspicillata*. Muestras totales de aproximadamente 600–1000 machos fueron necesarias para obtener límites de confianza del 95% dentro del 5% de la media estimada, con la exactitud de muestreo nivelándose cerca del 2% luego de estimarse la edad de 6000 o más machos. El reclutamiento entre las especies de Anseriformes es modelado

típicamente usando el cociente entre nuevas hembras y hembras en edad reproductiva. Basados en las estimaciones de cocientes de sexo y edad de los machos obtenidas en este estudio, calculamos un cociente de edad de las hembras de 0.23 (hembras del primer año: hembras adultas).

INTRODUCTION

Few reliable population indices or estimates of annual productivity are available for seaducks (Anatidae: Mergini) in North America. Analyses of existing survey data indicate declining population trends among 10 of the continent's 15 seaduck species (USFWS 1993, Goudie et al. 1994). These declines are poorly understood, and there is a need for new techniques to monitor populations. Typically, monitoring efforts focus on estimating total abundance. However, incorporating demographic data into monitoring programs can lend important insight into mechanisms underlying population change and help identify life stages at which changes are occurring.

Recruitment, the process by which young birds are added to the breeding population, is a crucial component of avian demographics. Thus, monitoring variation in recruitment rates is important from a management standpoint. Techniques traditionally used to assess waterfowl recruitment include pair:brood ratios (Kirby 1980, Rumble and Flake 1982), nesting success rates (Milne and Reed 1974, Klett et al. 1988) and age ratios based on wings turned in by hunters (Bellrose et al. 1961, Munro and Kimball 1982). Unfortunately, these techniques have been of limited value for many seaduck species, as most breed in low densities in remote portions of the continent (Bellrose 1980) and rarely appear in hunter bags (Bartonek 1994).

An alternative method for indexing recruitment by seaducks is the use of age ratios calculated from direct counts on nonbreeding areas. This technique relies upon delayed plumage maturation to distinguish cohorts and estimate population age structure. Age-related plumage variation has been described among males of all 15 North American seaduck species (Palmer 1976), and winter age-ratio estimation has recently been used to assess the age structure of Common Goldeneye (*Bucephala clangula*; Duncan and Marquiss 1993) and Harlequin Duck (*Histrionicus histrionicus*; Smith et al. 2001, Rodway et al; 2003, Robertson, in press) populations. However, use of male age ratios in population models requires several important con-

siderations. First, age ratios are subject to misinterpretation if factors such as geographic location, differential use of habitats, or variable group composition prevent representative sampling of age classes. Further, because waterfowl populations typically have male-biased sex ratios (Bellrose et al. 1961), estimating the number of potentially breeding females is of primary importance in models (Johnson et al. 1992). For seaducks, female age classes cannot be distinguished on the basis of plumage alone and must be calculated from male age ratios. Calculation of female age ratios is straightforward, so long as secondary sex ratios are equal (Blums and Mednis 1996) and prebreeding mortality rates are the same for subadult males and females; however, any sex-related distributional biases must be known.

The purpose of this study was to determine the age and sex composition of Surf Scoter (*Melanitta perspicillata*) populations wintering in southern coastal British Columbia, investigate age- and sex-specific distribution patterns, and infer the reliability of male age ratio as an index of recruitment. Until recently, the Surf Scoter has been among the least studied North American waterfowl (Savard et al. 1998). Current data indicate population numbers are declining in western North America (Goudie et al. 1994, Hodges et al. 1996; Nysewander et al., unpubl. data), and aerial surveys in Alaska suggest long-term (1957–2001) breeding population declines (Conant and Groves, unpubl. data). Surf Scoter breeding populations have been difficult to study because nesting occurs in low densities across remote boreal forest regions (Bellrose 1980). The demographic data that are available indicate variable, but generally low, reproductive rates and high adult survival (Savard and Lamothe 1991, Morrier et al. 1997). However, these data are from a few localized studies and systematic techniques for assessing breeding populations have not been implemented.

For most of the year, Surf Scoters frequent shallow marine habitats on wintering areas, where scoter flocks are a conspicuous part of the avifauna in many coastal areas. On the Pacific coast a vast majority of individuals occur within

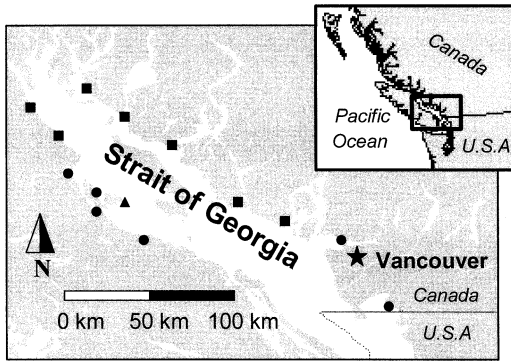


FIGURE 1. Map of the study area in the Strait of Georgia, British Columbia, Canada. Circles indicate areas used to survey Surf Scoters during 2000, 2001, and 2002; squares indicate survey areas used during 2001 and 2002; triangles indicate survey areas used during 2000.

1 km of shore (Vermeer 1981), making winter populations readily accessible to researchers. Iverson et al. (2003) determined first-year males in these flocks can be reliably distinguished from adult males and females on the basis of plumage, raising the possibility that winter age ratios could be used as an index of recruitment. For this paper, our four primary research objectives were to (1) estimate Surf Scoter winter age and sex ratios in the Strait of Georgia, British Columbia, Canada, and document annual variation in population composition; (2) investigate the potential effects that age and sex-related differences in flock composition, habitat use, and latitudinal distribution patterns might have on age-ratio estimates; (3) determine the sample sizes required to detect changes in age ratios among years; and (4) discuss the advantages and disadvantages of using winter age ratio as an index of recruitment by Surf Scoters and perhaps other migratory bird species.

