Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

C S A S

Canadian Science Advisory Secretariat

S C C S

Secrétariat canadien de consultation scientifique

Research Document 2005/067

Document de recherche 2005/067

Not to be cited without
permission of the authors *

Ne pas citer sans
autorisation des auteurs *

Estimation of grey seal population size and trends at Sable Island

Estimation de la taille et des tendances de la population de phoque gris de l'île de Sable

M. Kurtis Trzcinski, Robert Mohn and W. Don Bowen

Population Ecology Division
Bedford Institute of Oceanography
P.O. Box 1006
Dartmouth, N.S.
B2Y 4A2

ISSN 1499-3848 (Printed / Imprimé)

Canada

ABSTRACT

An age-structured population model with density-dependence parameterized using a theta-logistic function was used to estimate population size of grey seals at Sable Island through 2004 based on estimates of pup production, juvenile and adult survival and age-specific fecundity. The model incorporates parameter uncertainty in two ways. Estimates of pup mortality and population size at Sable Island were obtained by minimizing an objective function that is the sum of the negative log likelihoods for the pup count data assuming lognormal error structures which was carried forward to our final estimates. Birth rates and adult mortality rates were taken from other studies and uncertainty in these parameters was incorporated by adding the negative log of the probability density function to the objective function. In 2004, population size ranged between 208,720 (SE = 29,730) and 223,220 (17,376) depending on assumptions about carrying capacity and the strength of density dependence.

RÉSUMÉ

On s’est servi d’un modèle de population structuré par âge avec une dépendance à la densité paramétrée à l’aide d’une fonction logistique thêta pour estimer la taille de la population de phoques gris à l’île de Sable tout au long de 2004 d’après les estimations de la production de nouveau-nés, de la survie des jeunes et des adultes et de la fécondité selon l’âge. Le modèle incorpore l’incertitude des paramètres de deux façons. On a tout d’abord établi des estimations de la mortalité chez les nouveau-nés et de la taille de population de l’île de Sable par une réduction de la fonction objective, c’est-à-dire la somme des logarithmes négatifs du rapport de vraisemblance pour les dénombrements de nouveau-nés, en supposant des structures d’erreur lognormales, qui a été reportée à nos estimations finales. On a ensuite utilisé des taux de natalité et des taux de mortalité chez les adultes provenant d’autres études, et l’incertitude reliée à ces paramètres a été incorporée par l’ajout du logarithme négatif de la fonction de densité à la fonction objective. En 2004, la taille de la population a oscillé entre 208 720 (erreur-type = 29 730) et 223 220 individus (17 376), selon les hypothèses retenues au sujet de la capacité biotique et de la force de la dépendance à la densité.

INTRODUCTION

Contrary to the widespread declines of many marine predators, grey seals (*Halichoerus grypus*) have increased in eastern Canada. Grey seals are large (adults 100-350 kg), wide-ranging predators that exhibit marked seasonal changes in distribution and foraging effort (Austin et al. 2001; Beck et al. 2003). They are generalists, feeding on a wide range of pelagic and demersal fishes, including Atlantic cod (Bowen et al. 1993, Bowen et al. in press). Most grey seals are born at colonies located in the southern Gulf of St. Lawrence and on Sable Island located on the Eastern Scotian Shelf (ESS), but newer and smaller colonies are located along the eastern shore of Nova Scotia and at several sites in the north-eastern United States (Mansfield and Beck, 1977; Hammill et al., 1998; Waring et al. 1999). The population breeding on Sable Island, the largest colony, located on the Eastern Scotian Shelf has been a striking example of the exponential increase of a long-living marine mammal having increased at a rate of 12.8% annually for more than 40 years (Bowen et al. 2003).

Recently, the Canadian Department of Fisheries and Oceans approved a quota of 10,000 grey seals that could be taken over a 2-yr period from coastal sites along the eastern shore of Nova Scotia. The estimate of pup production in 2004 on Sable Island (Bowen et al. submitted) and the larger coastal colonies (Hammill et al. 2005) provides the bases for updating estimates of population size for the Scotian Shelf component of the grey seal population in Eastern Canada. The 2004 estimate of population size forms the basis for the estimate of N_{min} used to estimate the annual Potential Biological Removal from the Scotian Shelf component. Wade (1998) defined N_{min} as the 20th percentile of the log-normal distribution of population abundance.

