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Grey Seal Population Trends in Canadian Waters, 1960-2016 and Harvest Advice

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

A model of grey seal population dynamics was fitted to pup production estimates for the Sable Island, Coastal Nova Scotia (CNS), and Gulf of St. Lawrence (GSL) seal herds to provide estimates of the Canadian component of the Northwest Atlantic grey seal population from 1960 to 2016. The model was fit to the pup production estimates for the Scotian Shelf (CNS and Sable Island combined), and the GSL separately to allow for the GSL model to include an influence of ice on mortality. The 2014 assessment model was adjusted to use estimates of survival from mark-resighting data from Sable Island. The mark-resighting analysis of Sable Island indicates that males have higher mortality rates than females, which, assuming constant age structure, would result in a ratio of males to females in the population of 0.69:1, instead of 1:1 as previously assumed. A model incorporating the new sex ratio could not be developed in time for this assessment. Consequently, model estimates of total population were adjusted for the new sex ratio after model runs had been completed. Total grey seal pup production in 2016 estimated by the model was 101,500 (95% CI 80,600 to 121,600). The 2016 sex-ratio adjusted total population is 424,300 (95%CI=263,600 to 578,300). The estimated 2016 total population on the Scotian Shelf was 380,300 (95% CL=234,000 to 517,200), and 44,100 (95% CL=29,600 to 61,100), for the GSL. The models predict that the population size continues to increase at an overall rate of 4.4% per year, due primarily to the increase on Sable Island. The current estimate of abundance is less than that estimated in 2014 because of the adjustments for fewer males in the population, lower adult mortality estimated from the mark-resighting analysis and an increase in the assumed ratio of first year mortality to adult mortality. Total allowable removals depend on the age structure of the harvest and the objective of the removals. In the GSL, harvests of 4,500 and 2,400 animals comprising 95% YOY and 70% YOY, respectively, would meet the current management objective (i.e. have a probability of 0.8 of remaining above the Precautionary Reference Level (N_{70})). For the Scotian Shelf (combined Sable Island and CNS herds), harvests of 30,000 and 17,000 animals comprising 95% YOY and 70% YOY, respectively, would have a probability of 0.8 of remaining above N_{70}. The number of grey seals in different areas of Atlantic Canada varies seasonally. An illustrative example shows that the number of seals in the southern GSL can vary from 30,500 (SE=3,200) during January to March, increasing to a maximum of 73,100 (SE=8,400) animals during July-September and then declining again as animals leave the area in late fall.

Tendances de la population de phoques gris dans les eaux canadiennes de 1960 à 2016 et avis sur la récolte

RÉSUMÉ

Un modèle de la dynamique de la population de phoques gris a été adapté aux estimations de la production de jeunes pour les troupeaux de phoques de l’île de Sable, de la côte de la Nouvelle-Écosse (côte de la N.-É.) et du golfe du Saint-Laurent (GSL) afin de fournir des estimations de la composante canadienne de la population de phoques gris de l’Atlantique Nord-Ouest de 1960 à 2016. Le modèle a été adapté aux estimations de la production de jeunes pour le plateau néo-écossais (côte de la N.-É. et île de Sable combinées), et le GSL séparément afin de pouvoir inclure l’influence de la glace sur la mortalité dans le modèle du GSL. Le modèle d’évaluation de 2014 a été ajusté afin d’utiliser les estimations de la survie tirées des données sur les phoques marqués de l’île de Sable. L’analyse des phoques marqués de l’île de Sable indique que les mâles présentent un taux de mortalité plus élevé que les femelles, ce qui entraînerait, en supposant que la structure d’âge soit constante, une proportion mâles/femelles de 0,69:1 dans la population, au lieu d’une proportion de 1:1 comme précédemment supposé. Un modèle intégrant le nouveau sex-ratio n’a pas pu être élaboré à temps pour la présente évaluation. Par conséquent, les estimations du modèle de la population totale ont été rajustées pour tenir compte du nouveau sex-ratio après la réalisation des exécutions du modèle. La production totale de phoques gris nouveau-nés en 2016 estimée par le modèle s’élevait à 101 500 (intervalle de confiance [IC] à 95 % = 80 600 à 121 600). La population totale rajustée au moyen du sex-ratio de 2016 s’élevait à 424 300 (IC de 95 % = 260 600 à 578 300). La population totale estimée en 2016 sur le plateau néo-écossais s’élevait à 380 300 (IC de 95 %= 234 000 à 517 200), et à 44 100 (IC de 95 % = 29 600 à 61 100) pour le GSL. Les modèles prévoient que la taille de la population continuera d’augmenter à un taux global de 4,4 % par année, principalement en raison de l’augmentation à l’île de Sable. L’estimation actuelle de l’abondance est inférieure à celle estimée en 2014 en raison des réajustements à la baisse des mâles dans la population, de la diminution de la mortalité des adultes estimée d’après l’analyse des phoques marqués, et de l’augmentation du rapport supposé entre la mortalité pendant la première année et la mortalité des adultes. Les prélèvements totaux autorisés dépendent de la structure par âge des prélèvements et de l’objectif des prélèvements. Dans le GSL, des prélèvements de 4 500 et 2 400 animaux composés à 95 % de jeunes de l’année et à 70 % de jeunes de l’année, respectivement, permettraient d’atteindre l’objectif de gestion actuel (c.-à-d., avoir une probabilité de 0,8 de demeurer au-dessus du niveau de référence de précaution [N_{70}]). Dans le cas du plateau néo-écossais (troupeaux de l’île de Sable et de la côte de la N.-É. combinés), des prélèvements de 30 000 et de 17 000 animaux composés à 95 % et à 70 % de jeunes de l’année, respectivement, auraient une probabilité de 0,8 de demeurer au-dessus du seuil N_{70}. Le nombre de phoques gris dans les différentes zones du Canada atlantique varie selon la saison. Un exemple concret montre que le nombre de phoques dans le sud du GSL peut varier de 30 500 (ET = 3 200) de janvier à mars, augmenter à un maximum de 73 100 animaux (ET = 8 400) de juillet à septembre, et diminuer encore lorsque les animaux quittent la zone à la fin de l’automne.

INTRODUCTION

Little is known of historical abundance or harvests of grey seals (*Halichoerus grypus*) in Atlantic Canada. Grey seals appear to have been abundant throughout Atlantic Canada during the 16th and 17th centuries but, by the 18th century, their numbers had declined markedly due to high levels of harvesting for oil. In the late 1800s, Gilpin (1874) speaks of herds of only 20 or 30 seals on Sable Island, and in the early 1950s, they were rare throughout eastern Canada (Lavigueur and Hammill 1993, Fisher 1955, Bowen 2011). Government sponsored culls and a bounty program may have slowed grey seal recovery in the 20th Century (Bowen and Lidgard 2012), but over the last five decades the Canadian grey seal population has increased from approximately 15,000 animals in the 1960s to over 350,000 in 2007 (Mohn and Bowen 1996, Thomas et al. 2007).

Within Canadian waters the grey seal population is subdivided into three groups for management considerations based on the locations of the main breeding colonies: Sable Island, Gulf of St. Lawrence (GSL) and Coastal Nova Scotia (CNS) (Figure 1). These three herds represent a single genetic population (Boskovic et al. 1996, Wood et al. 2011). Sable Island is on the edge of the Scotian Shelf, approximately 160 km off the coast of Nova Scotia, Canada (44.8 N, 60.8 W). It is home to the largest breeding colony of grey seals in the world (Bowen et al. 2007). The second largest breeding colony in Atlantic Canada occurs in the GSL, where grey seals have their young on the pack-ice in the southern GSL or on small islands (Figure 1). A relatively small number of animals breed on isolated islands along coastal Nova Scotia. These have traditionally been in the area known as the Eastern Shore (Mansfield and Beck 1977). In the early 1990s, a small colony appeared along the southwestern shore of Nova Scotia on Flat and Noddy Islands. Outside of the breeding season, there is overlap in the distribution of animals from the different colonies (e.g., Lavigueur and Hammill 1993, Harvey et al. 2008, Breed et al. 2006, 2009). Grey seal pupping also occurs in the northeastern United States (Wood et al. 2007, 2011) with an estimated pup production of around 6,000 animals in 2016 (Wood, University of Massachusetts, Boston, pers. comm.).

The herds in the three regions have had different population trajectories. Prior to 1997, pup production increased at a rate of 13% a year on Sable Island (Bowen et al. 2011). Between 1997 and 2016, the rate of increase slowed to about 4% suggesting that the population may be facing resource limitation (Bowen et al. 2011, den Heyer et al. 2017). Pup production in the GSL has been much more variable than on Sable Island due to higher and more variable removals associated with bounty, culling and scientific harvests (Hammill et al. 1998), and higher mortality rates associated with pupping on the pack-ice (Hammill and Stenson 2011; Thomas et al. 2007). On the Eastern Shore, significant culling efforts, particularly in the Basque Island area limited pup production to the low 100s during the 1970s, and commercial hunting has occurred on Hay Island over the last decade.

McLaren et al. (2001) identified a need to manage seals under a framework that incorporated benchmarks and harvest control rules. In 2003, the Department implemented a management approach, referred to as the Atlantic Seal Management Strategy (ASMS), which incorporated the precautionary approach into the management of Atlantic seals. Grey seals are currently classified as being ‘Data Rich’. For such species, the framework identifies a precautionary reference level at 70% of the largest population size. A secondary reference level is set at 50% while the critical reference limit has been identified at 30% of the largest estimated population (Hammill and Stenson 2007, 2013). The primary goal of the management framework is to ensure that the population does not decline to levels where it falls below the critical reference level (N_{30}) and as such, is considered to have suffered serious harm. To minimize the risk the population is normally managed around the precautionary reference level.