METHODS

STUDY DESIGN

The age and sex composition of Surf Scoter populations was investigated in the Strait of Georgia, British Columbia (Fig. 1), during the winters of 2000, 2001, and 2002. Three replicate surveys were conducted per year, at 10–14 day intervals, commencing the third week of January each year. During 2000, counts were made at 36 sample stations, encompassing seven survey areas (survey area defined as a bay, inlet, sound,

or continuous section of coastline). An additional seven survey areas, each composed of 2–4 sample stations, for a grand total of 57 sample stations, were added in 2001 and 2002. All counts were made from shore during daylight hours (08:00–16:00), using a 20–60× spotting scope, when Beaufort scale sea conditions were rated as 3 (small scattered whitecaps, gentle breeze, wind speed 12–19 knots) or less. Each replicate required 3–5 days to complete.

At each sample station, the number of Surf Scoters within 400 m of shore was counted. After estimating abundance, a scan was performed to determine age and sex composition. This scan proceeded slowly over each flock while a minimum of birds were in motion or diving. For Surf Scoter flocks with more than 50 individuals, age and sex determinations often could not be made for every individual due to birds being underwater or obstructed from view by other birds. For these flocks, the age and sex determination scan was considered a random sample of flock composition, and the proportions obtained were treated as representative of the flock as a whole. Sample station estimates were averaged to produce a mean for each survey area.

Individual Surf Scoters were categorized by sex (M = male; F = female), and males were categorized by age (ADU = adult, ≥ 12 months old; IY = first-year, < 12 months old). These determinations were made on the basis of plumage and bill appearance (Iverson et al. 2003). During winter, first-year males (M_{IY}) are characterized by dull multicolored bills, light belly plumage, mottled black and brown feathering on the head and back, poorly defined nape patches, and the absence of forecrown patches. Adult males (M_{ADU}) are distinguished by their bright, bulbous, multicolored bills, lustrous black plumage, and large, clearly defined nape and forecrown patches. Both first-year and older females exhibit dark bills, brown plumage, and variable amounts of lighter feathering on the breast and belly. Female age is not distinguishable on the basis of appearance alone; therefore, we grouped them into a single category (F_{TOTAL} ; Iverson et al. 2003).

STATISTICAL ANALYSES

Age and sex ratio estimation. The proportion first-year males (M_{IY}/M_{TOTAL}), and proportion of females ($F_{TOTAL}/[M_{TOTAL} + F_{TOTAL}]$) were estimated for each year (\pm SE) using mean values for

each survey area weighted according to sample size. Recruitment among waterfowl is commonly indexed as the ratio of first-year females to adult females (Cowardin and Blohm 1992). To facilitate comparison with literature values, sex ratio (M_{TOTAL}/F_{TOTAL}) and male age ratio (M_{1Y}/M_{ADU}) were also calculated. Female age ratio ($M_{1Y}/[F_{TOTAL} - M_{1Y}]$) was derived, based upon the assumption of a 1:1 ratio among first-year males and females. Annual variation in these parameters was assessed using ANOVA, with $\alpha = 0.05$. Specifically, we used a general linearized model ANOVA appropriate for our binomial data, with the Wald-statistic, W (StatSoft 1995).

Flock composition patterns. A typical assumption of a random sampling protocol to estimate age and sex ratios would be that the classes assort themselves randomly within flocks in the sampled population. To determine if this was the case with Surf Scoters, we challenged a null hypothesis that aged and sexed individuals were independently distributed (i.e., no overdispersion) and that there was no trend in age and sex composition with respect to flock size. These hypotheses were tested by regressing the proportion first-year male (first-year males:total males), and the proportion female (total females:total birds), against flock size, in separate analyses. We wished to know (1) whether members of either age class (first-year males versus adult males) or sex class (females versus males) tended to occur more frequently in flocks of a particular size, and (2) whether members of either age or sex class tended to occur in flocks composed predominately of like individuals.

To effect our analyses we treated each flock as an independent sample unit, yielding a sample size of $n = 408$ for all years and replicates combined. These regressions used AIC_c and likelihood ratios to rank and test competing parametric hypotheses (Burnham and Anderson 2002) and were designed to respect the binomial error structure of the data by using a beta-binomial error distribution (Mood et al. 1985, McCullagh and Nelder 1989). The linear equations for the predicted proportions at each flock size were logit-transformed to retain the predictions within the range 0–1. Thus our statistical model was

$$p_{F_i} = \frac{1}{\{1 + e^{-(a+b \ln[F_i]) + \lambda_1 Y_{2001} + \lambda_2 Y_{2002}}\}} + \varepsilon_i$$

where $0 \leq p_{F_i} \leq 1$ is the predicted proportion first-year male (or proportion female, depending

upon the analyses being performed) for flock i of n with F_i birds; and a , b , λ_1 , and λ_2 are parameters to be estimated. Variables Y_{2001} and Y_{2002} are categorical (0 or 1), indicating the year. When all parameters except a equal zero, p_{F_i} is constant for all flock sizes. We chose the statistical error of this model (ε_i) to follow a beta-binomial distribution,

$$p[S_{F_i}] = BB[S_{F_i}; F_i, p_{F_i}, \theta_{F_i}^2]$$

where $p[S_{F_i}]$ is the probability of having observed S_F first-year males (or females) in a flock of size F_i , and where $0 \leq \theta_{F_i}^2 \leq 1$ is the overdispersion parameter of the beta-binomial distribution. To model the degree of overdispersion we used

$$\theta_{F_i}^2 = \frac{1}{\{1 + e^{-(c+d \ln[F_i]) + \gamma_1 Y_{2001} + \gamma_2 Y_{2002}}\}}$$

which allows $\theta_{F_i}^2$ to vary with flock size, where c , d , γ_1 , and γ_2 are parameters to be estimated and variables Y_{2001} and Y_{2002} are as above. When all parameters except c equal zero, $\theta_{F_i}^2$ is constant for all flock sizes.

