

Components of population growth rate for White-winged Scoters in Saskatchewan, Canada

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Abstract

Components of population growth rate for White-winged Scoters in Saskatchewan, Canada.— Breeding range and abundance of White-winged Scoters (*Melanitta fusca deglandi*) have declined in northwestern North America. Hypotheses proposed to account for this trend are that survival and/or recruitment of females had declined. Thus, we used a reverse-time capture-recapture approach to directly estimate survival, seniority and capture probabilities for females of breeding age at Redberry Lake, Saskatchewan, Canada for 1975–1980 and 2000–2003. We also estimated population size of breeding females for 1975–1985 and 2000–2003 using capture-recapture data. Initially, this local population was in serious decline [95% CL ($\hat{\lambda}_{75-80}$) = 0.89 ± 0.09], but has since stabilized and may be slowly increasing [95% CL ($\hat{\lambda}_{00-03}$) = 1.07 ± 0.11]. This reversal in trajectory apparently resulted from increased recruitment rather than increased apparent survival. Importantly, recent recruitment of adult females appeared to be driven solely by immigration of adult females with no detectable *in situ* recruitment, suggesting a hypothesis that the local population is being rescued by females produced elsewhere.

Key words: *Melanitta fusca deglandii*, Population growth, Saskatchewan, Survival, Recruitment, White-winged Scoter.

Resumen

Componentes de la tasa de crecimiento poblacional en el negrón especulado de Saskatchewan, Canadá.— El rango reproductivo y la abundancia del negrón especulado (*Melanitta fusca deglandi*) han disminuido en la zona noroeste de América del Norte. La hipótesis propuesta para explicar esta tendencia es que se ha producido una disminución en la supervivencia y/o el reclutamiento de hembras. Por consiguiente, utilizamos un enfoque de captura-recaptura con el tiempo invertido para estimar directamente la supervivencia, la jerarquía y las probabilidades de captura de las hembras en edad reproductora del lago Redberry, Saskatchewan, Canadá, durante los periodos 1975–1980 y 2000–2003. También estimamos el tamaño poblacional de las hembras reproductoras durante los periodos 1975–1985 y 2000–2003, mediante el empleo de datos de captura-recaptura. En un principio, esta población local experimentó una importante disminución [95% CL ($\hat{\lambda}_{75-80}$) = 0.89 ± 0.09], pero posteriormente se estabilizó, y es posible que poco a poco vaya aumentando [95% CL ($\hat{\lambda}_{00-03}$) = 1.07 ± 0.11]. Por lo visto, la inversión de esta trayectoria se produjo como consecuencia de un mayor reclutamiento, en lugar de una mayor supervivencia aparente. Es importante destacar que el reclutamiento reciente de hembras adultas parece haber obedecido exclusivamente a la migración de hembras adultas sin un reclutamiento detectable *in situ*, lo que sugiere la hipótesis de que la población local está siendo rescatada por hembras procedentes de otros lugares.

Palabras clave: *Melanitta fusca deglandi*, Crecimiento poblacional, Saskatchewan, Supervivencia, Reclutamiento, Negrón especulado.

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Introduction

Surveys done on the breeding grounds of White-winged Scoters in northwestern North America since 1955 demonstrate declines in continental population size, as well as northward retraction of breeding range (Trost, 1998; fig. 1). The contribution of changes in survival and recruitment to such population declines remains unknown. For instance, there have only been 142 recoveries of 4,006 White-winged Scoters banded in North America from 1923 to 2001. Kremenz et al. (1997) noted that such low recovery rates led to imprecise parameter estimates using band recovery models (e.g., Brownie et al., 1985). However, Kremenz et al. (1997) were able to estimate probabilities of apparent survival, ϕ , and capture, p , for a well-defined population of female White-winged Scoters captured during nesting from 1975 to 1985 on islands in Redberry Lake, Saskatchewan (52.66° N, 107.17° W). They drew inferences about temporal dynamics of productivity from range-wide harvest data and applied those inferences to the dynamics of the population breeding locally at Redberry Lake.

Since then, there have been additional developments in the direct estimation of population growth rate using reverse-time, capture-recapture models (Pradel, 1996; Nichols et al., 2000; Nichols & Hines, 2002). These approaches also permit inference in a more tractable fashion about local components of population growth. Seniority probability, γ , is a useful metric for understanding the proportional contribution of survival to population growth rate, i.e., $\gamma = \phi / \lambda$, and is analogous to elasticity for survival (Nichols et al., 2002). Values of seniority approaching 1.0 suggest that there is very little contribution to population growth rate by recruitment. If seniority and survival probabilities are estimable, then $\hat{\lambda}$ can be estimated by substitution. Similarly, local population size, \hat{N} , can be estimated from number of captures, n , and capture probability, \hat{p} . Finally, local recruitment, \hat{f} , defined as the *per capita* addition of individuals to the local population, can be calculated from the difference in local estimates of $\hat{\lambda}$ and $\hat{\phi}$.