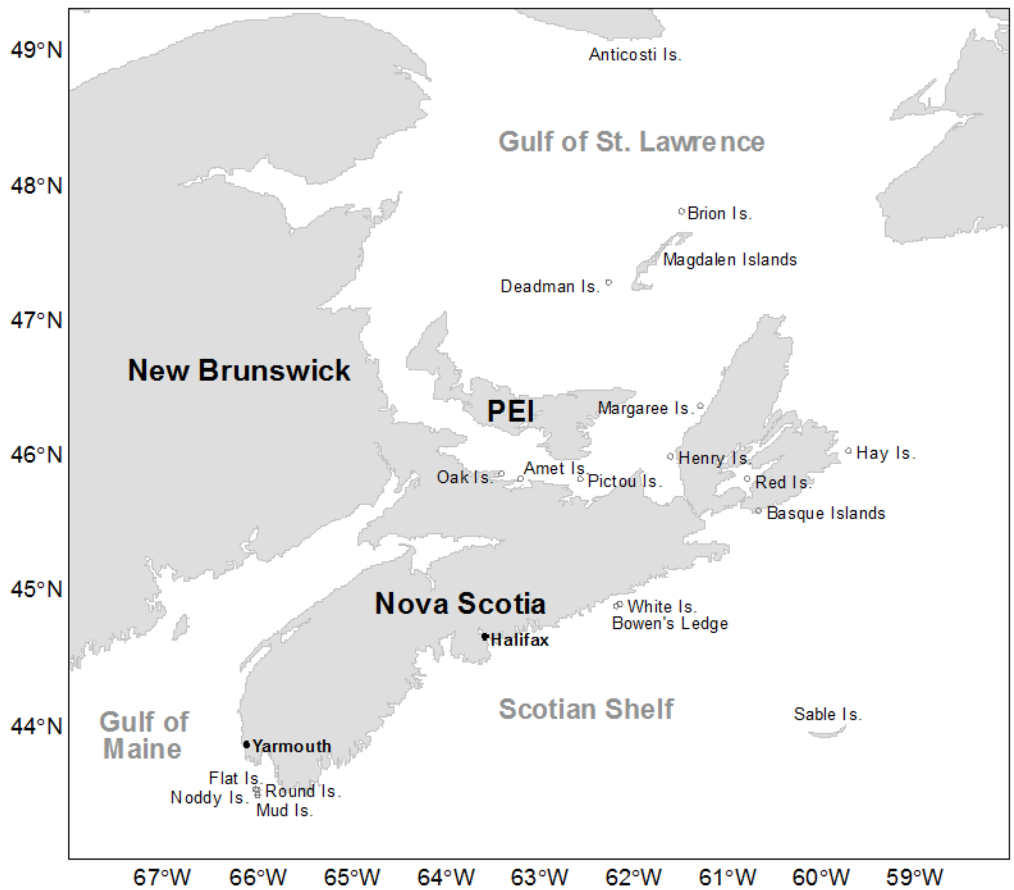


Figure 1. Map showing locations of main pupping colonies in Atlantic Canada.

Fisheries and Ecosystem Management requested that Science provide an update on the status of the grey seal population. Advice should include information on the status of the overall population, as well as changes in the status of the three herds known by sub-areas as Sable Island, Coastal Nova Scotia (CNS) and the Gulf of St. Lawrence (GSL). The following specific questions were addressed:

1. For the next five years (2017-2021) what would be the maximum sustainable harvest with an 80% confidence of remaining above N_{70}?
2. What is the risk that the grey seal population will drop below 50% and 70% of N_{max} at a total allowable catch of 60,000, 70,000 and 90,000, 100,000, 120,000 150,000 and 200,000 animals with a composition of 30% adults / 70% beaters, and 5% adults / 95% beaters?
3. If a target population was set at N_{70} (e.g. 70% of maximum population observed) what would be the total annual removals required to maintain that target over a range of 5 and 10 years?
4. Estimate the number of grey seals foraging in the Southern Gulf of St. Lawrence (4T).

Here we use a three-parameter age-structured model, similar to that developed for harp seals (*Pagophilus groenlandicus*; Hammill et al. 2015). The model inputs include age-specific reproductive rates, human removals and ice-related mortality of young of the year (YOY) seals (GSL only, Hammill et al. 2014). The model is also fitted separately to estimates of pup production for each of the three herds for comparison with earlier assessments. Data from CNS is more limited, but emigration from Sable Island to the CNS colonies is thought to occur. In this assessment, we estimate the total population for the Scotian Shelf by fitting the model to the combined pup production of Sable Island and CNS. New data on pup production, reproductive rates, adult survival rates and removals have been used to estimate total population size in Atlantic Canada and provide harvest advice. The new assessment includes estimates of juvenile and adult survival from mark-resighting analysis of individually marked grey seals that breed on Sable Island (den Heyer et al. 2014, den Heyer and Bowen 2017). The models were projected forward to evaluate the impacts of different harvest levels on the population.

MATERIALS AND METHODS

Modelling the dynamics of the Northwest Atlantic grey seal population occurs in two steps. In the first, using Monte Carlo sampling, the model is fitted to independent estimates of the total pup production by adjusting initial population size (α), adult (i.e., one year old and older, referred to as 1+) mortality rates (M) and the carrying capacity (K). The model was developed to consider density-dependent changes in mortality acting on first year survival as well as acting on reproduction (Hammill et al. 2015). Over the last 3 decades, little change in reproductive rates or adult mortality has been observed from Sable Island mark-resighting data (Schwarz and Stobo 1997, den Heyer et al. 2014, den Heyer and Bowen 2017) or in samples taken from the GSL (Hammill and Gosselin 1995, Hammill et al. 2013, 2014). Therefore, for all herds, it is assumed that the dynamics of the population can be described by density-dependent changes in mortality acting on first year survival only. The age-structured model assumes that the sex ratio is 1:1 (but see den Heyer and Bowen 2017), that removals of pups occurs at the beginning of the year and that removals of animals 1 year of age and older occurs mid-way through the year. A gamma parameter is a multiplier that specifies the relationship between first year mortality and adult female mortality such that first year mortality (M_1) is a fixed multiple of the adult mortality rate (M). In the last assessment, the models had gammas of 3 and 6, i.e., M_1= 3*M or 6* M (Hammill et al. 2014) for Scotian Shelf and GSL herds, respectively.

Here, we present an alternate model with an updated prior for adult mortality based on the high female survival estimated from the mark-resighting study on Sable Island (den Heyer and Bowen 2017). We also include a higher gamma (gamma=15) based on the mark-resighting estimates of adult (den Heyer and Bowen 2017) and juvenile survival (den Heyer et al. 2014). First year mortality was estimated as the sum of two components: pup mortality from birth to weaning and the estimated mortality from weaning to the end of the first year of life. This second component was estimated by discounting the mark-resighting estimate of juvenile mortality by three years of the adult mortality rate. In the 1990s, when the grey seal population was growing at maximum rate, mark-resighting analysis estimated 26% juvenile mortality from weaning to recruitment to the breeding colony (first reproduction at age 4; den Heyer et al. 2014). Assuming that juvenile (age 1+) mortality is constant and the same as adult mortality at approximately 2%/yr (den Heyer and Bowen 2017), we estimate post-weaning mortality in the first year to be 20%. Pup mortality of 4-5% has been estimated on the Sable Island breeding colony prior to aerial photographic surveys of pup production which are usually flown in early-January, just after peak pup production (Bowen et al. 2007, 2011, den Heyer et al. 2017). Assuming pup mortality on the breeding colony occurs at a constant rate, we estimate pre-weaning mortality on the colony (up until early February) to be roughly 10%. Therefore, total first year mortality is estimated to be 30% and the ratio of first year mortality to adult mortality (2%) is estimated to be 15.

MODEL STRUCTURE

Initial population size

$P = \sum_{i=1}^{26}(\alpha \times l_i)$ (1)

Survival

For age 1:

$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1}) \times e^{-M_1} \times (1 - (N_t/K)^{\theta})$ (2)

with $M_1 = \gamma \times M$ (3)

For age a, with 1<a<A:

$n_{a,t} = (n_{a-1,t-1} \times e^{-M/2} - c_{a-1,t-1}) \times e^{-M/2}$ (4)

For age A:

$n_{A,t} = [(n_{A-1,t-1} + n_{A,t-1}) \times e^{-M/2} - (c_{A-1,t-1} + c_{A,t-1})] \times e^{-M/2}$ (5)

Reproduction

$n_{0,t} = \sum_{a=1}^{A} n_{a,t} \times P_{a,t}$ (6)

For age a, with 1<a<8

$P_{a,t} \sim CorBin(n_{a.reprod,t}, P_{a.preg,t})$ (7)

For age a, with a ≥ 8 (i.e. 8+)

$P_{a,t} = P_{8,t} \sim CorBin(n_{8+.reprod,t}, P_{8+.preg,t})$ (8)

where

P_{init}	= size of the total initial population,
α	= multiplying factor,
l_i	= initial population size for the i[th] age class,
$n_{a,t}$	= population numbers-at-age *a* in year *t*,
$c_{a,t}$	= the numbers caught at age *a* in year *t*,
$P_{a,t}$	= per capita pregnancy rate of age *a* females in year *t*, assuming a 1:1 sex ratio,
$CorBin$	= multivariate distribution composed of binomial distributions which degree of correlation is controlled via an 8-dimension Gaussian copula (Hammill et al. 2015). Note: this function is only used during the fitting part (see below the point 4 of the projection part specifications),
$n_{a.reprod,t}$	= sample size used to obtain the observed pregnancy rate in year t,
$P_{a.reprod,t}$	= proportion of pregnancy in the observed group in year t,

$Psim_{8+,t}$	= per capita pregnancy rate of age 8+ females estimated by its relation with the carrying capacity. The value of 0.9 corresponds to the maximum pregnancy rate observed when the population was low (i.e. far from the carrying capacity). This estimation is used to fit the model with observed pregnancy rates obtained during the same period.
M	= the instantaneous rate of natural mortality,
M_1	= the instantaneous rate of natural mortality of animals in their first year,
γ	= a multiplier to allow for higher mortality of first year seals. For the previously accepted models, gamma was set to 3 for Sable Island and the GSL (Hammill et al. 2013; den Heyer et al. 2014). Here, based on the mark-recapture estimates of M, gamma has been adjusted to 15 for the assessment runs.
w	= the proportion of pups surviving an unusual mortality event arising from poor ice conditions or weather prior to the start of harvesting,
A	= the 'plus' age class (i.e., older ages are lumped into this age class and accounted for separately, taken as age 25 in this analysis),
N_t	= total population size,
K	= carrying capacity,
θ	= theta, set at 2.4 (Trzcinski et al. 2006).

PROJECTION MODEL

In the second step, a projection model predicts the impact of future catch scenarios based upon most recent estimates of population size (abundance at age). For the projections the Sable Island and CNS herds were combined and renamed the Scotian Shelf herd. It was also assumed that:

1. mortality from nuisance seal removals, culls and science harvests remain constant. For the Scotian Shelf herd, nuisance seal removals were assumed to follow a uniform distribution with limits of 3,000 to 4,000 animals. In the GSL, a uniform distribution allowed removals to vary between 100 and 200 animals.
2. ice-related mortality was set at 0 for the GSL (i.e. pupping occurs on land)
3. age-specific reproductive rates for each of the last 5 years were included in a vector and each year had an equal probability of being selected for a projection run
4. the dynamics of the population can be described assuming density-dependent mortality acting on first year survival by the relationship:

$$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1}) \times e^{-M_1} \times (1 - (N_t/K)^{\theta})$$

The model is projected forward to 2046 to determine if the catches will respect the management plan (i.e. 80% likelihood of population remaining above the Precautionary Reference Level, N_{70}, and 95% likelihood of population above Limit Reference Level, N_{30}). Grey seals are not fully recruited into the breeding population until age 8-10, and assessments are often spaced 5 years apart. Therefore, it is not possible to detect the impact of harvest activity for 15 or more years

(Hammill and Stenson 2008). For a 5-year management plan, the projection period of 30 years is used to assess the full impact of harvest strategies on the population.

Sex Ratio

Estimates of adult male and female survival from den Heyer and Bowen (2017) were used to estimate the population sex ratio. Adult female survival rates are consistently higher than males. Assuming a stationary age distribution, the weighted average ratio of males to females is 0.69. This ratio was used to adjust total population size.