Interpretation of the overdispersion parameter, $\theta_{F_i}^2$, is fundamental to understanding the degree to which cohorts group together into flocks. At one extreme, when $\theta_{F_i}^2 = 0$, all individuals are randomly distributed; that is, the beta-binomial distribution limits to the binomial distribution. At the other extreme, when $\theta_{F_i}^2 = 1$ individuals associate only with their kind. For example, with respect to the segregation of first-year and adult males, $\theta_{F_i}^2 = 1$ would indicate that each flock consisted entirely of either first-year males or adult males. To elucidate the magnitude of overdispersion, we calculated the *effective independent unit*, mathematically defined as the ratio of the beta-binomial variance to the equivalent binomial variance with no overdispersion, i.e.,

$$1 + \theta_{F_i}^2(F_i - 1).$$

Hence, an effective independent unit equal to one would indicate individuals were distributing themselves at random among flocks. A ratio greater than one would indicate individuals were not acting independently; rather, they could be interpreted as associating in numbers equal in size to the estimated effective independent unit.

One key consideration was the possible influence of random measurement error on the degree of overdispersion in p_{F_i} , since erroneous

counts of first-year or adult males would contribute to observed overdispersion. Since we had no independent assessment of measurement error, we used our estimates of p_{F_i} and $\theta_{F_i}^2$ to calculate the standard deviation of extrabinomial variance associated with each estimate of p_{F_i} . For these calculations we used

$$SD[p_{F_i}] = \sqrt{\theta_{F_i}^2 p_{F_i} (1 - p_{F_i})},$$

derived from the ratio of variance of the beta-binomial to the binomial distribution. We then made an *a posteriori* judgment if measurement error was likely to be a significant contributor to the value of $SD[p_{F_i}]$.

Habitat segregation. To determine whether first-year males or females segregated into different habitats, midwinter survey counts were related to habitat attribute data. We used the British Columbia Marine Ecosystem Classification (BCMEC) for the Pacific Coast of Canada (Zacharias et al. 1998) to characterize the substrate and exposure for each sample station. For the BCMEC ecounit themes, substrate categorizations were taken from Geological Survey of Canada sediment distribution maps, with sites classified as *rocky*: bedrock, boulders, or cobble, with gravel/sand interspersed; *sandy*: sand or sand/gravel; or *muddy*: mud or sand/mud. Wind and wave exposure were categorized as *low*: protected area, fetch <50 km; or *moderate*: open sound or strait, fetch 50–500 km. Variations in age and sex composition were investigated using the same ANOVA procedures described above for binomial data, where mean values were calculated for each survey area weighted according to sample size.

Latitudinal variation. Additional surveys were conducted during 2001 at locations along the Pacific coast to assess latitudinal variation in age and sex proportions. These surveys coincided with survey dates used in the Strait of Georgia and followed identical sampling protocols. They were conducted by volunteers with previous survey experience, whose assistance was solicited through birding organizations throughout the United States and Canada. Volunteers were trained using a website and written materials, which provided detailed instructions on identification of age classes and survey guidelines. Of 40 original respondents, 27 completed the three replicate surveys. Seven surveys were dropped due to insufficient sample size (<40 total birds per survey) leaving an overall sample size of 20.

Simple linear regression was used to evaluate latitudinal trends in age and sex proportions for wintering aggregations ranging from 35–58°N.

Power analysis. To determine our power to estimate the proportion of first-year male Surf Scoters with a specified confidence and make recommendations for future study design, we used a bootstrap resampling scheme to generate confidence intervals for various sampling intensities. Our motivation was to determine the sample size required to confidently estimate this proportion, given the overdispersion observed in our data. Such overdispersion increases the size of the effective independent unit, thus proportionately increasing the sample size required to achieve a desired confidence interval. In our power analysis, flock composition data from all three years and replicate samples were treated both individually and pooled into a single dataset composed of 408 flock observations, containing 6422 total males.

Our first step was to perform a jackknife procedure (Efron and Tibshirani 1998) to estimate the mean proportion of first-year males \bar{p}_{F_i} and $\hat{\theta}_{F_i}^2$, as well as their standard errors ($s_{p_{F_i}}$ and $S_{\hat{\theta}_{F_i}^2}$, respectively) using the model equations described above, but with all parameters except a and c equal to zero. Our choice to use a jackknife procedure to calculate these moments was motivated by the variable flock sizes and overdispersion attributes related to flock size and habitat in our data, features not captured when these moments are estimated using sample statistics. Given estimates for these population moments, which we treated as known values, we could randomly sample first-year and adult males from flock F_i , according to a beta-binomial probability distribution. This bootstrapping protocol was carried out for different sampling intensities, with the number of flock observations in each subsample increasing by sequential powers of 2 up to the maximum sample size of 408. For each subsample we used the model equations to estimate \hat{p}_{F_i} and $\hat{\theta}_{F_i}^2$, and repeated the procedure 100 times to generate stable estimates of $\hat{s}_{p_{F_i}}$ and $\hat{S}_{\hat{\theta}_{F_i}^2}$. These estimates were then used to infer the minimum number of sample stations and total males that would be required to estimate the proportion first-year male within 2% and 5% of the overall mean, using 95% confidence intervals for the upper and lower bounds. Note that for this procedure we presumed no knowledge of any relationship be-

TABLE 1. Number of Surf Scoters observed in the Strait of Georgia, British Columbia, Canada, 2000–2002, by sex and age class. Values are means \pm SE for three replicate midwinter surveys.