We analyzed the same capture histories used by Kremenz et al. (1997) to directly estimate survival, seniority and capture probabilities. We also initiated a capture-recapture study of nesting females and ducklings on the same population in 2000 because of: (1) declines in scoters over much of the continent (fig. 1); (2) availability of historical data (Kremenz et al., 1997); and (3) the location of Redberry Lake in an area of the continent with continuing declines (fig. 1). We reasoned that information gathered during 1975–1985 could serve as a useful historical benchmark for understanding current demography of the Redberry Lake population. While all of our conclusions apply to the Redberry Lake population, some of our inferences likely have range-wide relevance for North American White-winged Scoters (hereafter, scoters).

Material and methods

All scoters used in this analysis were captured during 1975–1985 or 2000–2003 on islands of Redberry Lake in the aspen parkland biome of west-central Saskatchewan, Canada. Redberry Lake is within a Migratory Bird Sanctuary, so there is no mortality of White-winged Scoters from hunting there. Scoters were captured by different sets of researchers in 1975–1980 (Brown, 1981), 1981–1983 (C. S. Houston, pers. comm.), and 1984–1985 (Kehoe, 1989). Details about 1975–1985 data representing 520 encounters of 280 nesting females were reported by Kremenz et al. (1997); their analysis of capture histories for 1981–1985 did not include captures of unmarked scoters, u_i , and only included recaptures of previously marked birds, m_i , but this nevertheless permits estimation of survival and detection probabilities. Although not used in their analyses, Kremenz et al. (1997) reported numbers of previously unmarked captures, u_i , in their table 1, from which we calculated total captures, $n_i = u_i + m_i$. Assuming equal capture probabilities of new captures and recaptures, we applied capture probabilities from 1981–1985 to n_i for respective years to estimate local population size, \hat{N}_i (see below). Data from 1975 to 1980 only were used for estimation of other vital rates (see below) before 2000–2003 field work. The 2000–2003 data represent 347 encounters of 184 nesting females. We analyzed both time series independently of one another, as there were no individuals common to both. During 1975–1985, scoters were marked only with legbands, and so reading marks required capture of females. From 2000–2003, all scoters were marked with legbands and nasal markers (Lokemoen & Sharp, 1985). Thus, the 2000–2003 dataset included captures as well as resights without capture. Hence, all inferences refer to the population of female scoters that nested on the study area during the course of the study; temporary emigrants were considered as part of the local population unless and until they permanently emigrated. We also applied plasticine-filled legbands (Blums et al., 1994), to 265 one-day-old ducklings of both sexes in 2000, 399 in 2001, 273 in 2002, and 622 in 2003.

We used Program MARK with capture-recapture/resight data to estimate probabilities of apparent survival, $\hat{\phi}_i$, capture, \hat{p}_i , and seniority, $\hat{\gamma}_{i+1}$, based on Pradel's (1996) model for survival and seniority (White & Burnham, 1999) for 1975–1980 and 2000–2003, using only adult females, i.e., those that had nested at least once. We also used the Cormack–Jolly–Seber (CJS) model to estimate \hat{p}_i for 1975–1985 data to derive estimates of population size, \hat{N}_i (see below), but used estimates of \hat{p}_i from Pradel's (1996) model mentioned above for estimation of \hat{N}_i for 2000–2003.

We used an information-theoretic approach for selection of models from a candidate set (Burnham & Anderson, 1998) using QAICc based on time dependence, (t), and time independence, (.), of