Monte Carlo resampling and parameter estimation

The model creates a population matrix with 26 age classes from 1952 until the current year. The initial population vector (26×1) was created as an initial population age structure which size is adjusted by a multiplying factor (α). We included the uncertainty in the pregnancy rates and the pup production estimates in the fitting model by resampling the parameters using Monte Carlo techniques. At each Monte Carlo iteration of the model (n=5000), pregnancy rates are resampled for each year assuming a binomial distribution (correlated among age classes) and pup production estimates are resampled assuming a normal distribution (with variance based on estimates of the survey errors) and the model minimizes the objective function by estimating three parameters: the initial population factor (α), the instantaneous mortality rate (*M*), and the carrying capacity (*K*). For each iteration, new parameter estimates (*M, K* and α) as well as total population size and pup production are estimated and stored to provide a distribution to estimate the means, medians and confidence intervals. The model runs in the programming language R.

DATA INPUT

Initial population

The initial population vector (26×1) was created as an initial population age structure. In the early 1960s there was little information on grey seal abundance, but the majority of animals were in the GSL, followed by CNS and then Sable Island, which had the smallest breeding population at that time. For the starting vector, pup production in 1960 was assumed to be 5000, 800, and 500 for the GSL, CNS and Sable Island herds, respectively. Subsequent age classes were created assuming that adult mortality (M) was approximately 6% and first year mortality was 3 times adult mortality. This adult mortality rate arose from some early simulations (Hammill unpublished data) and was similar to the 5% rate estimated by Mohn and Bowen (1996).

Pup production

The model was fit to independent estimates of pup production (Table 1) obtained for each herd. Not all herds have pup production estimates in the same years and a variety of methods have been used to estimate pup production. Nevertheless, for each herd there is a time series of estimates that begins in the 1960s.

Table 1. Pup production estimates used as input into the population models. Estimates from the Sable Island colony (1962-1971), the CNS (1962-1989) and GSL colonies (1962-1984) are very uncertain. The SE for these periods have been artificially increased to reflect this uncertainty (in bold italic).

Year	Sable Island		CNS		GSL	
	Estimate	SE	Estimate	SE	Estimate	SE
1962	-	-	130	***400***	-	-
1963	400	400	180	***400***	-	-
1964	550	550	190	***400***	-	-
1965	660	660	230	***400***	-	-
1966	-	-	180	***400***	900	***500***
1967	580	580	270	***400***	-	***-***
1968	700	700	-	***-***	-	***-***
1969	800	800	-	***-***	-	***-***
1970	800	800	100	***400***	-	***-***
1971	1000	1000	130	***400***	-	***-***
1972	950	950	-	***-***	-	***-***
1973	1200	1200	-	***-***	-	***-***
1974	1250	1250	135	***400***	-	***-***
1975	-	-	180	***400***	3800	***3800***
1976	2000	2000	130	***400***	-	***-***
1977	2181	173	-	***-***	3900	***3900***
1978	2687	192	-	***-***	-	***-***
1979	2933	201	-	***-***	-	***-***
1980	3344	214	-	***-***	-	***-***
1981	3143	208	-	***-***	-	***-***
1982	4489	248	-	***-***	-	***-***
1983	5435	273	-	***-***	-	-
1984	5856	283	142	***400***	7169	911
1985	5606	277	135	***400***	6706	795
1986	6301	294	151	***400***	5588	679
1987	7391	318	179	***400***	-	-
1988	8593	343	-	***-***	-	-
1989	9712	365	179	***400***	9352	1756
1990	10451	575	-	-	9176	649
1993	15500	463	-	-	-	-
1994	-	-	900	-	-	-
1996	-	-	395	148	10717	1306
1997	25400	750	1061	242	6839	800
2000	-	-	799	210	5260	910
2004	41500	4381	2469	152	14210	1200
2007	54482	8909	3017	80	11413	1077
2010	62054	4973	2960	272	11228	6442
2016	83594	10170	4556	395	10497	815

Pregnancy rates

Late-term pregnancy data are available from sampling programs conducted in the GSL (Hammill and Gosselin 1995). Samples were collected between late May and November. Fall samples represent late-term pregnancy rates since they were collected only a few months prior to pupping in December. It is assumed that there were no abortions after the samples were taken. To the extent that abortions do occur, these late-term rates are likely to over-estimate birth rates. The mean birthdate is assumed to be the first of January, and the age of all animals advances by one year on this date. Females enter the model at their age on the first of January of each year. There are gaps in the time series of reproductive data, and in some years sample sizes are small (Table 2) (Figure 2). When sample sizes were <25, reproductive rates were estimated by smoothing the data using a local likelihood estimator (Hammill et al. 2015).

Table 2. Year, age (years), number of females collected between 1969 and 2012 (N) and number of females pregnant (Preg). Note age 8 refers to females 8 years of age and older.

Year	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate
1969	4	12	0.25	5	7	0.71	6	9	1	7	6	1	8	36	0.81
1982	4	4	0.00	5	4	0.75	6	8	0.88	7	1	1	8	48	0.90
1986	4	4	0.25	5	2	1.00	6	4	0.75	7	7	0.86	8	34	0.94
1987	4	7	0.14	5	10	0.50	6	8	0.63	7	9	0.67	8	71	0.94
1988	4	7	0.29	5	14	0.71	6	10	0.90	7	5	0.80	8	57	0.89
1992	4	16	0.06	5	16	0.75	6	15	0.87	7	7	0.86	8	36	0.89
1994	4	1	0.00	5	3	0.00	6	1	1.00	7	2	1.00	8	0	-
1998	4	0	-	5	0	-	6	1	0.00	7	1	1.00	8	10	0.80
1999	4	0	-	5	2	0.00	6	2	1.00	7	2	1.00	8	12	1.00
2000	4	5	0.40	5	3	0.67	6	6	0.83	7	2	1.00	8	18	0.89
2001	4	1	0.00	5	0	-	6	1	1.00	7	0	-	8	6	0.83
2002	4	7	0.29	5	3	0.33	6	3	1.00	7	7	0.86	8	22	0.86
2003	4	2	0.00	5	4	0.50	6	3	1.00	7	0	-	8	9	0.67
2004	4	5	0.00	5	6	0.83	6	3	0.33	7	4	0.75	8	28	0.93
2005	4	1	0.00	5	3	1.00	6	1	0.00	7	0	-	8	1	1.00
2006	4	1	0.00	5	0	-	6	0	-	7	0	-	8	0	-
2007	4	1	0.00	5	3	0.67	6	3	1.00	7	0	-	8	10	0.90
2008	4	0	-	5	0	-	6	5	1.00	7	2	1	8	9	0.78
2009	4	0	-	5	0	-	6	0	-	7	0	-	8	0	-
2010	4	4	0	5	1	1	6	2	1.00	7	1	1	8	11	1.00
2011	4	1	1	5	2	0	6	0	-	7	1	1	8	16	0.75
2012	4	0	-	5	3	0	6	2	0.50	7	4	0	8	13	0.92
2013	4	3	0	5	1	0	6	0	-	7	1	1	8	6	5
2014	4	1	0	5	2	0	6	5	3	7	4	3	8	23	22
2015	4	2	1	5	4	2	6	3	2	7	0	-	8	11	10
2016	4	0	-	5	0	-	6	0	-	7	0	-	8	0	-
2017	4	0	-	5	0	-	6	0	-	7	0	-	8	0	-

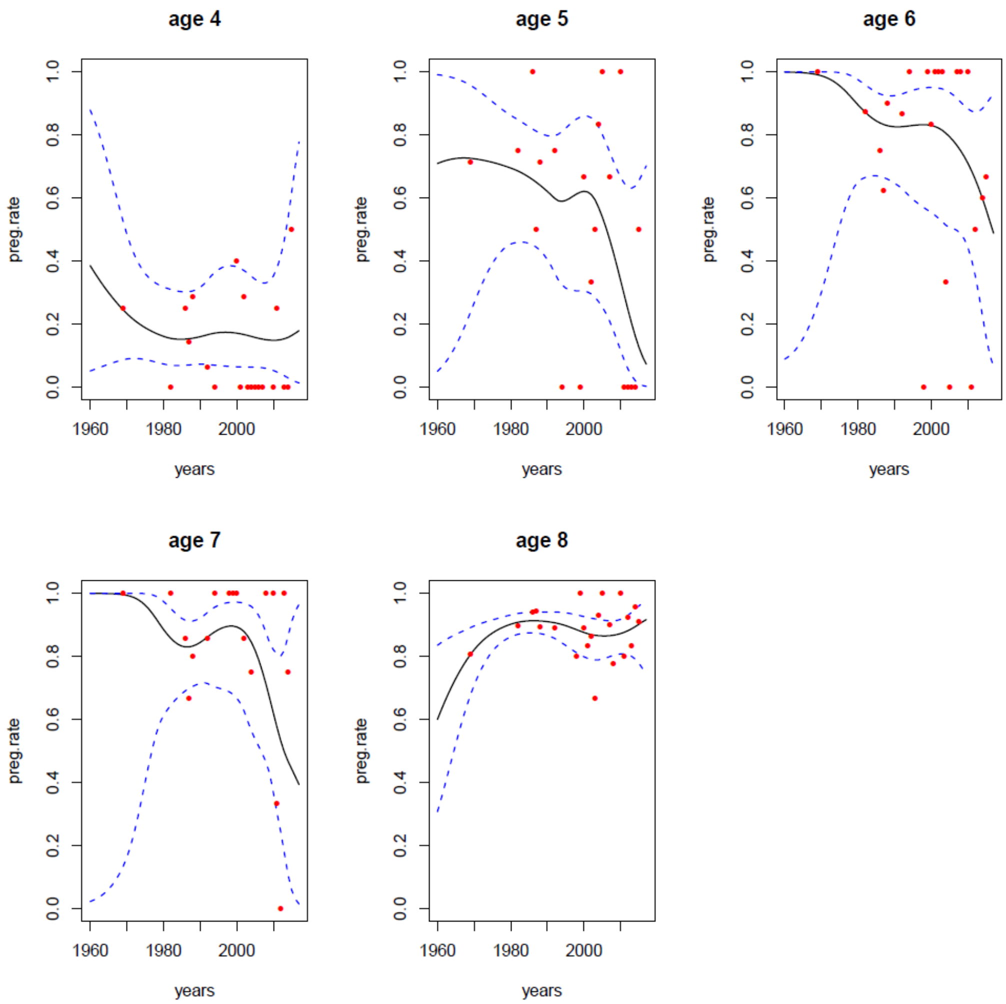


Figure 2. Age specific reproductive rates (red circles) and non-parametric smoothed rates (solid line) for the period 1969-2012 for ages 4-8+ years. Dotted lines represent 95% CI.

Removals

Data on removals from the herds are available since 1960. There are four types of removals: the Canadian commercial harvest (Department of Fisheries and Oceans, Statistics Branch); seals killed under nuisance seal licenses, bounty kills and culls, and science sampling programs (Appendix 1). The Canadian commercial hunt consists of 99% young of the year (YOY). The commercial hunts and culls occur on land or on the ice. For these hunts all animals were assumed to have been recovered, landed and reported. For the scientific collections, animals are shot in the water. It was assumed that struck and loss rates were 30% (Hammill unpublished data). Reports of nuisance seal harvests are not corrected for struck and loss since there is no requirement to recover the animal.