	2000	2001	2002	Total
Total Surf Scoters	1221 \pm 218	1316 \pm 238	1080 \pm 36	1206 \pm 56
Total females	442 \pm 66	422 \pm 77	379 \pm 23	414 \pm 15
Total males	779 \pm 152	894 \pm 162	701 \pm 12	791 \pm 46
Adult males	680 \pm 132	833 \pm 150	629 \pm 26	714 \pm 50
First-year males	100 \pm 21	62 \pm 16	72 \pm 14	78 \pm 9
Proportion first-year males ^a	0.13	0.07	0.11	0.10
Sex ratio ^b	1.76	2.12	1.87	1.91
Female age ratio ^c	0.29	0.17	0.23	0.23

^a The number of first-year males/the total number of males.

^b The number of males/the number of females.

^c The number of first-year males/(the number of females – the number of first-year males).

tween these moments and flock size (i.e., only parameters a and c were estimated), contrary to what we will report in this manuscript. The reason for this is that (1) these relationships would not necessarily exist in other data collections, and (2) if they exist but are not identified, our power analysis will provide a conservative estimate of the sample size required to overcome the variance added by any such relationship. Means are presented \pm SE.

RESULTS

Age and sex ratios. Similar numbers of Surf Scoters were counted each year, with survey means ranging from 1080 \pm 36 birds in 2002 to 1316 \pm 238 in 2001. Estimates for the proportion first-year males differed among years ($W_2 = 41.6$, $P < 0.001$), with annual estimates of 0.13 \pm 0.03 in 2000, 0.07 \pm 0.02 in 2001, and 0.11 \pm 0.02 in 2002. For males, these values yielded an overall age composition estimate of 0.10 first-year males:total males. With respect to sex, the population composition was strongly male biased, with an overall estimate of the proportion female of 0.35 total females:total birds. Annual variations were significant ($W_2 = 11.3$, $P = 0.04$), with estimates of 0.36 \pm 0.02 in 2000, 0.32 \pm 0.02 in 2001, and 0.35 \pm 0.02 in 2002. This male-biased estimate for population composition contributed to calculated female age ratios that were more than twice as high as male age ratios (female age ratio = 0.23 first-year females:adult females, range 0.17–0.29; male age ratio 0.11 first-year males:adult males, range 0.07–0.15; Table 1).

Flock composition patterns. On the basis of model selection using AIC_c and judgment of

statistical significance using likelihood-ratio tests, our best model could not support a slope different from zero for the proportion first-year males, \hat{p}_F , ($b = 0$, $P = 0.78$), suggesting no strong age-related differences in flock composition with respect to flock size. However, the corresponding estimates of $\hat{\theta}_{F_i}^2$ were significantly greater than zero ($P < 0.001$), and changed with flock size ($d = -0.46$, $P < 0.001$), indicating that first-year males did not independently sort into flocks (Fig. 2). As in our age-ratio analysis above, we also identified interannual differences in the estimated mean proportion of first-year males, \hat{p}_F , in this analysis. Our best model including year effects was 378 times more likely than its direct competitor lacking them, and thousands of times more likely than the null model (constant \hat{p}_F and $\hat{\theta}_{F_i}^2$). The effective independent unit for males (averaged over all years 2000–2002) increased from about 3.4 in flocks of 10 males, to 8.4 in flocks of 50, and 12.6 in flocks of 100, indicating a tendency for first-year males to increasingly associate with other first-year males as flock size increased. The standard deviation of extrabinomial variance $SD[p_{F_i}]$ was estimated to range from 0.1 to 0.2 for flock sizes of 1 to 100 birds.

With respect to sex, our best model indicated that the proportion female, p_{F_i} , tended to be higher in larger flocks ($b = 0.08$, $P < 0.001$, Fig. 2). The estimate of $\theta_{F_i}^2 = 0.02$ was significantly different from zero ($P < 0.001$), but there was no trend in $\theta_{F_i}^2$ with flock size ($d = 0$, $P = 0.74$). As in our sex ratio analysis above, we also identified interannual differences in the mean proportion of females, \hat{p}_F , in this analysis. Our best model including year effects was 41