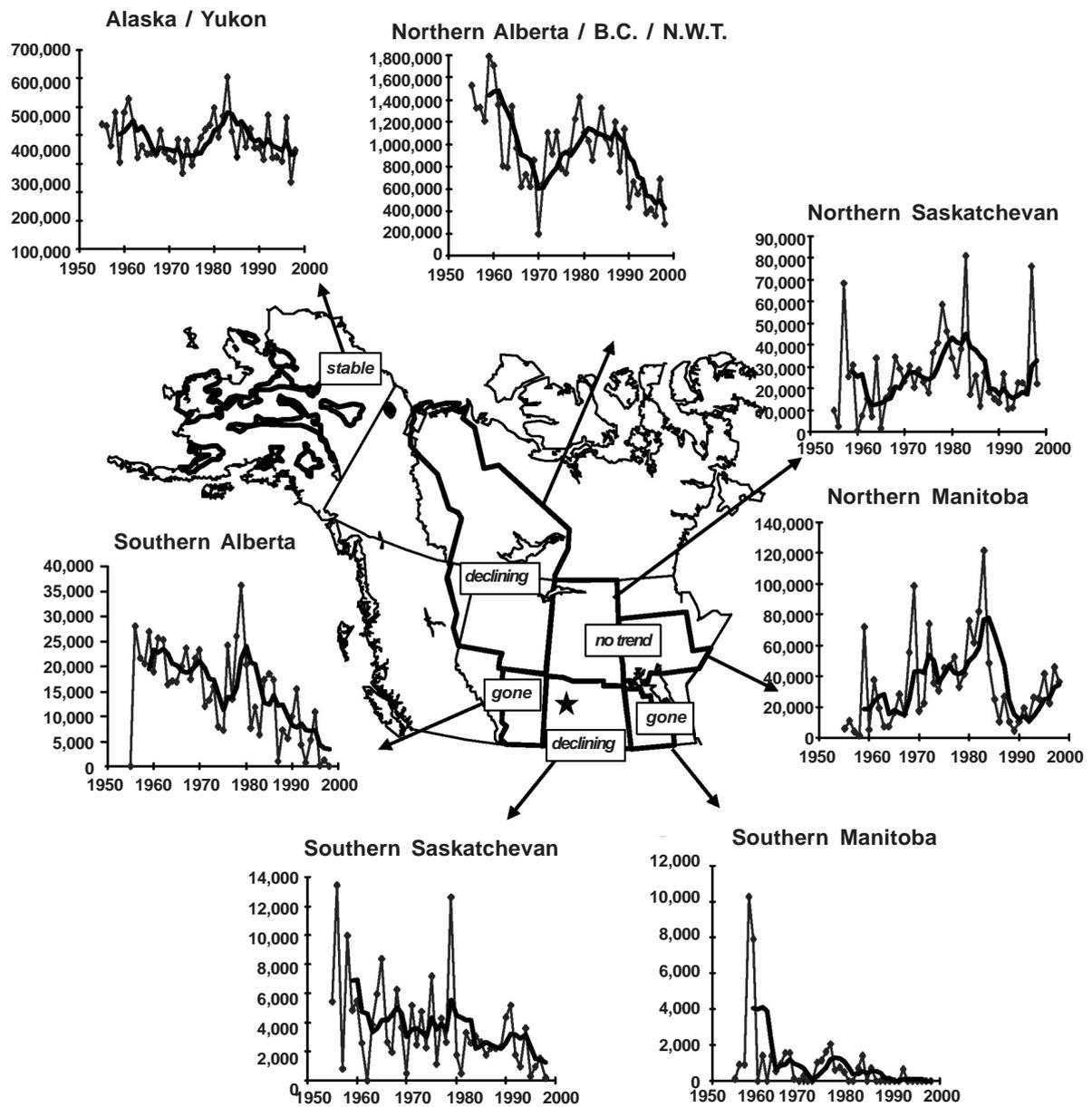


Fig. 1. Combined population estimates of White-winged (*Melanitta fusca deglandi*), Surf (*Melanitta perspicillata*), and Black (*Melanitta nigra americana*) Scoters from surveys conducted in Canada and Alaska, 1955 to 1998 (Trost, 1998). Although northern strata represent trends in all 3 species, strata in Southern Alberta, Saskatchewan and Manitoba are south of the main breeding distributions of Surf and Black Scoters, and contain mostly White-winged Scoters. Shown are annual estimates for different strata in the survey area with corresponding 5-year running averages. Approximate location of Redberry Lake, Saskatchewan, Canada, is indicated by the star.

Fig. 1. Estimaciones poblacionales combinadas del negrón especulado (*Melanitta fusca deglandi*), negrón careto (*Melanitta perspicillata*) y negrón especulado (*Melanitta nigra americana*) a partir de estudios realizados en Canadá y Alaska, entre 1955 y 1998 (Trost, 1998). Aunque los estratos del norte representan tendencias en la totalidad de las tres especies, los estratos de Alberta del Sur, Saskatchewan y Manitoba se encuentran al sur de las principales distribuciones reproductivas del negrón careto y del negrón común americano, y contienen principalmente negretas de alas blancas. Se indican las estimaciones anuales de distintos estratos del área de estudio, junto con los correspondientes promedios de cinco años consecutivos. La estrella indica el emplazamiento aproximado del lago Redberry, Saskatchewan, Canadá.

Table 1. Models for evaluating annual variation in estimates of probabilities for apparent survival (ϕ) capture (p) and seniority (γ) for female White-winged Scoters nesting at Redberry Lake, Saskatchewan, Canada, 1975–1980. Temporal variation was either constant (.), annual (t), or linear trend on a logit scale (T). Δ AICc for the best model was 1737.78 with $\hat{c}=1.0$: w. Model weight; L. Model likelihood; K. Estimable parameters; D. Deviance.

Tabla 1. Modelos para evaluar la variación anual en las estimaciones de probabilidades de supervivencia aparente (ϕ), captura (p), y experiencia (γ) para negretas de alas blancas hembras que anidaron en el lago Redberry, Saskatchewan, Canadá, entre 1975 y 1980. La variación temporal fue constante (.), anual (t), o una tendencia lineal en una escala logit (T). El Δ AICc correspondiente al mejor modelo fue 1737,78 con $\hat{c}=1,0$: w. Peso modelo; L. Modelo de probabilidad; K. Parámetros estimables; D. Desviación.

Model	Δ AICc	w	L	K	D
{ $\phi(\cdot)$ $p(t)$ $\gamma(\cdot)$ }	0.00	0.80	1.00	8	1039.39
{ $\phi(t)$ $p(t)$ $\gamma(\cdot)$ }	4.73	0.08	0.09	11	1037.84
{ $\phi(\cdot)$ $p(T)$ $\gamma(\cdot)$ }	4.74	0.07	0.09	4	1052.38
{ $\phi(\cdot)$ $p(t)$ $\gamma(t)$ }	5.69	0.05	0.06	11	1038.81
{ $\phi(t)$ $p(t)$ $\gamma(t)$ } global	10.45	0.00	0.01	14	1037.20
{ $\phi(t)$ $p(\cdot)$ $\gamma(t)$ }	19.71	0.00	0.00	11	1052.83
{ $\phi(\cdot)$ $p(\cdot)$ $\gamma(t)$ }	21.28	0.00	0.00	7	1062.75
{ $\phi(\cdot)$ $p(\cdot)$ $\gamma(\cdot)$ }	30.20	0.00	0.00	3	1079.87
{ $\phi(t)$ $p(\cdot)$ $\gamma(\cdot)$ }	32.35	0.00	0.00	7	1073.82

each of the parameters. A linear time trend (T) was considered for \hat{p}_i estimated from Pradel's (1996) model for both 1975–1980 and 2000–2003 data, because we reasoned that capture efficiency by field researchers may have improved with increased experience at finding and capturing nesting scoters even over only 4–6 years.