Ice-related mortality of YOY in the GSL

Grey seals in the GSL give birth on the ice as well as on islands. In heavy ice years, most animals are born on the ice, whereas in years of light ice a greater proportion of pups are born on the islands (Hammill and Stenson 2011). Pup mortality appears to be higher in the GSL herd than on Sable Island and, in poor ice years, we have observed that pups disappeared during the surveys (e.g., 1997, 2010) although the numbers have been difficult to quantify. Hammill and Stenson (2011) used an ice anomaly index to attempt to account for this disappearance based on the late January Northumberland Strait ice cover (km^2).

Ice index = (Ice cover - mean ice cover) / mean ice cover

If the ice index had a value greater than -0.25, M_{ice} was set to 1. If the ice index value was below -0.25, M_{ice} was set to the value of the ice index (Table 3, Figure 3). The proportion of pups born on the ice has declined as total ice cover has declined (Figure 3). The survival coefficient (Table 3), or proportion of pups that are estimated to have survived to be counted, was estimated as

$$S_{ice} = 1 - (M_{ice} * Prop_{ice})$$

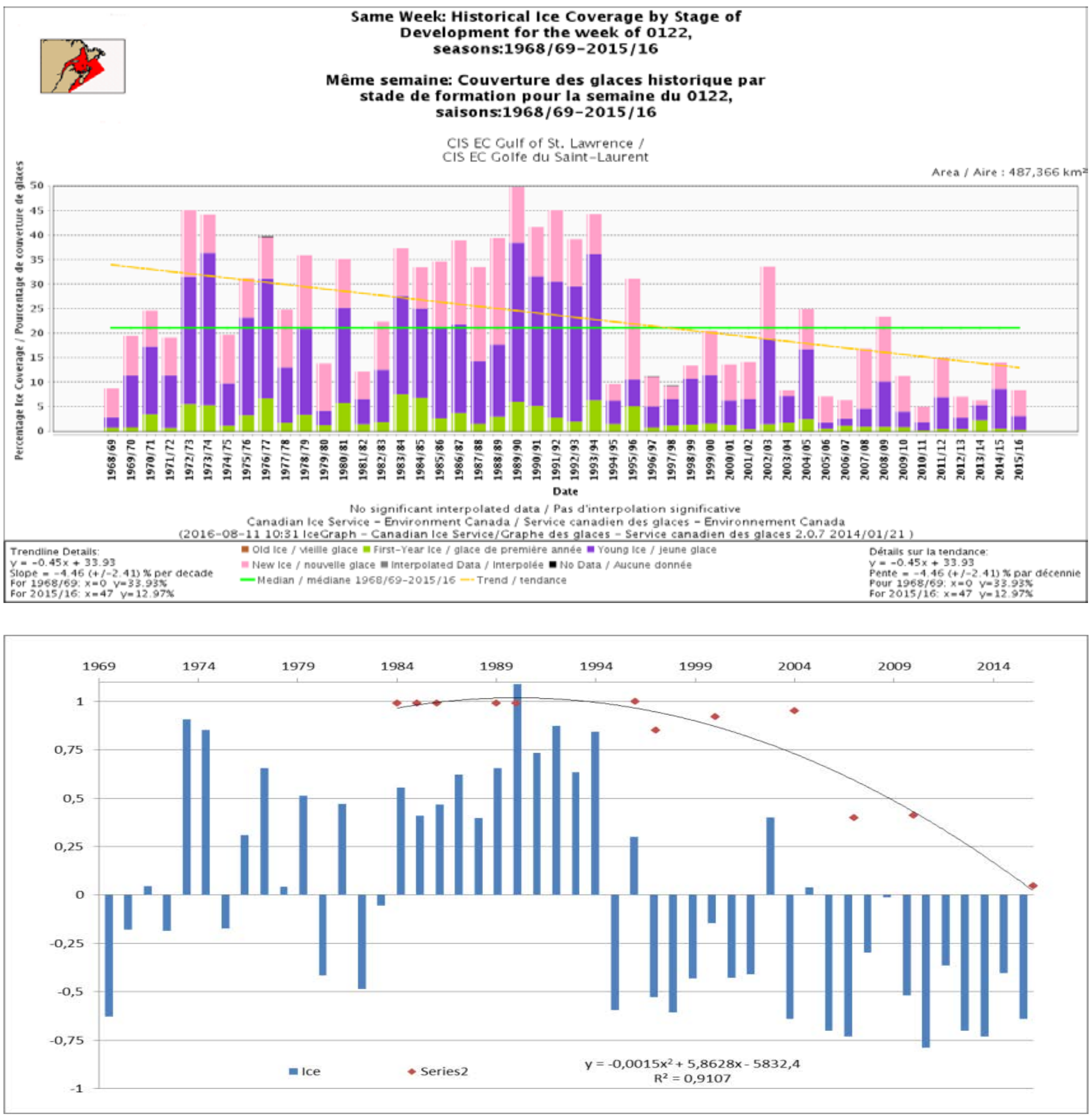


Figure 3. Total ice cover (%) in GSL during the week of January 22, 1969-2016 (top) and the proportion of animals pupping on the ice compared to the ice anomaly (ice index) (bottom). Ice data are from Environment Canada.

Table 3. Survival coefficient (S_{ice}) used to account for pups drowning before surveys were completed in the GSL, taking into account the proportion of pups that are born on the ice.

Year	Survival	Year	Survival	Year	Survival
1960	1.0	1980	0.8	2000	0.7
1961	1.0	1981	1.0	2001	0.7
1962	1.0	1982	1.0	2002	0.4
1963	1.0	1983	0.5	2003	1.0
1964	1.0	1984	1.0	2004	1.0
1965	1.0	1985	1.0	2005	0.7
1966	1.0	1986	1.0	2006	0.1
1967	1.0	1987	1.0	2007	0.5
1968	1.0	1988	1.0	2008	0.6
1969	0.8	1989	1.0	2009	1.0
1970	1.0	1990	1.0	2010	0.6
1971	1.0	1991	0.9	2011	1.0
1972	0.9	1992	1.0	2012	1.0
1973	1.0	1993	0.8	2013	0.7
1974	1.0	1994	1.0	1014	0.9
1975	0.4	1995	0.2	2015	0.8
1976	0.8	1996	1.0	2016	1.0
1977	1.0	1997	0.7	-	-
1978	0.6	1998	0.7	-	-
1979	1.0	1999	0.2	-	-

Survival on Sable Island

The mark-resighting estimates of juvenile and adult survival for the Sable Island herd (den Heyer et al. 2014, den Heyer and Bowen 2017) have been used to parameterize the model. The priors for adult M were set to tightly describe adult mortality (M) of 2% and juvenile mortality ($M_{age\ 0\text{-}4}$) of 26% estimated from female seals branded on Sable Island in the late 1980s (den Heyer et al. 2014; den Heyer and Bowen 2017). In the model, all of the higher juvenile mortality is assumed to occur in the first year (M_1) ie age 0-1 year, with adult mortality rates applying to animals aged 1 year and older (M)

For age 1:

$$n_{1,t} = ((n_{0,t-1} \times w) - c_{0,t-1})e^{-M_1} \times (1 - (N_t/K)^{\theta})$$

with $M_1 = \gamma \times M$

For age a, with 1<a<A:

$$n_{a,t} = (n_{a-1,t-1} \times e^{-M/2} - c_{a-1,t-1}) \times e^{-M/2}$$

For age A:

$$n_{A,t} = \left[(n_{A-1,t-1} + n_{A,t-1}) \times e^{-M/2} - (c_{A-1,t-1} + c_{A,t-1})\right] \times e^{-M/2}$$

Seasonal abundance in the GSL

An estimate of the seasonal abundance of grey seals in the southern GSL (NAFO zone 4T) was calculated from the seasonal distribution of animal locations as determined from satellite telemetry (Table 4) (Benoit et al. 2011). We assumed a CV around the proportions of 20%. The number of animals in each fishing zone (Ni) was estimated by multiplying the proportion of animals from each herd in each zone (Pi) by the total estimated GSL population (GSL) and the estimated combined Scotian Shelf (SS) herd, where

$N_i = N_{GSL\ female} * P_{GSL\ female} + N_{GSL\ male} * P_{GSL\ male} + N_{SS\ male} * P_{SS\ male} + N_{SS\ female} * P_{SS\ female}$.

The variance (V_i) was estimated as the sum of the variances for each component where:

$V_i = (N_{Hs})^2 * V_{proportion\ H\ S} * (P_{iHS})^4 + (V_N) * (P_{iHS})^2$,

where i is the NAFO division, and H is the herd (GSL or Scotian Shelf), and S is the sex (Mood et al. 1974).

Table 4: Seasonal distribution of male and female seals from the GSL and Scotian Shelf herds in NAFO fishing zones based upon telemetry data obtained prior to 2011(Benoit et al. 2011). Note there are no recent telemetry estimates for the distribution of seals.

Area	Male				Female			
	Jan-Mar	Apr-Jun	Jul-Oct	Nov-Jan	Jan-Mar	Apr-Jun	Jul-Oct	Nov-Jan
GSL Herd								
3PsPnLK	0,135	0,012	0,000	0,000	0,039	0,000	0,000	0,000
4RS	0,001	0,090	0,124	0,034	0,001	0,118	0,203	0,106
4T	0,570	0,678	0,876	0,875	0,446	0,379	0,704	0,789
4Vn	0,133	0,020	0,000	0,079	0,116	0,000	0,015	0,011
4VsW	0,064	0,139	0,000	0,006	0,397	0,503	0,078	0,095
4X	0,068	0,018	0,000	0,005	0,000	0,000	0,000	0,000
5Z	0,001	0,000	0,000	0,000	0,000	0,000	0,000	0,000
Other	0,028	0,044	0,000	0,000	0,000	0,000	0,000	0,000
Scotian Shelf Herd								
3PsPnLK	0	0	0,021	0,003	0	0,012	0,05	0,004
4RS	0,000	0,000	0,055	0,010	0,008	0,049	0,099	0,035
4T	0,026	0,000	0,054	0,021	0,021	0,081	0,138	0,097
4Vn	0,008	0,006	0,068	0,029	0,061	0,053	0,033	0,001
4VsW	0,600	0,806	0,753	0,833	0,908	0,801	0,679	0,861
4X	0,170	0,111	0,036	0,073	0,000	0,000	0,000	0,000
5Z	0,190	0,077	0,000	0,031	0,000	0,000	0,000	0,000
Other	0,006	0,000	0,013	0,000	0,002	0,004	0,001	0,002

RESULTS

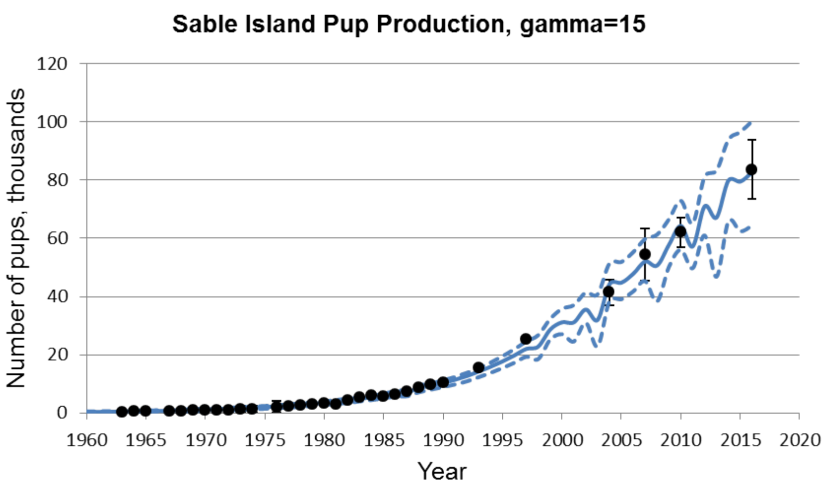
REPRODUCTIVE DATA

A smoother fitted to the reproductive data provided a means of interpolating for missing years and attempting to characterize inter-annual variability (Figure 2). Overall, reproductive rates for age 8 years and older were high throughout most of the time-series. There appears to have been a decline in the reproductive rates for age classes 5-7 year olds since the early 2000s, but samples sizes are too small for these age classes (evidenced by large confidence intervals) to draw firm conclusions (Table 2)(Figure 2).