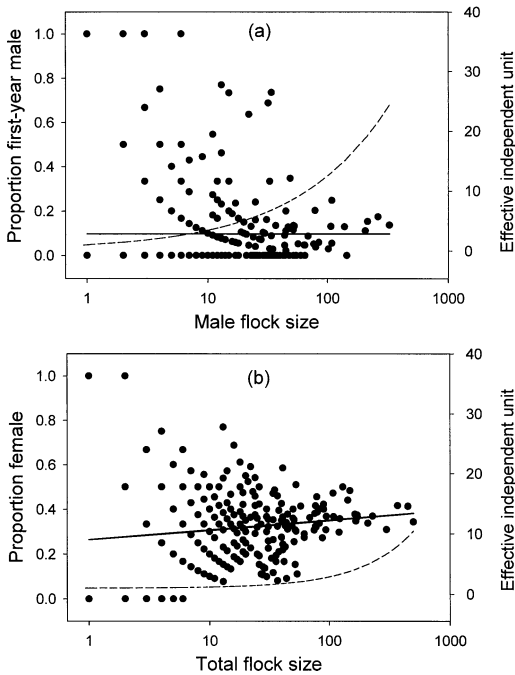


FIGURE 2. Relationship between Surf Scoter flock size and (a) proportion first-year male or (b) proportion female. Points indicate observed proportions, solid line indicates predicted proportions averaged over all years, and dashed line indicates the effective independent unit, a measure of the degree to which individuals in a given age or sex cohort tend to associate, and thus behave as a unit for statistical purposes. Interannual differences in the trends portrayed were statistically detected, but to retain clarity only the mean values are presented.

times more likely than its direct competitor lacking them, and thousands of times more likely than the null model (constant \hat{p}_F and $\hat{\theta}^2_{F_i}$). The effective independent units differed only slightly from unity (complete independence) in the smallest flocks (averaged over all years 2000–2002), increasing to about 1.2 in flocks of 10 birds, then approximately 3 in flocks of 100. The standard deviation of extrabinomial variance $SD[p_{F_i}]$ was estimated to range from 0.05 to 0.06 for flock sizes of 1 to 100 birds.

Habitat segregation. When relating the composition of flocks to substrate type, age-related segregation was not evident among males ($W_2 = 1.8, P = 0.41$). However, sex-related habitat segregation was evident, with females being underrepresented in sandy substrate and overrepresented in rocky and muddy substrate ($W_2 = 61.2, P < 0.001$). Female proportions (total females:

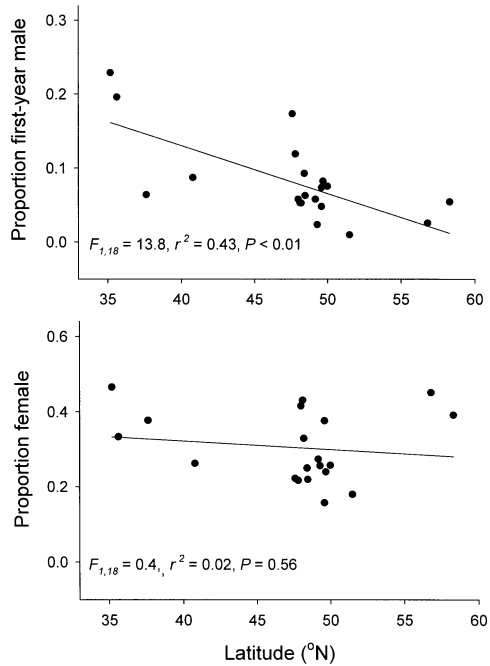


FIGURE 3. Geographic variation in age and sex composition of Surf Scoter flocks on the Pacific coast of North America. Data were collected during January and February 2001 by volunteers at 20 coastal locations between Alaska and California.

total birds) in the three habitats were estimated as 0.38 ± 0.01 in rocky habitats, 0.34 ± 0.01 in muddy habitats, and 0.29 ± 0.01 in sandy habitats. First-year male proportions were higher in sites with low exposure to wind and waves, 0.11 ± 0.01 , than in sites with moderate exposure, 0.08 ± 0.01 ($W_1 = 16.3, P < 0.001$). With respect to sex, there was no difference in proportion female between low and moderate exposure sites ($W_1 = 1.2, P = 0.27$).

Latitudinal variation. Results of the volunteer surveys suggested that latitudinal variation in the age composition of Surf Scoter populations may exist (Fig. 3). The proportion of first-year males was negatively related to latitude ($M_{1Y}/M_{TOTAL} = 0.38 - 0.01 \text{ latitude}, F_{1,18} = 13.8, r^2 = 0.43, P < 0.01$). Sex ratios did not exhibit a latitudinal trend ($F_{TOTAL}/(M_{TOTAL} + F_{TOTAL}) = 0.41 \text{ latitude}, F_{1,18} = 0.4, r^2 = 0.02, P = 0.56$). These results, however, should be treated with caution, as the survey was conducted only for a single year and the number of samples at both the northern ($>55^\circ\text{N}$) and southern ($<45^\circ\text{N}$) ends of the range was small.

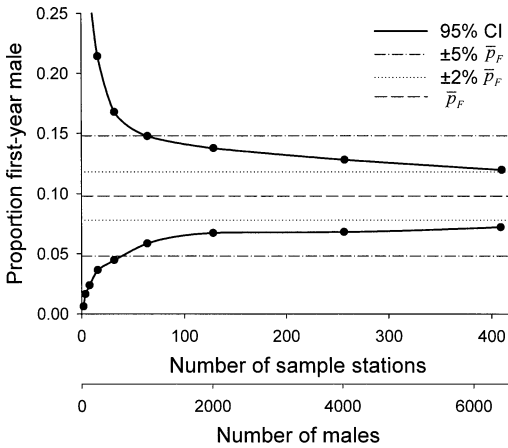


FIGURE 4. Number of sample stations and total number of male Surf Scoters necessary to estimate the proportion first-year male Surf Scoters (p_{F1}) within specified confidence limits.