We adjusted for goodness-of-fit by calculating variance inflation factors, \hat{c} , for estimates of $\hat{\phi}_i$ and \hat{p}_i from CJS models with 1975–1985 data by performing 100 bootstrap simulations of expected deviance for the global model (White & Burnham, 1999); the quotient of observed deviance/simulated deviance for the global model was $\hat{c} = 1.1168$. Similarly, we calculated \hat{c} from 1975–1980 and 2000–2003 data sets used for variance estimation of $\hat{\phi}_i$, \hat{p}_i and $\hat{\gamma}_{i+1}$ by performing bootstrap simulation on respective global models using forward capture histories $\{\phi(t) p(t)\}$, and applied respective adjustments to variance in estimates from Pradel's (1996) models: $\hat{c}_{75-80} = 1.0$, $\hat{c}_{75-85} = 1.1168$, and $\hat{c}_{00-03} = 1.2457$. Hence, we used AICc for model selection involving 1975–1980 data, but applied the corresponding variance inflation factor for calculation of QAICc and adjustment of variance in parameter estimates for 2000–2003 data.

Direct estimates of $\hat{\phi}_i$, \hat{p}_i , and $\hat{\gamma}_i$ were used to calculate derived estimates, \hat{N}_i and $\hat{\lambda}_i$. We estimated population size in year i as

$$\hat{N}_i = \frac{n_i}{\hat{p}_i}$$

where n_i equals the number of scoters captured in year i , and

$$v\hat{a}r(\hat{N}_i) = \frac{n_i(1 - \hat{p}_i)}{\hat{p}_i^2} + \left(\frac{n_i^2}{\hat{p}_i^4} \right) v\hat{a}r(\hat{p}_i)$$

is the associated approximate variance suggested by Williams et al. (2002: 503). We estimated population growth rate in year i as a parameter derived by Program MARK, i.e.,

$$\hat{\lambda}_i = \frac{\hat{\phi}_i}{\hat{\gamma}_{i+1}}$$

We estimated recruitment probability, \hat{f}_i , ourselves as

$$\hat{f}_i = \hat{\lambda}_i - \hat{\phi}_i$$

and the complement to seniority, $\hat{\gamma}_i$ referred to as entry probability, is the proportional contribution of recruitment to population growth rate related to these as

$$(1 - \hat{\gamma}_{i+1}) = \frac{\hat{f}_i}{\hat{\lambda}_i}$$

(Nichols et al., 2000).

Approximate 95% confidence limits for derived parameters ($\hat{\theta}$) were constructed as

$$\hat{\theta} \pm 1.96 \sqrt{v\hat{a}r(\hat{\theta})}$$

Table 2. Models for evaluating temporal variation in estimates of probabilities for apparent survival (ϕ), capture (p), and seniority (γ), for female White-winged Scoters nesting at Redberry Lake, Saskatchewan, Canada, 2000–2003. Temporal variation was either constant (\cdot), annual (t), or linear trend on a logit scale (T). Δ QAICc for the best model was 703.49 with $\hat{c} = 1.2457$: w . Model weight; L . Model likelihood; K . Estimable parameters; QD . Quasi deviance.

Tabla 2. Modelos para evaluar la variación temporal en las estimaciones de probabilidades de supervivencia aparente (ϕ), captura (p), y experiencia (γ), para negrones especulares que anidaron en el lago Redberry, Saskatchewan, Canadá, entre 2000 y 2003. La variación temporal fue constante (\cdot), anual (t), o una tendencia lineal en una escala logit (T). El Δ QAIC correspondiente al mejor modelo fue 703,49 con $\hat{c} = 1.2457$: w . Modelo de peso; L . Modelo de probabilidad; K . Parámetros estimables; QD . Quasi desviación.