MODEL ESTIMATES

Sable Island

Fitting the model assuming gamma=15, generated parameter estimates of α=0.22 (SE=0.039), M=0.039, (SE=0.005) and K=542,900 (SE=191,000). The model estimated pup production in 2016 is 82,700 (95% CL=64,400-100,300) and the estimated total population is 368,800 (95% CL=70,900-504,500) assuming a sex ratio of 1:1 (Figure 4).



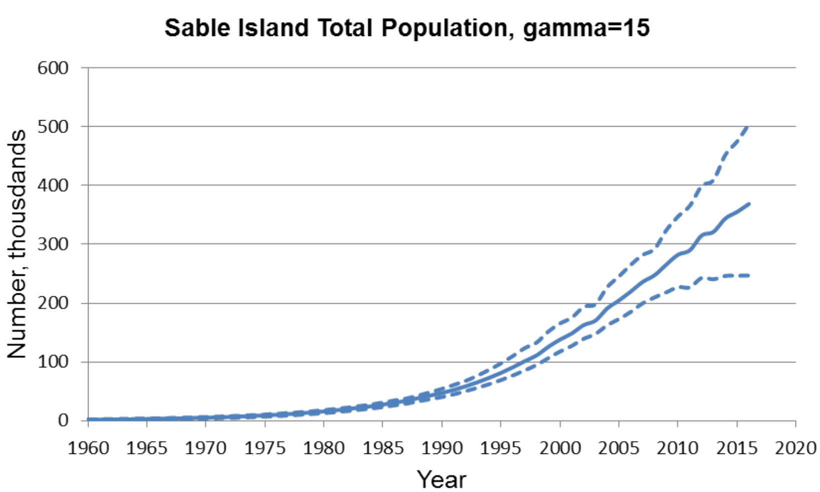


Figure 4. Sable Island pup production estimates from model (solid line, dotted lines 95%CL) and survey estimates (square, 95% CL) (top) and total population size (bottom) through 2016. Model fit gamma=15.

Scotian Shelf

A single model was fit to pup production on the Scotian Shelf, by combining Sable Island and CNS. Prior to 1994 there were no estimates for pupping for CNS. Since 1994, there are estimates of CNS pup production in all years that Sable pup production was estimated. Estimates for only CNS, but not Sable Island, are not included in the pup production time series. The assessment model with a more restricted adult female mortality and gamma=15, generated parameter estimates of α = 0.243 (SE =0.049), *M*=0.063 (SE=0. 007) and *K*=727,900 (SE=247,700). Again, the model predicts that the rate of increase in pup production has slowed (Figure 5), with pup production in 2016 predicted to be 87,100 (95% CI=70,200-103,300) and total population to be 447,400 (95% CI 275,300 to 608,500) assuming a sex ratio of 1:1. Adjusting the population estimate for a sex ratio of 0.69M:1F, the estimated population in 2016 is 380,300 (95% CI=234,000 to 517,200) (Figure 5).

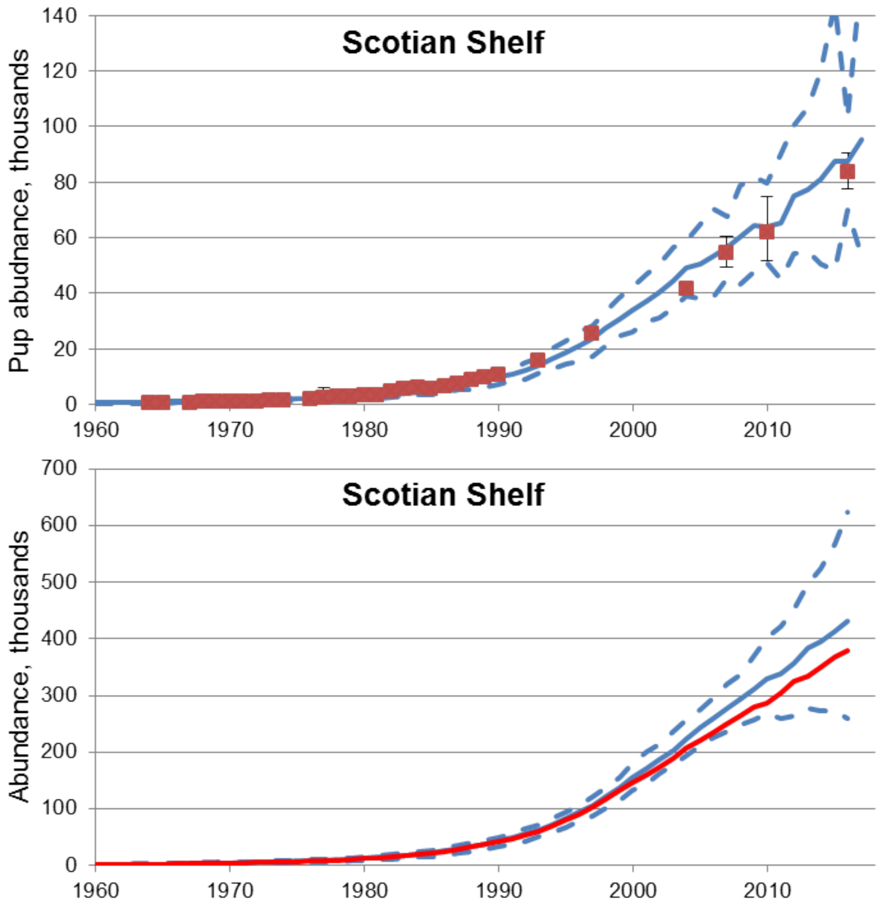


Figure 5. Model (gamma =15) estimates for total population for combined Scotian Shelf. Pup production estimates from model (solid line, dotted lines 95%CL) and survey estimates (square, 95% CL) (top) and total population size assuming a 1:1 male:female sex ratio (bottom) through 2016 using reproductive data from 1969-2015. The red line is the population trajectory assuming a male:female sex ratio of 0.69:1.

Gulf of St. Lawrence (GSL)

Fitting the model assuming gamma=15, generated parameter estimates of α=0.072 (SE=0.031), M=0.032 (SE=0.009), and K=55,600 (SE=14,300) and resulted in a 2016 pup production estimate of 14,200 (95% CL=10,500-18,300) and a total population of 51,800 (95% CL=34,800-

71,900) assuming a sex ratio of 1:1. Using a sex ratio of 0.69M:1F, the estimated population in 2016 is 44,100 (95% CI=29,600 to 61,100) (Figure 6).

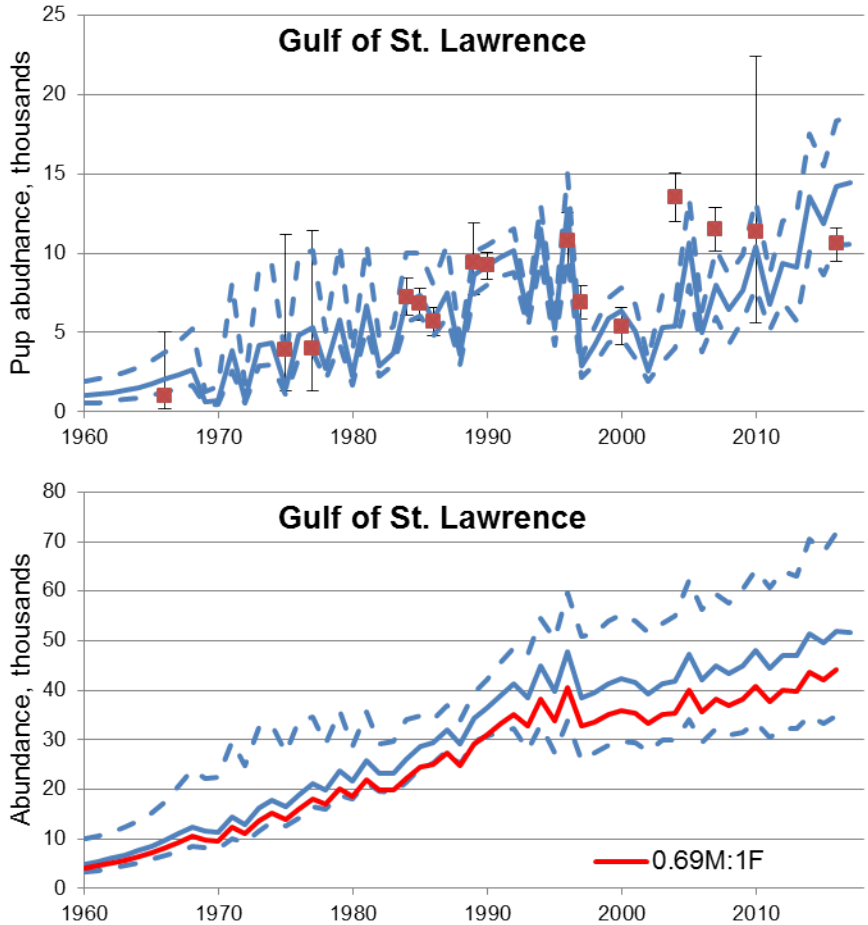


Figure 6. Gulf of St. Lawrence pup production estimates from model (solid line, dotted lines 95%CL) and survey estimates (square, 95% CL) (top) and total population size assuming a 1:1 male:female sex ratio (bottom) through 2016 using reproductive data from 1969-2015 and accounting for increased pup mortality due to poor ice conditions. Model fit gamma=15. The red line is the population trajectory assuming a male:female sex ratio of 0.69:1.

TOTAL ESTIMATED ABUNDANCE

Total grey seal pup production in 2016 estimated by the model is 101,500 (95% CI 80,600-121,600). The associated total population is 499,200 (95% CI=310,100-680,400) (Figure 7) assuming a sex ratio of 1:1. Correcting for the higher mortality rate observed among males results in a male to female sex ratio of 0.69:1. Applying this ratio to the population results in a total estimated population of 424,300 (95% CI=263,600-578,300) (rounded to the nearest 100).