Power analysis. Our power analysis, designed to calculate confidence levels for various sampling intensities, allowed us to assess the efficacy of winter age-ratio estimation. In our dataset that included samples from all three years combined, a jackknifed mean proportion first-year male, \bar{p}_F , of approximately 0.10 was estimated, with $s_{\bar{p}_F} = 0.01$. The value for θ^2_{F1} was estimated as 0.22, with $S_{\theta^2_{F1}} = 0.04$. Bootstrap simulation results suggest that in order to narrow 95% confidence intervals to within 5% of \bar{p}_F , 40–60 sample stations or 630–960 male Surf Scoters would need to be surveyed. For an estimate within 2%, sampling intensity would have to increase to 400–600 sample stations or 6280–9420 males (Fig. 4).

DISCUSSION

At a regional scale, such as the Strait of Georgia, Surf Scoter winter population composition can be estimated with confidence. However, in order to avoid potential biases resulting from age- and sex-related differences in flock composition and habitat use patterns, large samples drawn representatively from available habitats must be obtained. In this study, we estimated an overall proportion first-year male of 0.10 first-year males:total males, with annual estimates ranging between 0.07 and 0.13. The population was also strongly male biased, with a sex ratio of 1.9 males per female. From these estimates we calculated a male age ratio of 0.11 first-year males: adult males and a female age ratio of 0.23 first-

year females:adult females. These relatively low age-ratio estimates are consistent with expectations for a seabird species, whose life history strategies are characterized by high annual adult survival and variable, but generally low, annual productivity (Goudie et al. 1994).

Flock composition and habitat use patterns suggest Surf Scoter winter distributions are not entirely independent with respect to age and sex class. There was a tendency for first-year males to cluster into flocks with other first-year males, particularly within larger flocks. The grouping of male age classes is not surprising, given the strong flocking behavior of Surf Scoters in general (Savard et al. 1998) and the postulated role of dominance interactions within waterfowl flocks (Nichols and Haramis 1980, Hepp and Hair 1984, Alexander 1987). Relatively high values for the estimated extrabinomial variance, $SD[p_{F1}]$, which ranged from about 0.1 to 0.2, suggest that our measure of overdispersion for first-year males is not due entirely to measurement error. That is, it seems unlikely that our standard error of measurement would be equal to or double the estimated proportion first-year male ($\hat{p}_F = 0.10$).

In contrast to first-year males, there was little evidence that females were joining flocks composed primarily of other females. Our estimates of the effective independent unit (Fig. 2) for females differed only slightly from unity in smaller flocks, and the magnitude of overdispersion was not sufficient to distinguish it from potential measurement error in larger flocks. Although there was no trend in the overdispersion parameter, a positive relationship between proportion female and flock size was evident. We speculate that this relationship is related principally to habitat preferences, which appear to differ between the sexes. Female proportions were highest over rocky substrates, where Surf Scoters forage primarily on mussels (Vermeer 1981). Flocks in these rocky habitats tended to be larger and more densely packed than in sandy areas, where clams are the principal prey item and flocks were typically smaller and more dispersed (Iverson 2002). First-year males did not segregate from adult males according to substrate type, but they were underrepresented relative to adults in more exposed sites. The most obvious explanation for the small number of first-year males in exposed sites would be body size differences; however females, which are smaller

and 10–20% lighter than males (Palmer 1976), did not exhibit the same pattern. It should be noted, however, that we sampled only under relatively calm weather conditions, and it is possible that exposure-related distributional differences are more pronounced under extreme wind and wave conditions.

Our power analyses, which incorporated the tendency for individuals of various age and sex classes to associate with like individuals, and thus behave as a group for statistical purposes, were designed to assess the level of precision attainable at various sampling intensities. These analyses indicated that approximately 600–1000 total males were needed to obtain estimates within 5% of the population mean, and that precision could be further improved with larger samples, reaching roughly 2% from a sample of 6000 or more total males. While sampling intensities of such a magnitude would be logistically feasible in many areas, and could act as a guide for other researchers when designing monitoring programs, we caution that demographic parameters may differ among populations. Our analyses indicated that the sample size required to achieve a chosen level of confidence depends upon the mean age proportion, mean flock size, and overdispersion characteristics, all of which may vary from location to location.

While the potential estimation complications resulting from age-related differences in flock composition, overdispersion, and habitat association patterns can be remedied by sampling design, the data from volunteer surveys conducted at sites along the Pacific coast may present a greater challenge for the application of winter age ratios in population monitoring schemes and demographic models. This study was the first to investigate the possibility of differential migration according to age class among wintering seaducks. Latitudinal variation in Surf Scoter age ratios was evident, with a higher proportion of first-year male Surf Scoters wintering farther south. Differential migration is common among migratory birds, with prey and habitat differences, competitive exclusion by adults, and lower cold tolerance among young all potentially underlying geographic distribution patterns during winter (Cristol et al. 1999). If latitudinal variation in Surf Scoter winter age ratios exists, then estimates taken at a regional scale would be greatly complicated by interannual fluctuations in productivity in the larger population.

However, sample sizes in this part of the study were small, and there is a danger of committing a Type I error if too much credence is given to an extrapolation from a single year's observation. Future research will be necessary to evaluate the trend, determine if it is authentic, and if so investigate whether distributional differences are related primarily to site preferences by young or competitive exclusion by adults.