Model	Δ QAICc	w	L	K	QD
$\{\phi(\cdot) p(T) \gamma(\cdot)\}$	0.00	0.36	1.00	4	408.707
$\{\phi(\cdot) p(t) \gamma(\cdot)\}$	0.86	0.23	0.65	6	405.436
$\{\phi(t) p(\cdot) \gamma(t)\}$	1.43	0.17	0.49	6	406.004
$\{\phi(t) p(t) \gamma(\cdot)\}$	2.66	0.09	0.26	7	405.156
$\{\phi(\cdot) p(t) \gamma(t)\}$	2.79	0.09	0.25	7	405.287
$\{\phi(t) p(t) \gamma(t)\}$ global	4.66	0.03	0.10	8	405.056
$\{\phi(\cdot) p(\cdot) \gamma(t)\}$	6.27	0.02	0.04	5	412.922
$\{\phi(t) p(\cdot) \gamma(\cdot)\}$	9.09	0.00	0.01	4	417.799
$\{\phi(\cdot) p(\cdot) \gamma(\cdot)\}$	12.06	0.00	0.00	3	422.812

Results

Of 4 CJS models considered for 1975–1985 data, $\{\phi(\cdot) p(t)\}$ had $w = 0.997$, so we estimated \hat{N}_i using numbers of scoters captured, n_p , and capture probability, \hat{p}_i , in turn estimated from this model. Numbers captured or resighted, n_r , were highly variable, ranging from only 2 to 114/yr during 1975–1985, but increasing from 47 to 127 during 2000–2003. Most annual variation in n_i (fig. 2A) appeared to be strongly related to capture probability (fig. 2B).

We considered the same 9 candidate Pradel models for analysis of 1975–1980 (table 1) and 2000–2003 data (table 2). There was very little uncertainty about the best model $\{\phi(\cdot) p(t) \gamma(\cdot)\}$ for 1975–1980 data with model weight, $w = 0.80$. There was less certainty for 2000–2003 data, but the two best models were merely variants of temporal variation in \hat{p}_i (table 2), with cumulative $w = 0.59$. Hence we used the best models from analysis of each time series for parameter estimation (table 3).

On a logit scale, slope between capture probability and year for 1975–80 was 0.44 ± 0.16 (95% CL) estimated from $\{\phi(\cdot) p(T) \gamma(\cdot)\}$, and 0.73 ± 0.34 for 2000–03 estimated from $\{\phi(\cdot) p(T) \gamma(\cdot)\}$. These results support the notion of increased efficiency of capture with experience by respective teams of researchers during 1975–1980 (Brown, 1981) and 2000–2003 (this study).

Estimated population size of females that had bred at least once showed a strong decline from ~450 in 1975 to ~100 in 1985 (fig. 2). There was no evidence of substantial recovery between 1985 and 2000–2003 as shown by overlapping 95% CL (\hat{N}) for these years. Most recent estimates of population size remained below estimates from 1975–1979.

Annual rate of population change for 1975–1980 indicated a population decline with 95% CL ($\hat{\lambda}$) < 1 (table 3). Most recently, $\hat{\lambda}$ suggests absolute population growth with 95% CL ($\hat{\lambda}$) non-overlapping with those for 1975–1980, but with inclusion of unity. The 20% increase in $\hat{\lambda}$ between 1975–1980 and 2000–2003 was accounted for more by a 92% increase in recruitment, than it was by a 9% increase in survival probability (fig. 3). Apparent survival was constant in each time series, but had increased from 1975–1980 to 2000–2003; however 95%CL($\hat{\phi}$) overlapped between the two time series (table 3, fig. 3). During 1975–1985, survival probability constituted a higher proportion of $\hat{\lambda}$ for which upper 95% CL ($\hat{\gamma}_i$) < 1.0 (table 3, fig. 3). When the population was declining in 1975–1980, only ~0.12 new females, on average, entered the breeding population each year for every female that had bred the previous year at Redberry Lake; the annual recruitment rate of breeding females had almost doubled by 2000–2003 (table 3).

We marked 1559 male and female ducklings marked with permanent plasticine bands during 2000–2003, but could only have recaptured the females because our sampling did not include males. However, no females had been recaptured up to 3 years later. Thus, contrary to expectation, all recruitment at Redberry Lake apparently was through immigration of adults from elsewhere, or possibly of some unmarked ducklings > 4-years-old hatched at Redberry Lake before 2000.

Discussion

Our retrospective analysis indicated that the population of White-winged Scoters nesting at Redberry Lake was in serious decline during 1975–1985, shrinking from at least 283 [i.e., lower 95% (\hat{N}_{1975})] females to, at most, 136 [upper 95% (\hat{N}_{1985})] females capable of breeding (fig. 2C). Since then, findings from our own mark-recapture study during 2000–2003 suggested that the population had increased somewhat, and most recently was at least stable or continuing to increase slowly. Precision of some of our recent estimates was poor compared to 1975–1985, but we anticipate that this will improve with additional years of study.

The acute local population decline during 1975–1985 was accompanied by stable survival rates (table 3, fig. 3), as also found by Kremetz et al. (1997). The striking change in population trajectory between 1975–1985 and 2000–2003 was largely the result of improved recruitment, although estimates of apparent survival of female scoters that had bred at least once had also increased from 0.77 to 0.84. Vital rates that contribute to in situ recruitment include age of first reproduction, breeding propensity, clutch size, nest success, duckling survival, annual survival after fledging before breeding age, and duckling philopatry. Additionally, immigration rate, ψ_{i+1} (expressed as the ratio of immigrants in year $i+1$, I_{i+1} , to adults from the previous year, N_i), added to in situ recruitment equals total recruitment. We have not yet estimated breeding probability, which may have declined. However, Traylor et al. (in press) found that White-winged Scoters at Redberry Lake nested later in 2000–2001 and had protracted nesting of 41 days between nest initiation and hatch, compared to 1977–1980 when mean nesting duration was 36–39 days. They suggested that later and protracted nesting may have resulted from poor nutrition of breeding females which may impinge on their ability to successfully complete incubation and to raise offspring. Nest success and egg hatchability in 2000–2001 (Traylor et al., 2004) was comparable to that estimated by Brown (1981). However, Traylor (2003) estimated that 95% CL ($\hat{S}_{\text{duckling}}$) was only 0.016 ± 0.015 and 0.021 ± 0.021 in 2000 and 2001, respectively, for the first 28 days after hatch at Redberry Lake; to our knowledge, these are the lowest estimates ever published for any North American duck species.