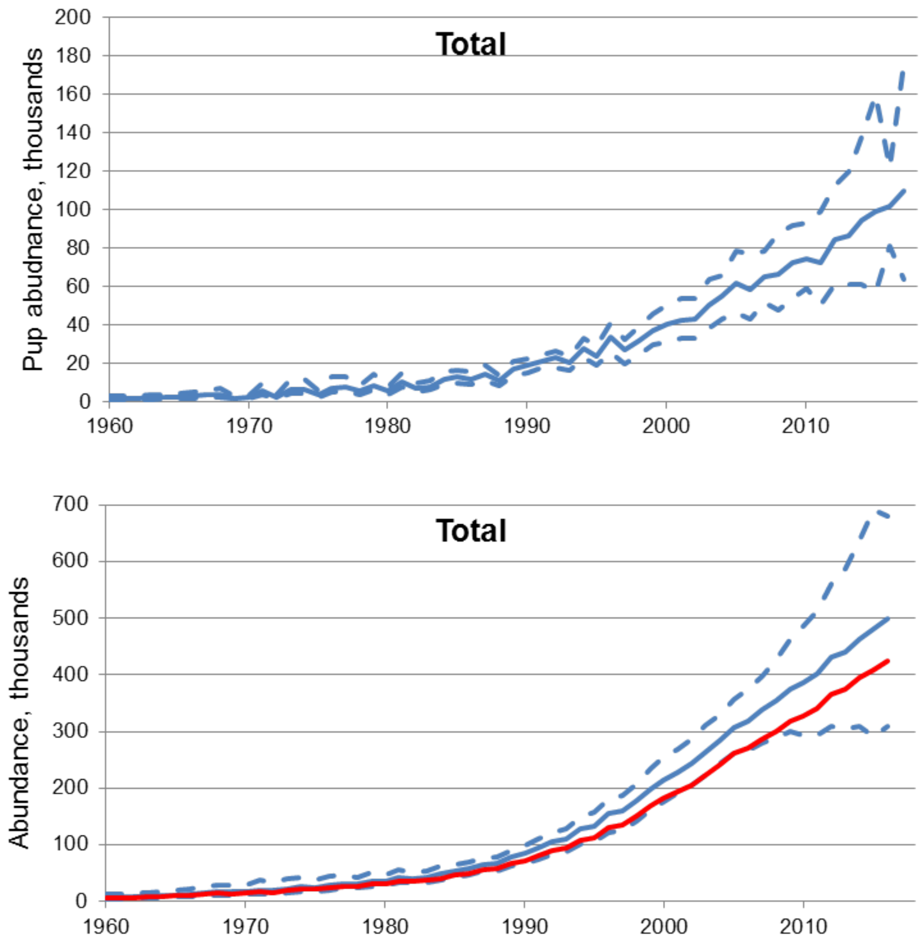


Figure 7. Canadian grey seal pup production estimates from model (solid line, dotted lines 95%CL) and survey estimates (square, 95% CL) (top) and total population size assuming a 1:1 male:female sex ratio (bottom) through 2016 reproductive data from 1969-2015. Model fit gamma=15. The red line is the population trajectory assuming a male:female sex ratio of 0.69:1.

HARVEST ADVICE

In GSL, annual harvests of 4,500 and 2,400 animals comprising 95% YOY and 70%YOY respectively would have a probability of 0.8 of remaining above N_{70} (Figure 8). A harvest of 6,700 and 7,000 would have a probability of 0.5 of the population declining to N_{70} and N_{50} respectively, if the harvest comprised 95% YOY. If the harvest comprised 70% YOY, then a harvest of 4,000 and 4,500 would have a 0.5 probability that the population will decline to N_{70} and N_{50} respectively (Figure 8).

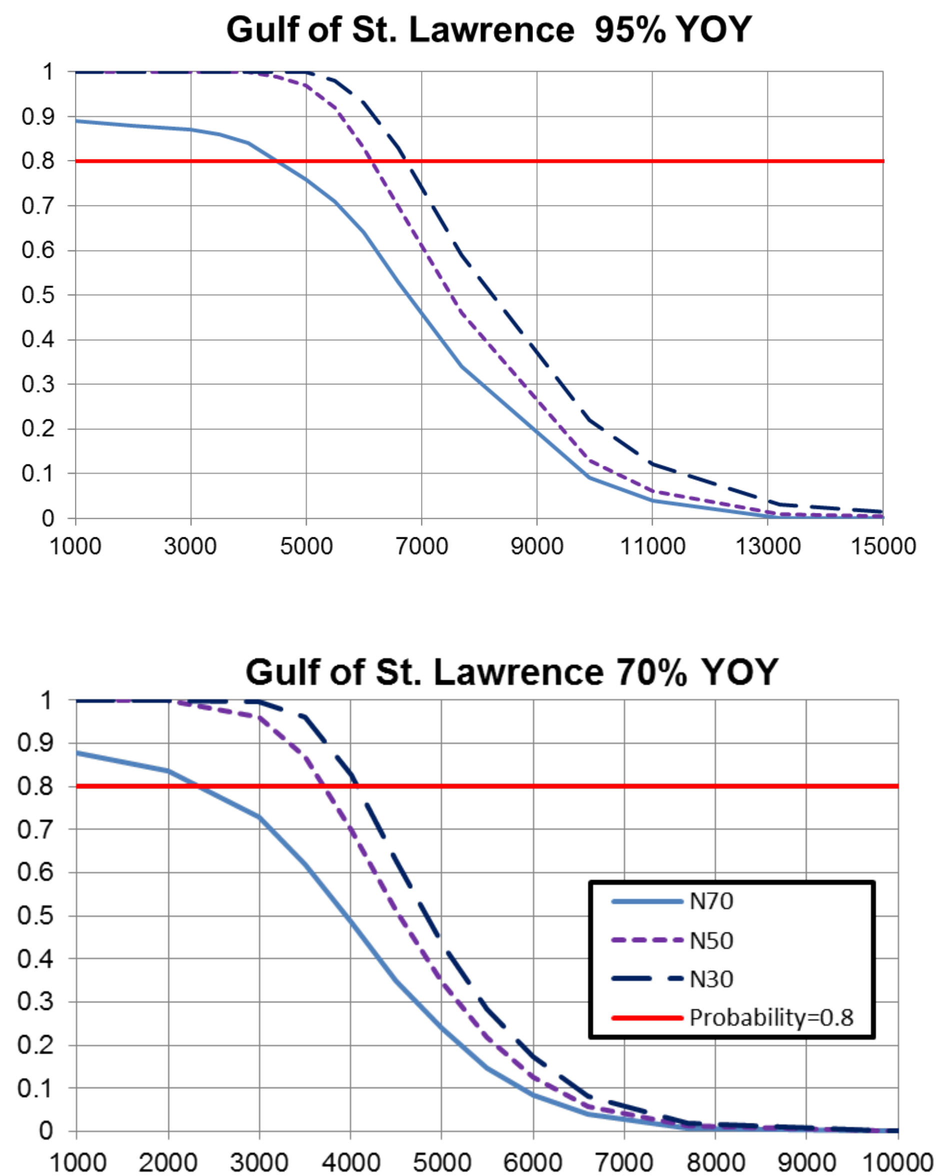


Figure 8. The probability (Y-axis) that different levels of harvest (x-axis) from the GSL herd would decline below N_{70}, N_{50} and N_{30} depending on the age composition of the harvest. The two options were 95% Young of the year (YOY) or 70% YOY. Scenarios are for annual harvests during a 5 year management plan.

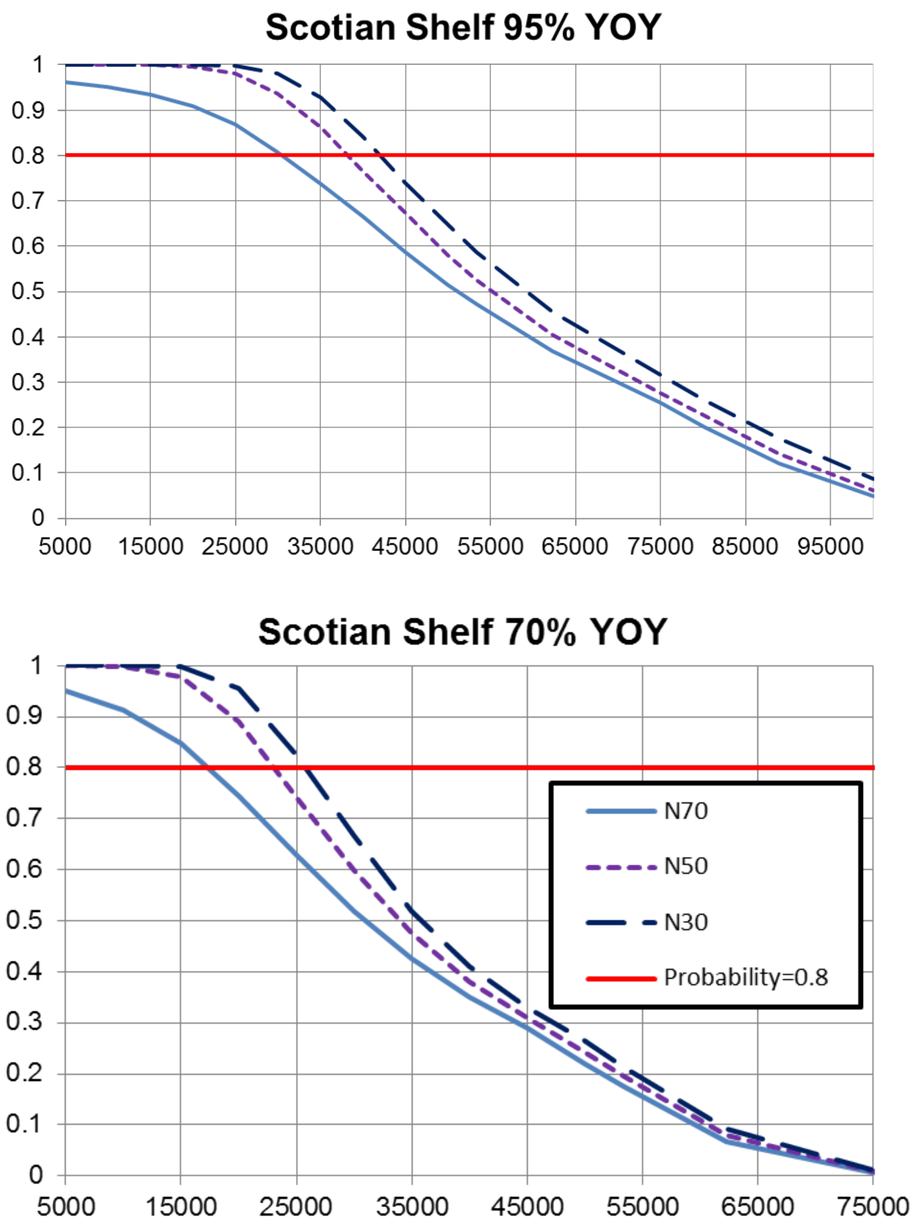


Figure 9. The probability (Y-axis) that different levels of harvest (x-axis) from the combined Scotian Shelf herd would decline below N_{70}, N_{50} and N_{30} depending on the age composition of the harvest. The two options were 95% Young of the year (YOY) or 70% YOY. Scenarios are for annual harvests during a 5 year management plan.