The potential for differential distribution of the age classes at a latitudinal scale during winter also raises the issue of how migratory populations are linked through the annual cycle, as migratory movements often confound efforts to delineate distinct population units for management purposes (Esler 2000, Webster et al. 2002). Population models most often focus on breeding aggregations, in part due to the direct implications for reproductive dynamics (Lindberg et al. 1998). Use of demographic data derived from wintering areas, however, requires that additional consideration be given to seasonal movements and potential linkages between breeding and nonbreeding areas.

Seaduck species exhibit a wide range of association patterns between breeding and nonbreeding areas. Common Eider (*Somateria mollissima*) populations, for example, are among the most geographically structured, with birds breeding in specific areas in arctic and western Alaska known to have separate wintering ranges (Petersen and Flint 2002). In such cases, age-ratio estimates made on wintering areas should correspond directly with productivity estimates from specific breeding locations. However, when migratory movements produce wintering aggregations which include multiple breeding populations, interpretation is more complex. For example, Pacific populations of Steller's Eiders (*Polysticta stelleri*) assort into three distinct breeding aggregations, but combine to form a single wintering population (Dau et al. 2000). Winter age ratios in such a population would represent a pooled estimate of productivity from multiple breeding areas, and would have to be treated as such in population models. Finally, for species such as Long-tailed Ducks (*Clangula hyemalis*), where little to no population structure has been identified (M. Petersen and P. Flint, unpubl. data), winter age ratios can serve only as a rough measure of age composition, with fine-scale linkages between specific breeding and wintering areas not being possible. To date, mi-

gratory movements and potential linkages between breeding and nonbreeding areas have not been elucidated for Pacific Surf Scoter populations. Therefore, caution must be applied when attempting to relate winter age-ratio estimates to productivity and recruitment estimates at specific breeding locations, and when extrapolating regional estimates to larger geographic scales during winter.

At present there is a clear need for new techniques to assess and monitor seaduck populations. Demographic data can be particularly useful for understanding the mechanisms underlying population changes. For species such as the Surf Scoter, which breed in low densities in remote portions of the continent, estimation of recruitment from winter age ratios offers an attractive alternative to traditional methods. Further, because distribution patterns can reveal important relationships to food resources, as well as adaptive social organization important to survival, understanding age- and sex-related differences is important from an ecological standpoint (Haramis et al. 1994). Results of this study suggest the use of male winter age ratios may be a practicable method for indexing recruitment by Surf Scoters; however, considerable care must be taken to plan for sample sizes that ascertain the desired precision of estimates. With such an effort, incorporating demographic data such as these into monitoring efforts and population models can better equip conservation agencies to understand declining seaduck populations and manage them for sustainability.

ACKNOWLEDGMENTS

The CWS/NSERC Centre for Wildlife Ecology and the Georgia Basin Ecosystem Initiative funded this project. Cyndi Smith helped in the early stages of project planning and Julian Hudson assisted with fieldwork. John Eadie, Paul Flint, Dan Esler, Sean Boyd, Michael Rodway, Heidi Regehr, and Jean-Pierre Savard provided critical comments that improved earlier versions of this manuscript. Special thanks are owed to Stephanie Hazlitt, from Bird Studies Canada, and the many volunteer naturalists who collected data: H. Higley, R. Carlson, R. Orr, G. Smith, B. Hunter, B. Pawuk, P. Suchanek, J. Anderson, G. Kordowski, R. Toochin, I. Raudzins, D. Carrick, H. Sigler, B. Merrick, D. Watkins, B. Heybroek, K. Rogers, J. Black, J. Phillips, B. Moorehead, P. Crawford, M. Dunn, P. Geoffray, R. Chappel, M. Stahnke, J. Stahnke, N. Robins, M. Robins, N. Morton, B. Goodman, and S. Niscail.

LITERATURE CITED

- ALEXANDER, W. C. 1987. Aggressive behavior of wintering diving ducks (Aythyini). *Wilson Bulletin* 99:38–47.
- BARTONEK, J. C. 1994. Waterfowl harvests and status, hunter participation and success, and certain hunting regulations in the Pacific Flyway and United States. USDI Fish and Wildlife Service, Pacific Flyway Data Book, Portland, OR.
- BELLROSE, F. C. 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BELLROSE, F. C., T. G. SCOTT, A. S. HAWKINS, AND J. B. LOW. 1961. Sex ratios and age ratios in North American Ducks. *Illinois Natural History Survey Bulletin* 27:391–474.
- BLUMS, P., AND A. MEDNIS. 1996. Secondary sex ratio in Anatinae. *Auk* 113:505–511.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York.
- COWARDIN, L. M., AND R. J. BLOHM. 1992. Breeding population inventories and measures of recruitment, p. 432–445. *In* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [EDS.], *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, MN.
- CRISTOL, D. A., M. B. BAKER, AND C. CARBONE. 1999. Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology* 15:33–88.
- DAU, C. P., P. L. FLINT, AND M. R. PETERSEN. 2000. Distribution of recoveries of Steller's Eiders banded on the lower Alaska Peninsula, Alaska. *Journal of Field Ornithology* 71:541–548.
- DUNCAN, K., AND M. MARQUISS. 1993. The sex/age ratio, diving behaviour and habitat use of Goldeneye *Bucephala clangula* wintering in northeast Scotland. *Wildfowl* 44:111–120.
- EFRON, B., AND R. J. TIBSHIRANI. 1998. An introduction to the bootstrap. Chapman and Hall/CRC, New York.
- ESLER, D. 2000. Applying metapopulation theory to conservation of migratory birds. *Conservation Biology* 14:366–372.
- GOUDIE, R. I., S. BRAULT, B. CONANT, A. V. KONDRATYEV, M. R. PETERSEN, AND K. VERMEER. 1994. The status of seaducks in the north Pacific Rim: toward their conservation and management. *Transactions of the North American Wildlife and Natural Resource Conference* 59:27–49.
- HARAMIS, G. M., E. L. DERLETH, AND W. A. LINK. 1994. Flock sizes and sex ratios of Canvasbacks in Chesapeake Bay and North Carolina. *Journal of Wildlife Management* 58:123–131.
- HEPP, G. R., AND J. D. HAIR. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. *Condor* 86:251–257.
- HODGES, J. I., J. G. KING, B. CONANT, AND H. A. HANSON. 1996. Aerial surveys of waterbirds in Alaska 1957–94: population trends and observer variability. USDI National Biological Service, Information and Technology Report 4. Washington, DC.