Our findings are consistent with Traylor's (2003) and indicate that improved recruitment during 2000–2003 was not the result of in situ production of ducklings. White-winged Scoter females are physiologically capable of nesting as 2-year-olds; of 1,740 ducklings marked with webtags over 4 years (1977–1980) by Brown (1981), 3 were detected nesting at Redberry Lake as 2-year-olds, and 7 as 3 years olds. We marked a comparable number of 1,559 ducklings over the same number of years (2000–2003). Despite (1) our use of more permanent plasticine-filled legbands (Blums et al., 1994) compared to webtags with lower retention used by Brown (1981), and (2) generally higher capture probabilities in 2000–2003 compared to 1977–1980 (fig. 2B), we had not detected any as breeding adults originally marked as ducklings. Although probability of duckling survival to 28 days of age was very low at Redberry Lake in 2000–2001 (Traylor, 2003), the discrepancy in return rates between 1975–1985 and 2000–2003 may also have resulted from delays in age of first nesting. If some recruitment during 2000–2003 resulted from in situ production of ducklings, these could only have been produced before 2000 and so would be at least 4-years-old. If true, then age of first reproduction may have increased in this population. Permanent emigration of ducklings from Redberry Lake may have increased recently. However, we suspect that low survival rate of ducklings is the most important factor behind low in situ production and, instead, recruitment into the Redberry Lake population appeared to be entirely from immigration of adults produced elsewhere.

While the scope of our inferences is most pertinent to the Redberry Lake population, we also suggest that attention be focused on ecological factors that influence recruitment to better understand dynamics of White-winged Scoter populations in southern Saskatchewan. Estimates of apparent survival provide a minimal estimate of true survival, and may be representative continentally. If true, our results suggest that long-term changes in survival played only a minimal role, at best, in declines in Prairie Canada and possibly in the boreal forest (fig. 1). Kehoe (1994) suggested that disappearance of White-winged Scoters from some historic breeding sites may have been related to local harvest pressure, although this seems unlikely for widespread declines that have occurred until recently. There is no hunting on Redberry Lake, a migratory bird sanctuary, so local harvest pressure was not a factor during this study. Afton & Anderson (2001) similarly suggested that harvest likely was not related to recent continental declines in Greater (*Aythya marila*) and Lesser (*A. affinis*) Scaup.

White-winged Scoters (Dobush, 1986) and waterfowl in general (Alisauskas & Ankney, 1992) rely on nutrient reserves, often stored great distances from nesting areas, for use during breeding. Annual variation in levels of prebreeding nutrient reserves can influence continental production