METHODS

Estimating grey seal abundance

As in Mohn and Bowen (1996), we estimated population trends on Sable Island separately from other Canadian colonies. The pup production of grey seals on Sable Island was estimated from 1962 to 1990 for most years based on tagging all weaned pups (Mansfield and Beck 1977, Stobo and Zwanenburg 1990). High population abundance in recent years required that pup production be estimated from aerial photography (Bowen et al. 2003), with the most recent estimate for the spring of 2004 (Bowen et al. submitted). Pup production along the eastern shore of Nova Scotia, the other components of the Scotian Shelf population, was determined by visual counts or year-class tagging (Hammill 2005). However, only estimates of pup production on Sable Island were used to generate an estimate of total population size in the model described below.

Previously, a simple exponential population model was fit to the data on pup production (Mohn and Bowen 1996, Bowen et al. 2003), however, the Sable population appears to have started to show evidence of density dependence. This conclusion is based on two sources of information. First, the age of first reproduction has increased from 4 to 5 yr, and second, the upper 95% confidence interval for pup production in

2004 is well below the lower confidence interval predicted from the exponential model (Bowen et al. submitted). Consequently, we parameterized a theta-logistic model using several assumptions about the strength and timing of density dependence and the level of carrying capacity.

We denoted the total number of seals as $N_{t,a,s}$, where the subscript t indexes the year, a age, and s sex. In our model, age-0 refers to pups in their first year of life (birth to January 1st the following year). Males ages 1 to 9 yr and females ages 1 to 5 yr were considered as juveniles, even though some females can give birth as early as age 4. Males older than 9 yr and females older than 5 yr were referred to as adults. We distinguished between mortality at different life stages using superscripts (e.g. M^{Pup}), and use subscripts to denote rates for different sex or age classes. Mohn and Bowen (1996) argued that mortality rates should be different for males and females based on their differences in longevity, however there is little data which can be used to evaluate this assumption. Consequently, we fixed the mortality rates of juveniles, adult males and females at the values guided by Mohn and Bowen (1996), Schwarz and Stobo (2000), Manske et al. (2002), and Hall et al. (2002). Schwarz and Stobo (2000) noted that their estimates of adult female survival (0.92) was probably biased low, while Manske et al. (2002) indicated that their estimate of adult male survival (0.97) was probably biased high. We split the difference and assumed that adult survival for male and females was 0.95 which corresponds to an instantaneous mortality of 0.05 with Schwarz and Stobo`s (2000) estimate of variance. Juveniles were assumed to have the same mortality as adults. The rates concur with observations that males and females often live to their mid 30's, while a few survive into their early 40's.

Reviews of population dynamics in large mammals indicate that one of the first signs of density dependence is a decrease in juvenile survival (Fowler 1987). It is at this stage that we model density dependence in the Sable population with the theta-logistic function. We assume that all other natural mortality rates were instantaneous, density-independent and constant over our study period. Given the observed exponential rate of increase of pup production in the Sable population over the period from 1976 to 1997 these assumptions seem warranted (Bowen et al. 2003), but will need to be modified as the population approaches carrying capacity. The age-specific birth rate b_a, was based on pregnancy rates reported in Zwanenburg and Bowen (1990) and Hammill and Gosselin (1995), and we assumed a 1:1 sex ratio at birth (Bowen unpublished data).

The number of pups produced in the next year, $P_{t+1,s}$, is the sum of the number of females, $N_{t,a,f}$, times the age-specific pregnancy rate b_a.

$$P_{t+1,s} = 0.5 \left(\sum_a N_{t,a,\mathrm{f}} b_a \right) \quad . \tag{1}$$

The survival of pups to the next year in the Sable population is given by

$$J_{t+1,1,s} = P_{t,s} e^{-M^{\text{Pup}}} \left[1 - \left(\frac{N_t}{K} \right)^{\theta} \right], \tag{2}$$

where *N* is total population size, *K* is carrying capacity, and *θ* is the degree of density dependence. Further survival (juvenile males ages 1 to 9, females ages 1 to 5 yr) in the Sable population is given by

$$J_{t+1,a,s} = J_{t,a,s} e^{-M} \left[1 - \left(\frac{N_t}{K} \right)^{\theta} \right], \tag{3}$$

where M is the mortality rate taken from Schwarz and Stobo (2000), and Manske et al. (2002). The degree of density dependence in grey seals is unknown, however Harting (2002, p. 101) argued that *θ* for marine mammals should be around 2.4, which he found support for in monk (*Monachus schauinslandi*) and fur seals (Taylor and DeMaster 1993). However, theta is unknown for grey seals. We explored this uncertainty by running our model at three different levels of theta. Since carrying capacity can not be estimated without more data, we varied *K* until the 2004 model estimate of pup production fell within the confidence interval of the 2004 aerial survey estimate. We did not allow adults to survive beyond age 39. Adult survival (males ages >9, female ages >5) is given by

$$A_{t+1,a+1,s} = \begin{Bmatrix} J_{t,a,s} e^{-M} \\ A_{t,a,s} e^{-M} \end{Bmatrix}. \tag{4}$$