For the Scotian Shelf herd, harvests of 30,000 and 17,000 animals comprising 95% YOY and 70% YOY, respectively, would have a probability of 0.8 of remaining above N_{70} (Figure 9). A harvest of 50,000 and 55,000 would have a 0.5 probability in the population declining to N_{70} and N_{50} if the harvest comprised 95% YOY. If the harvest comprised 70% YOY, then a harvest of 30,000 and 34,000 would have a 0.5 probability of declining to the thresholds of N_{70} and N_{50} (Figure 9).

Combining harvests from the two main groups, a total harvest of 34,500 and 19,400 animals comprising 95% YOY and 70% YOY respectively would have a probability of 0.8 of remaining above N_{70}. A total harvest of 56,700 and 62,500 would reduce the population to N_{70} and N_{50} respectively, for a harvest comprised of 95% YOY. A harvest of 34,000 and 38,500 comprising 70% YOY would decline to N_{70} and N_{50}, respectively.

The probability of dropping below N_{70} and N_{50} for total allowable catches of 60,000, 70,000 and 90,000, 100,000, 120,000 150,000 and 200,000 animals with a composition of 95% YOY and 70% YOY were estimated (Table 5). For a total catch of 60,000 with 89% and 11% of the catch allocated to Scotian Shelf and GSL respectively (i.e. the relative population sizes), the probabilities of dropping below N_{70} for the Scotian Shelf is 53% (95% YOY) and 83% (70% YOY), and below N_{50} is 48% (95% YOY) and 80% (70% YOY). The probabilities of dropping below N_{70} for the GSL is 46% (95% YOY) and 94% (70% YOY), and below N_{50} is 30% (95% YOY) and 96% (70% YOY). Higher harvest levels increase the probability of dropping below N_{70} and N_{50}.

Table 5. Probabilities that the Gulf of St. Lawrence and Scotian Shelf grey seal herds will be below 50% and 70% of N_{max} at different total allowable catches with a catch compositions of 95% YOY and 70% YOY.

95% YOY

Total Catch	Gulf of St. Lawrence			Scotian Shelf		
	Catch	50% N_{max}	70% N_{max}	Catch	50% N_{max}	70% N_{max}
60000	6600	30%	46%	53400	48%	53%
70000	7700	44%	66%	62300	60%	63%
90000	9900	88%	91%	80100	77%	80%
100000	11000	94%	96%	89000	86%	88%
120000	13200	99%	100%	106800	97%	98%
150000	16500	100%	100%	133500	100%	100%
200000	22000	100%	100%	178000	100%	100%

70% YOY

Total Catch	Gulf of St. Lawrence			Scotian Shelf		
	Catch	50% N_{max}	70% N_{max}	Catch	50% N_{max}	70% N_{max}
60000	6600	96%	94%	53400	80%	83%
70000	7700	99%	98%	62300	91%	92%
90000	9900	100%	100%	80100	100%	100%
100000	11000	100%	100%	89000	100%	100%
120000	13200	100%	100%	106800	100%	100%
150000	16500	100%	100%	133500	100%	100%
200000	22000	100%	100%	178000	100%	100%

Seasonal abundance in the GSL

Based upon the assumed seasonal distribution of seals from the GSL and Scotian Shelf components, the estimated number of grey seals in NAFO division 4T would vary between

30,500 (SE=3,200) during January to March, increasing to a maximum of 73,100 (SE=8,400; rounded to the nearest 100) animals during July-September, then declining during the fall as animals that will breed on the Scotian Shelf leave the area (Table 6).

Table 6. Estimated number of seals (top) and standard error (bottom) from the Sable Island, CNS and GSL herds in NAFO divisions throughout the year. Total numbers have been adjusted for sex ratio assuming that there are 0.6 males for every female, based on the survival estimated from mark-recapture analysis on Sable Island (den Heyer and Bowen 2017).

Abundance	**Jan-Mar**	**Apr-Jun**	**Jul-Oct**	**Nov-Jan**
3PsPnLK	3439	2898	14426	1358
4RS	1833	15623	38095	12729
4T	30460	40058	73112	61006
4Vn	20262	13139	18271	6394
4VsW	307154	319088	270132	323741
4X	27458	17454	5557	11364
5Z	29337	11885	0	4785
Other	1882	1679	2230	447
Total	421825	421824	421824	421824

SE	**Jan-Mar**	**Apr-Jun**	**Jul-Oct**	**Nov-Jan**
3PsPnLK	492	538	2329	202
4RS	358	2286	4862	1681
4T	3242	4795	8383	7395
4Vn	2833	2379	2567	936
4VsW	56245	51961	42816	57265
4X	5255	3427	1111	2254
5Z	5869	2377	0	957
Other	227	232	404	89

DISCUSSION

Total population was estimated by fitting a model that incorporated information on age-specific reproductive rates and removals to the pup production estimates. Pup production was estimated for all breeding colonies in Canadian waters in 2016. Pup production continues to increase on Sable Island and on small colonies in southwest Nova Scotia. A new, small colony has appeared in the Bras d'Or lakes (eastern Nova Scotia), while pup production has stabilized on Hay Island (eastern Nova Scotia) and in the GSL. Age-specific reproductive rates were obtained from females shot in the GSL. This sample contains a mix of animals that breed in the GSL and on the Scotian Shelf. However, the samples from the GSL are collected in summer and early fall (up to start of October). If there are late-term abortions, as has been reported for harp seals (Stenson et al. 2016), then the reproductive rates used in the model will overestimate true values.

The Canadian grey seal population has been increasing since the 1960s. Assuming a sex ratio of 1:1, the estimated total population from the current model is 499,200 (95% CI=310,100-680,400). While the sex ratio at birth is 1:1, subsequent mortality differs by sex. In the Northeast Atlantic, it has been found that juvenile males have higher morality than females (Hall et al. 2001) and recent analysis of the mark-resighting data from Sable Island has shown that males have higher mortality rates than females at all ages (den Heyer and Bowen 2017). Assuming a constant age structure in population, the male and female survival estimated from mark-resighting analysis of individually marked seals on Sable Island suggests that there are 0.69 males for every female (den Heyer and Bowen 2017). Assuming that the other two herds have similar age structures, applying this ratio to our estimate of total population results in a 15% reduction from 499,200 (95% CI=310,100-680,400) to 424,300 (95%CI=263600-578,300) (Figure 8).

The model predicts that the grey seal population continues to increase at an overall rate of 4.4%, with increases observed in all three management areas although at different rates. The CNS herd appears to be increasing at the fastest rate (6%) due to the increase in abundance in the small colonies off southwest Nova Scotia. This increase is probably being driven by a combination of increased production and immigration, probably from Sable Island. The Sable Island colony is also increasing, but at a slightly slower rate of around 5%. This decline in the rate of increase on Sable Island is thought to be due to a combination of an increase in density-dependent mortality of juveniles and/or emigration of juveniles to the CNS colonies, as well as to the United States where marked animals from Sable Island have been reported. The model predicts that the GSL herd is also increasing, but at a rate of around 3% per year.

Mark-resighting estimates of juvenile and adult survival from Sable Island were used to inform the model. This analysis estimates apparent survival, where emigration and mortality are indistinguishable. Assuming low emigration from the breeding colony, mortality of adult female grey seals is estimated to be 0.024 while juvenile mortality (ages 0-4) was 0.26 during the period of rapid expansion of the Sable Island herd, increasing to 0.67 (den Heyer et al. 2014; den Heyer and Bowen 2017) in the 2000s when population increase had slowed to 4-5% per year. The population model estimated adult mortality on Sable Island to be 0.039. Several factors likely account for the discrepancy between the mark-resighting estimates and the population model estimates of M. In the model, M_1 is assumed to equal 15xM. After their first year, all animals are assumed to have the same mortality rate of adults. However, animals surviving their first year are not likely to assume adult survival rates immediately. Instead there is likely some improvement in survival as animals approach maturity, however, there is little information on the rate or the functional form of this improvement in survival with age. Secondly, although mark-resighting estimate mortality over the first 4 years ($M_{age\ 0\text{-}4}$), until animals are recruited to the breeding population this estimate may overestimate true mortality because juveniles are more likely to disperse than adults and may not return to Sable Island to breed. Given the large size of the Sable Island herd compared to the other breeding colonies we know that the juvenile emigration must be a small proportion of the apparent survival, but a small rate of emigration from Sable Island can have a large impact on the smaller herds.

For this study, we have assumed theta=2.4 (Trzcinski et al. 2006). Unfortunately, little is known of the functional form of the density dependent relationship for juvenile mortality. Nevertheless, the estimated large reduction in juvenile survival of seals born at Sable Island indicates that the population is likely experiencing resource limitation as the population continues to grow (den Heyer et al. 2014).

Grey seals along CNS have received less attention than in the GSL and on Sable Island. This is because the main CNS colony is relatively new and all coastal colonies combined still contribute little to the overall Canadian grey seal population. Historically, small colonies have persisted in spite of repeated harvesting activity, particularly around Basque Island off the east coast of Cape Breton Island. Erosion has altered the island so that little of it remains to serve as a pupping site and this area did not have a breeding colony in 2016. Based on bounty and science collections during the 1960s-1970s the Gaborus/Fourchu area on eastern Cape Breton Island near Hay Island was an area where grey seals were locally abundant. Currently, the CNS herd is dominated by pupping activity on Hay Island, a relatively new colony discovered in 1994.

The pup production on this island has remained stable for last three pup production surveys and the photographs suggests that this colony may be limited by available breeding habitat. A new colony was also identified in Cape Breton on Red Island, in the Bras d'Or lakes. The source of these animals (GSL, Sable Island, or CNS) is not known. The model does not fit well to the CNS trend in pup production even when the early, less reliable (those from 1984 to 1989) estimates of production are not used to fit the model. The 'best' fit generates an adult mortality estimate that is high compared to empirical estimate from Sable Island. At present the CNS component is the smallest of the three, and its location and small size mean that it is likely influenced by immigration from the larger herds.

Variable ice conditions in the GSL, particularly since the early 1990s, have complicated attempts to estimate pup production and total population. Correcting estimates for variable pup mortality at birth provides a better fit overall to the survey data. In some years, when some ice forms, limiting access to the islands, animals pup on the ice and mortality can be high if this ice breaks up before animals are weaned. If suitable ice has not formed in the GSL, then animals have their pups on land, e.g., Brion Island, Pictou Island and Anticosti Island (Hammill and Stenson 2011). These conditions are likely more favourable to the survival of grey seal pups, although human disturbance and storm surges may offset the advantages of pupping on these islands.