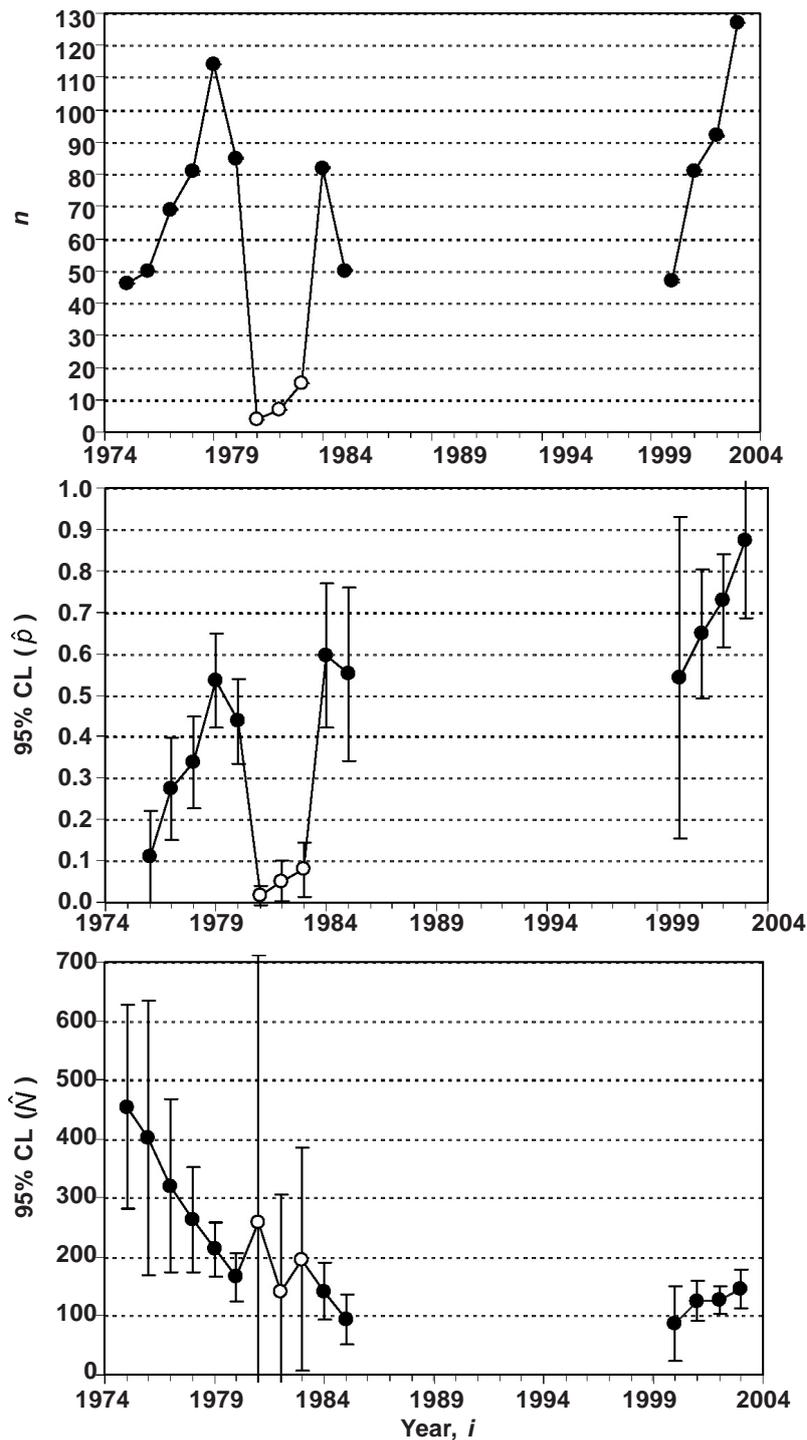


Fig. 2. A. Numbers of nesting scoters captured or sighted, n ; B. Detection probabilities, 95% CL (\hat{p}_i); and C. Annual estimates of population size, 95% CL (\hat{N}_i), for female White-winged Scoters nesting at Redberry Lake, Saskatchewan, 1975–1985 and 2000–2003. Open circles denote numbers of annual captures, n_i , range 4–15, otherwise closed circles denote $n_i > 45$.

Fig. 2. A. Número de negrones comunes anidados que fueron capturados o avistados, n ; B. Probabilidades de detección, 95% CL (\hat{p}_i); C. Estimaciones anuales del tamaño poblacional, 95% CL (\hat{N}_i), para los negrones especulares que anidaron en el lago Redberry, Saskatchewan, entre 1975 y 1985, y entre 2000 y 2003. Los círculos blancos indican el número de capturas anuales, n_i , rango 4–15, mientras que los círculos negros indican $n_i > 45$.

of young waterfowl subsequent to the storage of such reserves (Alisauskas, 2002). Several hypotheses related to the connection between events during winter or spring migration and subsequent recruitment have been proposed to explain the decline in population estimates of scoters and other duck species nesting in the boreal forest and prairie biomes of northwestern North America. For example, Afton & Anderson (2001) suggested that declines in estimates of continental scaup (*Aythya* spp.) populations may stem from females arriving on breeding areas with lower nutritional reserves than in the past, possibly due to diminished food resources. As noted above, Traylor et al. (2004) speculated that depleted body reserves may have protracted incubation duration, thereby delaying hatch date in scoters at Redberry Lake. A general delay in nesting often lowers nest success in waterfowl (Flint & Grand, 1996) reducing the number of recruits to local populations (Dzus & Clark, 1998; Blums et al., 2002).

Large-scale changes (i.e., degradation) in quality of nesting habitat, and human alteration of lakes used by breeding waterfowl through development for recreational use or agriculture may have affected recruitment (Turner et al., 1987). Agriculture, commercial forestry, and mineral extraction may favor increased abundance and foraging efficiency of generalist predators (Krasowski & Nudds, 1986; Turner et al., 1987). The main predators of ducklings at Redberry Lake were California (*Larus californicus*) and Ring-billed (*L. delawarensis*) Gulls (Traylor, 2003). Thus, increased predation pressure from growing populations of gulls, in response to the growth in size and number of garbage dumps associated with human activity, may impinge directly on recruitment of White-winged Scoters.

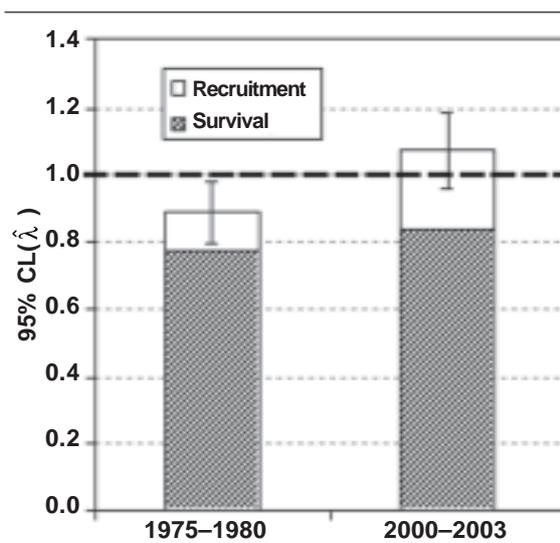


Fig. 3. Estimates of annual rate of population change, 95% CL ($\hat{\lambda}_t$), for female White-winged Scoters breeding at Redberry Lake, Saskatchewan, Canada, 1975–1985 and 2000–2003. Also shown are estimates of survival ($\hat{\phi}_t$) and recruitment (\hat{f}_t) the components of $\hat{\lambda}_t$.