Total population size is given by

$$N_t = \sum_{a,s} P_{t,s} + \sum_{a,s} J_{t,a,s} + \sum_{a,s} A_{t,a,s} \ . \tag{5}$$

Estimates of the number of pups in 1962 (intercept) and pup mortality were obtained by minimizing an objective function that is the sum of the negative log likelihoods for the pup count data (Quinn and Deriso 1999). We used lognormal error structures for all likelihoods.

The model incorporates parameter uncertainty in two ways. The variance of the number of pups in 1962 and pup mortality were estimated directly from the pup count data and carried through the model. However, birth rates and the mortality of juveniles and adults were taken from other studies (Table 1). For the age specific birth rates, the probability density function was calculated and converted into a negative log likelihood. These likelihoods were added to the objective function and acted as penalty functions (Breen et al. 2003). Variances were carried through the model and are reflected as uncertainty in the final estimates of grey seal population size.

RESULTS

Grey seals have continued to increase on Sable Island, but the 2004 estimate of pup production indicates that the rate of population increase has slowed (Bowen et al. 2005, Fig. 1). Estimates of pup mortality in 1962 (i.e., at the beginning of the time series), and population size and N_{min} in 2004 under three different assumptions of theta are presented in Table 2. The carrying capacity of the Sable Island population was estimated to be between 430,000 and 850,000 grey seals, depending on the density-dependent parameter, θ (Fig. 2).

Increasing age of first reproduction of females from 4 to 5 yr, did not have a significant effect on our model estimates causing only a 1% change in our estimate of population size.

DISCUSSION

Our estimate of Sable Island population size is dependent on several factors. The first level of uncertainty is whether density dependence is incorporated. The upper 95% confidence interval for pup production in 2004 is lower than predicted from the exponential model (Bowen et al. submitted). This result along with an increase in a female's age of first reproduction from 4 to 5 yr, strongly suggests that the rate of population growth is slowing. Therefore, we no longer consider the model of exponential increase viable. However, it is also impossible to fully parameterize the theta-logistic model without future estimates of pup production. Thus, the next survey will be particularly informative and we suggest that 2007 would be the earliest practical year.

Our method of taking theta from the literature and varying carrying capacity is a first-order approximation of future grey seal population dynamics. However, we stress that currently there is much uncertainty in our estimate of theta and carrying capacity, and this can only be remedied by adding additional estimates of pup production and estimating changes in vital rates. Research on vital rates is important because density dependent changes in mortality and fecundity have quite different implications for estimated total population size. For example, a decline in age-specific fecundity for a given level of pup production implies a larger adult female and thus total population size.

Although pup production trend data exists from the early 1960's, the Sable Island population should be considered 'data poor' because of the inability to parameterize population models with more complex dynamics. Estimated population size was relatively insensitive to our assumptions about the values of theta and carrying capacity, but N_{min} quite sensitive to those assumptions and the uncertainly in mortality rates used in the model. The more conservative estimate of total population size on Sable Island produced from the theta-logistic model also lowers the estimate of N_{min} which in turn will lower the estimate of Potential Biological Removal. Our uncertainty in population size increases the further we project from the 2004 estimate of pup production. Harvest strategies should take this uncertainty into account reducing their impact as time elapses.

ACKNOWLEDGEMENTS

This work would not have been possible without the foresight and work of those studying grey seals since the 1960's to whom we are greatly indebted. We thank M. Hammill, for sharing data, J. Gibson for modeling advice.

LITERATURE CITED

Austin, D., W. D. Bowen, and J. I. McMillan. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos **105**:15-30.

Beck, C. A., W. D. Bowen, J. I. McMillan, and S. J. Iverson. 2003. Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. Journal of Animal Ecology **72**:979-993.

Bowen, W. D., J. I. McMillan, W. Blanchard. submitted. Pup production and age of primiparity indicated reduced rate of population increase of grey seals at Sable Island. Marine Mammal Science.