Grey seals were last assessed in 2014. The estimated pup production from that assessment was 93,000 (95% CI=48,000 to 137,000) with a total population estimate of 505,000 (95% CI=329,000 to 682,000). The current model produces a comparable estimate for 2014 pup production (94,500 (95%CI=60,700 to 137,500) but an estimate of total population for 2014 of 394,400, which is about 22% lower than the previous estimate. Most (approx. 64%) of the change in the total population estimate between the two assessments is due to changes in assumptions concerning the sex ratio, with new model estimates of mortality accounting for the remaining difference. In the previous assessment it was assumed that the male:female sex ratio was 1:1 while new sex-specific survival estimates from Sable Island, indicate that this is not correct and suggests that the male:female sex ratio is closer to 0.69:1 (den Heyer and Bowen 2017). In the current model runs, information from the mark-resighting program (den Heyer et al. 2014; den Heyer and Bowen 2017) was used to modify the multiplier (gamma), which sets the ratio between M and M_1 from the traditional value of 3 to 15. Limits on M were also applied as priors, which restricted estimates of this parameter within values of 0.01 to 0.07 instead of letting M range as high as 0.1 as in earlier modeling. The new model estimates of adult mortality were 0.039 and 0.032 (compared to 0.07 and 0.08 from the previous assessment) for Sable Island and the GSL respectively, which are more similar to the adult female mortality estimate of 0.024 obtained from the mark-resighting program (den Heyer and Bowen 2017). With the lower estimates for adult mortality rates, a smaller adult population is needed to account for the pup production estimates from the aerial surveys. The model responded to the lower estimates of adult mortality by increasing first year mortality, and adjusting K (equation 2). On Sable Island, estimated K declined slightly from 804,000 (SE=260,000) to 745,000 (SE=252,000) while in the GSL, larger changes in estimated K were observed. In the 2014 assessment K was 298,000 but this estimate declined to 55,600 in the current assessment. The leveling off in K is a model response to the leveling off in pup production (Figure 7b). These changes resulted in a much smaller GSL population, reducing the 2014 population estimate from 98,000 animals in the 2014 assessment to 51,500 animals in 2014 in the current assessment.

New information on demographic rates from the mark-recapture analyses, including the differences in the survival schedule for males and females and the spatial redistribution of the grey seal breeding colonies, needs to be represented in the population model to provide more robust harvest advice and allow for the assessment of ecosystem impact of grey seals. At present, projecting future trends of this population is highly uncertain. Other factors that would necessitate changes to the science advice include significant changes in age-specific reproductive rates and in juvenile mortality rates.

In this study, we provided estimates of total number of removals from the Canadian grey seal population and the probabilities that the population would decline below the maximum population size (N_{max}) which, for all areas, is the current population size. The Canadian grey seal population forms a single population (Wood et al. 2011) that has been separated into three herds for management and assessment purposes. We examined the impacts of removals by fitting the models to the GSL and Scotian Shelf herds separately. This allowed for the GSL model to include increased ice mortality. As well, the model fit to the CNS herd is relatively poor, arguably because it is being subsidized by the much larger Sable Island herd, so harvest advice is provided based on the model fit to the combined pup production for Sable Island and CNS. The impact of removals on the population varies with respect to the age composition of the harvest. The number of animals that can be removed also depends upon where animals are being harvested and the time of year. Season has an important impact because animals (adults) from both groups tend to return to their natal colonies during the breeding season but forage throughout the Scotian Shelf and in the GSL the rest of the year. Less is known about the seasonal distribution of pups and juveniles although grey seals are known to have wide distribution (Mansfield and Beck 1977; Breed et al. 2013) and recent unpublished data confirms that weaned pups from Sable Island range widely, including waters off Cape Cod, the GSL and around Newfoundland.

The estimates of total removals are associated with several caveats. Currently the population model fitted to the aerial survey estimates and the projection model, assume that both the population sex ratio and the sex ratio of the harvest are 1:1. However, there is strong evidence from the Sable Island mark-resighting that the survival of males is lower than females over all ages (den Heyer and Bowen 2017) which would result in fewer adult males in the population than females. Additional work is needed to examine the sex ratio since it is also affected by the population age structure. As recruitment slows and the age structure of the population becomes dominated by older animals, the discrepancy between the number of males and females in the population will increase. An unequal sex ratio means that we have under-estimated the impact of harvests on the population in scenarios where seals aged 1 year and older represent a large fraction of the seals removed. For harvests that comprise 95% YOY there will little impact since mortality rates of males and females in their first year are similar and the sex ratio at birth is 1:1. Also, in the model, harvest mortality is treated as additional sources of mortality. In reality, some of the animals that would be harvested would die anyway, particularly animals in their first year, which would reduce the actual impact of harvest mortality on the population. Additional uncertainties include the assumptions that future reproductive rates fall within the range of rates observed over the last five years, and that there are no changes in assumptions related to struck and loss, and the number of animals removed under the nuisance license program. It is also assumed that there is no unusual mortality event occurring over the projection period. Although the estimates of allowable removals from the CNS colonies have been combined with Sable Island in the assessment model, it is important to note that the CNS colonies alone are too small to support the total Scotian Shelf removals. Excessive harvest at the coastal colonies could jeopardize their continued use as viable breeding sites.

Information from satellite telemetry, observations from resightings of individually marked seals and tag returns show that grey seals move extensively across the GSL, Scotian Shelf and into Gulf of Maine, USA (Lavigueur and Hammill 1993, Breed et al 2006, 2009, 2013, Harvey et al 2008). In this study information on the relative distribution of male and female seals from the GSL and Sable Island herds obtained from seals that had been equipped with satellite transmitters prior to the 2010 review of grey seals (DFO 2011) was used to underline how grey seal abundance can change seasonally and spatially. The estimated number of grey seals in the southern GSL (NAFO Div. 4T) varies from 30,500 during the first quarter to as many as 73,100 animals during the third quarter. These estimates were also corrected for the differential sex ratio resulting in a 20% reduction in the number of seals present compared to a model that assumes the sex ratio is 1:1. These estimates should only be considered as illustrative since they are based on satellite transmitter deployments in the GSL and at Sable Island only and animals of all age classes have been grouped together. Since this earlier work, there have been several more deployments in both areas as well as in the CNS herd on males and females of different age classes. These additional deployments have shown that more animals move into American waters than suggested in earlier analyses.

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APPENDIX

Appendix 1. Reported removals of grey seals.

Sable

YEAR	Nuisance	Science	YOY	1 plus	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0
1969	0	0	0	0	0	0
1970	43	2	0	0	0	0
1971	1	12	0	0	0	0
1972	0	0	0	0	0	0
1973	0	0	0	0	0	0
1974	0	2	0	0	0	0
1975	22	0	0	0	0	0
1976	0	9	0	0	0	0
1977	0	69	0	0	0	0
1978	0	0	0	0	0	0
1979	0	0	0	0	0	0
1980	0	0	0	0	0	0
1981	0	69	0	0	0	0
1982	0	0	0	0	0	0
1983	0	214	0	0	0	0
1984	0	20	0	0	0	0
1985	0	0	0	0	0	0
1986	0	0	0	0	0	0
1987	0	0	0	0	0	0
1988	0	46	0	0	0	0
1989	0	477	0	0	0	0
1990	0	197	0	0	0	0
1991	0	0	0	0	0	0
1992	0	6	0	0	0	0
1993	0	0	0	0	0	0
1994	0	0	0	0	0	0
1995	0	0	0	0	0	0
1996	0	24	0	0	0	0
1997	0	7	0	0	0	0
1998	0	0	0	0	0	0
1999	1638	0	0	0	0	0
2000	1743	0	0	0	0	0
2001	1820	0	0	0	0	0

2002	1953	0	0	0	0	0
2003	2079	0	0	0	0	0
2004	2660	0	0	0	0	0
2005	2751	0	0	0	0	0
2006	3437	0	0	0	0	0
2007	3373	0	0	0	0	0
2008	3018	0	0	0	0	0
2009	5218	0	0	0	0	0
2010	1853	0	0	0	0	0
2011	1722	0	0	0	0	0
2012	5428	0	0	0	0	0
2013	3500	0	0	0	0	0

Coastal Nova Scotia

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	293	0	0	0	0
1964	0	6	0	0	0	0
1965	0	1	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	17	212
1968	0	104	0	0	18	134
1969	0	1	0	0	31	104
1970	0	0	0	0	125	450
1971	0	0	0	0	97	382
1972	0	0	0	0	32	408
1973	0	0	0	0	36	431
1974	0	0	0	0	51	482
1975	0	0	0	0	87	512
1976	0	0	0	0	80	466
1977	0	0	0	0	34	373
1978	0	0	0	0	90	290
1979	0	0	0	0	45	269
1980	0	0	0	0	211	115
1981	0	46	0	0	35	197
1982	0	69	0	0	42	276
1983	0	197	0	0	45	152
1984	0	0	0	0	34	80
1985	0	0	0	0	0	0
1986	0	0	0	0	0	0
1987	0	0	0	0	0	0
1988	0	0	0	0	0	0
1989	0	24	0	0	0	0
1990	0	9	0	0	0	0
1991	0	0	0	0	0	0
1992	0	0	0	0	0	0

1993	0	0	0	0	0	0
1994	0	0	0	0	0	0
1995	0	0	0	0	0	0
1996	0	0	6	0	0	0
1997	0	0	0	0	0	0
1998	0	0	0	0	0	0
1999	0	0	0	0	0	0
2000	0	0	82	0	0	0
2001	0	0	1301	0	0	0
2002	0	0	0	0	0	0
2003	0	0	0	0	0	0
2004	0	0	0	0	0	0
2005	0	0	494	0	0	0
2006	0	0	830	0	0	0
2007	0	0	868	0	0	0
2008	0	0	1261	0	0	0
2009	0	0	263	0	0	0
2010	0	0	50	0	0	0
2011	0	0	0	0	0	0
2012	0	0	0	0	0	0

Gulf

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0
1969	0	0	0	0	159	485
1970	0	22	0	0	0	70
1971	0	0	0	0	45	361
1972	0	0	0	0	80	191
1973	0	0	0	0	39	127
1974	0	1	0	0	75	560
1975	0	1	0	0	447	1238
1976	0	1	0	0	16	79
1977	0	0	0	0	308	673
1978	0	0	0	0	57	267
1979	0	9	0	0	190	215
1980	0	0	0	0	336	994
1981	0	0	0	0	552	1242
1982	0	199	0	0	880	961
1983	0	12	0	0	814	1721
1984	0	12	0	0	135	96

1985	0	0	0	0	141	113
1986	0	230	0	0	402	180
1987	0	249	0	0	456	593
1988	0	298	0	0	379	90
1989	0	45	0	0	138	1700
1990	0	16	50	0	48	38
1991	0	0	50	0	0	0
1992	0	260	50	0	0	0
1993	0	6	50	0	0	0
1994	0	39	50	0	0	0
1995	0	5	50	0	0	0
1996	0	33	50	0	0	0
1997	0	25	50	0	0	0
1998	0	20	50	0	0	0
1999	0	69	50	0	0	0
2000	0	89	50	0	0	0
2001	0	39	50	0	0	0
2002	0	100	50	0	0	0
2003	0	13	50	0	0	0
2004	0	93	50	0	0	0
2005	0	12	579	0	0	0
2006	0	28	1027	0	0	0
2007	0	87	879	0	0	0
2008	0	100	210	0	0	0
2009	0	0	0	0	0	0
2010	0	150	58	25	0	0
2011	0	210	200	18	0	0
2012	0	159	200	18	0	0
2013	25	58	200	18	5	20
2014	0	82	82	0	0	0
2015	0	42	1151	0	0	0
2016	0	30	1588	0	0	0