- IVERSON, S. A. 2002. Recruitment and the spatial organization of Surf Scoter (*Melanitta perspicillata*) populations during winter in the Strait of Georgia, British Columbia. M.Sc. thesis, Simon Fraser University, Burnaby, BC.
- IVERSON, S. A., D. ESLER, AND W. S. BOYD. 2003. Plumage characteristics as an indicator of age class in the Surf Scoter. *Waterbirds* 26:56–61.
- JOHNSON, D. H., J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl, p. 446–485. *In* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [EDS.], *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, MN.
- KIRBY, R. E. 1980. Waterfowl production estimates of forested wetlands from pair and brood counts. *Wildlife Society Bulletin* 8:273–278.
- KLETT, A. T., T. L. SHAFFER, AND D. H. JOHNSON. 1988. Duck nest success in the prairie pothole region. *Journal of Wildlife Management* 52:431–440.
- LINDBERG, M. S., J. S. SEDINGER, D. V. DERKSEN, AND R. F. ROCKWELL. 1998. Natal and breeding philopatry in a Black Brant (*Branta bernicla nigricans*) metapopulation. *Ecology* 79:1839–1904.
- MCCULLAGH, P., AND J. A. NELDER. 1989. *Generalized linear models*. 2nd edition. Chapman and Hall/CRC, New York.
- MILNE, H., AND A. REED. 1974. Annual production of fledged young from the eider colonies of the St. Lawrence estuary. *Canadian Field Naturalist* 88:163–170.
- MOOD, A. M., F. A. GRAYBILL, AND D. C. BOES. 1985. *Introduction to the theory of statistics*. Third edition. McGraw-Hill, New York.
- MORRIER, A., L. LESAGE, A. REED, AND J.-P. L. SAVARD. 1997. Étude sur l'écologie de la Macreuse à front blanc au lac Malbaie, Réserve des Laurentides—1994–1995. Technical Report Series No. 301, Canadian Wildlife Service, Québec Region, Québec, Canada.
- MUNRO, R. E., AND C. F. KIMBALL. 1982. Population ecology of the Mallard: VII. Distribution and derivation of the harvest. USDI Fish and Wildlife Service Resource Publication 147, Laurel, MD.
- NICHOLS, J. D., AND G. M. HARAMIS. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. *Condor* 82:406–416.
- PALMER, R. S. 1976. *Handbook of North American birds*. Vol. 3. Yale University Press, New Haven, CT.
- PETERSEN, M. R., AND P. L. FLINT. 2002. Population structure of Pacific Common Eiders breeding in Alaska. *Condor* 104:780–787.
- ROBERTSON, G. J. In press. Using winter juvenile/adult ratios as indices of recruitment in population models. *In* G. J. Robertson and P. W. Thomas [EDS.], *Harlequin Ducks in the Northwest Atlantic*. Canadian Wildlife Service Occasional Paper Series, Ottawa, ON, Canada.
- RODWAY, M. R., H. R. REGEHR, AND F. COOKE. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment. *Canadian Journal of Zoology* 81:492–503.
- RUMBLE, M. A., AND L. D. FLAKE. 1982. A comparison of two waterfowl brood survey techniques. *Journal of Wildlife Management* 46:1048–1053.
- SAVARD, J.-P. L., D. BORDAGE, AND A. REED. 1998. Surf Scoter (*Melanitta perspicillata*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 363. The Birds of North America, Inc., Philadelphia, PA.
- SAVARD, J.-P. L., AND P. LAMOTHE. 1991. Distribution, abundance, and aspects of breeding ecology of Black Scoters, *Melanitta nigra*, and Surf Scoters, *Melanitta perspicillata*, in northern Quebec. *Canadian Field-Naturalist* 105:488–496.
- SMITH, C. M., R. I. GOUDIE, AND F. COOKE. 2001. Winter age ratios and the assessment of recruitment of Harlequin Ducks. *Waterbirds* 24:39–44.
- STATSOFT. 1995. *Statistica for Windows*. Version 6.1. StatSoft Inc, Tulsa, OK.
- USFWS. 1993. Status of seaducks in eastern North America. USDI Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, MD.
- VERMEER, K. 1981. Food and populations of Surf Scoters in British Columbia. *Wildfowl* 32:107–116.
- WEBSTER, M. S., P. P. MARRA, S. M. HAIG, S. BENSCH, AND R. T. HOLMES. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–82.
- ZACHARIAS, M. A., D. E. HOWES, J. R. HARPER, AND P. WAINWRIGHT. 1998. The British Columbia Marine Ecosystem Classification: rationale, development, and verification. *Coastal Management* 26:105–124.