Bowen, W. D., C. A. Beck, S. J. Iverson, D. Austin, and J. I. McMillan. in press. Linking predator foraging behaviour and diet with variability in continental shelf ecosystems: grey seals of eastern Canada. *in* I. L. Boyd and S. Wanless, editors. Management of Marine Ecosystems: Monitoring changes in upper trophic levels. The Zoological Society of London, London, UK.

Bowen, W. D., J. W. Lawson, and B. Beck. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian shelf. Canadian Journal of Fisheries and Aquatic Sciences **50**:1768-1778.

Bowen, W. D., J. I. McMillan, and R. Mohn. 2003. Sustained exponential population growth of the grey seal on Sable Island. ICES Journal of Marine Science **60**:1265-1374.

Breen, P. A., R. Hilborn, M. N. Maunder, and S. W. Kim. 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). Canadian Journal of Fisheries and Aquatic Sciences **60**:527-541.

Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Current Mammalogy **1**:401-441.

Hall, A. J., B. J. McConnell, and R. J. Barker. 2002. The effect of total immunoglobulin levels, mass and condition on the first-year survival of grey seal pups. Functional Ecology **16**:462-474.

Hammill, M.O. 2005. Abundance of Northwest Atlantic grey seals in the Gulf of St. Lawrence and along the Nova Scotia Eastern Shore. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/036.

Hammill, M. O., and J. F. Gosselin. 1995. Grey seal (*Halichoerus grypus*) from the Northwest Atlantic: female reproductive rates, age at first birth, and age of maturity of males. Canadian Journal of Fisheries and Aquatic Sciences **52**:2757-2761.

Hammill, M. O., G. B. Stenson, R. A. Myers, and W. T. Stobo. 1998. Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences **55**:423-430.

Harting, A. L. 2002. Stochastic simulations model for the Hawaiian monk seal. PhD Thesis. Montana State University.

Mansfield, A.W. and Beck, B. 1977. The grey seal in eastern Canada. Fish. Mar. Ser. Tech. Rep. **704**: 1-81.

Manske, M., W. T. Stobo, and C. J. Schwarz. 2002. Estimation of age-specific probabilities of first return and annual survival rates for the male grey seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. Marine Mammal Science **18**:145-155.

Mohn, R., and W. D. Bowen. 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences **53**:2722-2738.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Schwarz, C. J., and W. T. Stobo. 2000. Estimation of juvenile survival, adult survival, and age-specific pupping probabilities for the female grey seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. Canadian Journal of Fisheries and Aquatic Sciences **57**:247-253.

Stobo, W. T., and K. C. T. Zwanenburg. 1990. Grey seal (*Halichoerus grypus*) pup production on Sable Island and estimates of recent production in the Northwest Atlantic. Pages 171-184 *in* W. D. Bowen, editor. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Canadian Bulletin of Fisheries and Aquatic Sciences, No. 222.

Taylor, B. L., and D. P. DeMaster. 1993. Implications of non-linear density dependence. Marine Mammal Science **9**:360-371.

Wade, P.R. 1998. Calculating the limits to allowable human-caused mortality in cetaceans and pinnipeds. Marine Mammal Science 14:1-37.

Waring, G.T., Palka, D.L., Clapham, P.J., Swartz, S., Rossman, M.C., Cole, T.V.N., Hansen, L.J., Bisack, K.D., Mullin, K.D., Wells, R.S., Odell, D.K. and Barros, N.B. 1999. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 1999. NOAA Technical memorandum NMFS-NE-153.

Zwanenburg, K. C. T., and W. D. Bowen. 1990. Population trends of the grey seal (*Halichoerus grypus*) in eastern Canada. Pages 185-197 *in* W. D. Bowen, editor. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Canadian Bulletin of Fisheries and Aquatic Sciences, No. 222.

Table 1. Values used in grey seal population model. B = binomial, N = normal distribution.

Parameter	Symbol	Group	Value	Distribution	S. D.	Reference
Birth rate	b	age				
		4	0.15	B	0.0442	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		5	0.70	B	0.0618	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		6	0.85	B	0.0457	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		7	0.83	B	0.0446	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		8	0.96	B	0.0418	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		9	0.96	B	0.0400	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
		10+	0.90	B	0.0202	Zwanenburg and Bowen 1990 Hammill and Gosselin 1995
Mortality	M	juveniles, adults	0.05	N	1.08	Schwarz and Stobo 2000 Manske et al. 2002

Table 2. Assumed values of theta, carrying capacity (K), estimated parameters of pup mortality (SE) in 1962, and population size (SE) and N_{min} in 2004.