Fig. 3. Estimaciones de la tasa anual de cambio poblacional, 95%CL ($\hat{\lambda}_t$) correspondientes al nedrón especular que se reprodujeron en el lago Redberry, Saskatchewan, Canadá, entre 1975 y 1985, y entre 2000 y 2003. También se indican las estimaciones de supervivencia ($\hat{\phi}_t$) y el reclutamiento (\hat{f}_t) así como los componentes de $\hat{\lambda}_t$.

Table 3. Ninety-five % confidence limits of estimates of population parameters for female White-winged Scoters nesting at Redberry Lake, Saskatchewan, Canada, 1975–1980 and 2000–2003. Estimates shown are from the best of Pradel's (1996) models considered from separate analysis of 1975–1980 data $\{\phi(\cdot) p(t) \gamma(\cdot)\}$ and 2000–2003 data $\{\phi(\cdot) p(T) \gamma(\cdot)\}$: $\hat{\phi}$. Apparent survival; $\hat{\gamma}$. Seniority; $\hat{\lambda}$. Annual rate of population change; \hat{f} . Recruitment; $(1-\hat{\gamma})$. Entry.

Tabla 3. Límites de intervalos de confianza del 95% en las estimaciones de parámetros poblacionales para los negrones especulares que anidaron en el lago Redberry, Saskatchewan, Canadá, entre 1975 y 1980, y 2000 y 2003. Las estimaciones indicadas corresponden al mejor de los modelos de Pradel (1996) considerados en análisis independientes de datos obtenidos entre 1975 y 1980 $\{\phi(\cdot) p(t) \gamma(\cdot)\}$ y entre 2000 y 2003 $\{\phi(\cdot) p(T) \gamma(\cdot)\}$: $\hat{\phi}$. Supervivencia aparente; $\hat{\gamma}$. Precedencia; $\hat{\lambda}$. Tasa anual de cambio poblacional; \hat{f} . Reclutamiento; $(1-\hat{\gamma})$. Entrada.

Year	$\hat{\phi}$	$\hat{\gamma}$	$\hat{\lambda}$	\hat{f}	$(1-\hat{\gamma})$
1975–1980	0.77 ± 0.08	0.87 ± 0.09	0.89 ± 0.09	0.12	0.13 ± 0.09
2000–2003	0.84 ± 0.07	0.78 ± 0.09	1.07 ± 0.11	0.23	0.22 ± 0.09

Heavy metals acquired on winter or migration areas (White & Finley, 1978) and subsequent biomagnification of other contaminants (Di Giulio & Scanlon, 1984) may disrupt reproductive potential by reducing breeding propensity, egg size, egg hatchability, clutch size, and/or duckling survival. Contaminants also reduce adult survival (DeKock & Bowmer, 1993; Perkins & Barclay, 1997), although this has never been tested directly in free-ranging waterfowl, in either a design-based (i.e., experimental) or model-based fashion other than by Grand et al. (1998) to our knowledge. Thus, identification of wintering/migration areas of breeding females and associated levels of contaminants may provide further insights on reduced breeding success and survival of scoter nests and ducklings.

Changing food resources, varying harvest pressures and contaminants on wintering areas all have potential to limit reproductive success and local recruitment on breeding areas in a multifactorial fashion. As events on these areas are not mutually exclusive, it is important to link breeding and wintering areas to address conservation issues and to understand factors that influence population dynamics. Consequently, we have expanded our research scope with a view toward a better understanding of ecological processes behind variation in survival and recruitment in White-winged Scoters. In conjunction with continued mark-recapture of nesting females, our objectives have expanded to include development of methodology based on stable isotope analyses for assigning breeding females from this population to winter areas, as was done successfully for King Eiders (*Somateria spectabilis*; Mehl et al., in press). As well, we have taken blood samples during 2001–2003 to evaluate concentrations of Cadmium, Mercury, Lead and Selenium on annual survival and on components of recruitment. Linkage of individuals nesting at Redberry Lake to respective wintering areas may uncover differences in contaminant loads, nest success, and egg hatchability in relation to winter origin, and identify areas responsible for limiting recruitment. Inferences from those findings could have relevance to much of the continental population.

Finally, as have others (e.g., Nichols, 1992; Anderson, 2001), we caution against drawing inferences about population change strictly from counts or number of animal captures. Numbers of White-winged Scoters captured annually (fig. 2A) increased regardless of whether the local population was in a precipitous decline ($\hat{\lambda} \approx 0.89$) during 1975–1980, or was increasing ($\hat{\lambda} \approx 1.07$) during 2000–2003 (fig. 2C). Instead, annual number of captures was related largely to increasing capture efficiency of field researchers in each phase of study (fig. 2B). Inferences about size or dynamics of free-ranging populations should be based on methods that account for variation in capture or detection probabilities, and that provide unbiased estimates. This seems particularly critical in situations for which there may be great conservation concerns.

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