	Θ	K	M^{Pup}		N_{2004}		N_{min}
Model 1	2.4	430,000	0.116	(0.40)	208,720	(29,730)	125,541
Model 2	2.0	550,000	0.115	(0.31)	216,490	(24,447)	144,610
Model 3	1.5	850,000	0.122	(0.21)	223,220	(17,376)	169,064

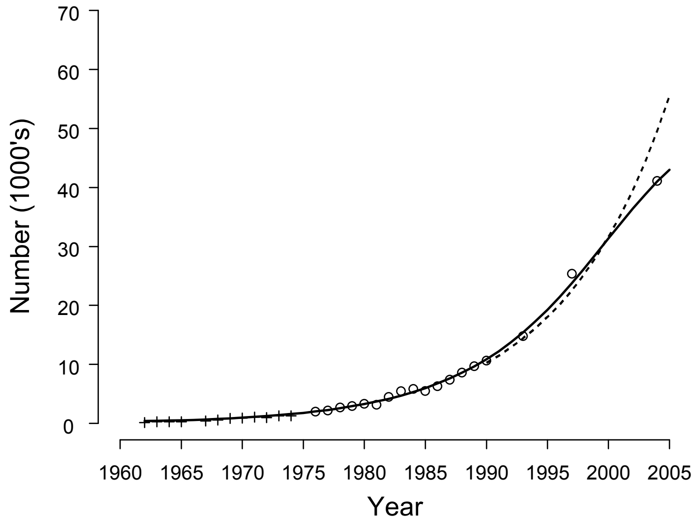
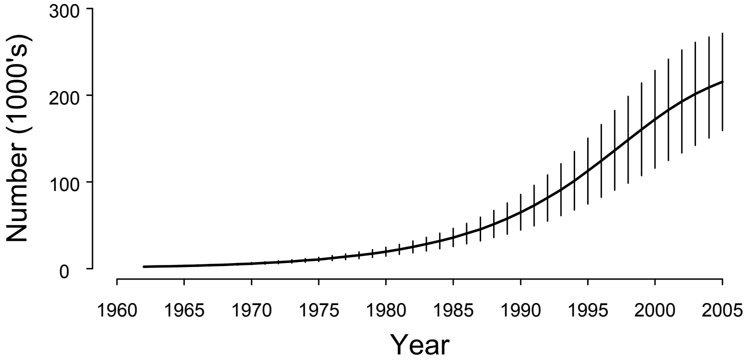
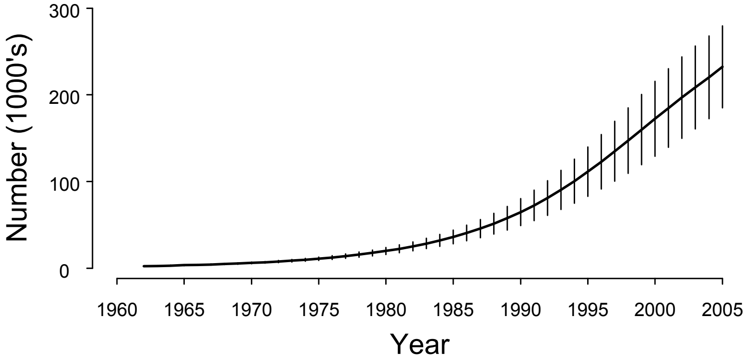


Figure 1. Census counts and model fit (solid line) to the pup production of the Sable Island grey seal population. The model of exponential increases (dotted line) was not used but was added for comparison.

(a) Theta = 2.4, K = 430,000



(b) Theta = 2, K = 550,000



(c) Theta = 1.5, K = 850,000

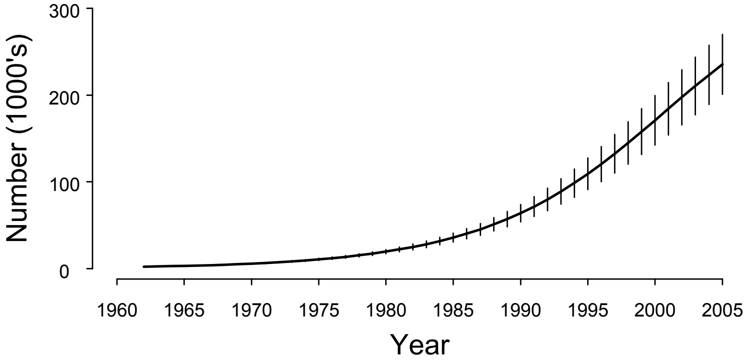


Figure 2. Model estimates of total population size assuming three different levels of theta. Horizontal lines indicate the 95% C.I.