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### Trends in abundance of harp seals, *Pagophilus groenlandicus*, in the Northwest Atlantic, 1952-2019

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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.

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## ABSTRACT

Harp seals require pack ice as a platform for resting, to give birth and nurse their young. They are also subject to commercial and subsistence harvesting. We examined the status of the Northwest Atlantic harp seal population using a three parameter population model that fits to estimates of pup production and reproductive rates, and incorporates information on annual catches in Canada and Greenland (including by-catch and struck and lost), and unusual pup mortality due to poor ice conditions. After applying the model formulation used during previous assessments, the fit to the reproductive data and aerial survey data was poor. Using an alternative formulation where adult mortality was fixed and juvenile mortality estimated, and a Comprehensive Environmental Index used to vary the population carrying capacity, improved the model fit to the data. Based upon a population model that included pup production estimates up to 2017, annual estimates of age-specific reproductive rates, removals and ice related mortality up to 2019, the harp seal population appears to have been relatively stable since the mid-1990s, but has been increasing in recent years likely due to higher reproductive rates and lower removals. The model estimated a pup production of 1,039,000 (95% CI 927,000 - 1,100,000) animals and a total population size of 6.8 (95% CI 5.8 - 8.0) million animals in 2017. Projecting forward to 2019, the model estimated that the population increased to 7.6 (95% CI 6.6 - 8.8) million harp seals. Climate change is having an impact on ice-cover, particularly in the Gulf of St Lawrence, but even the northeast Newfoundland area is expected to be ice-free by the end of the century. This will have a negative impact on harp seals unless new areas for pupping are found to the north of current whelping areas.

Key words: harp seal, *Pagophilus groenlandicus*, abundance, juvenile survival, environmental index, Northwest Atlantic

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## INTRODUCTION

The harp seal (*Pagophilus groenlandicus*) is a medium sized, migratory phocid distributed over continental shelf regions of the north Atlantic. The Northwest Atlantic population summers in the Arctic, but migrates south along the Canadian continental shelf in the autumn to overwinter and reproduce off northeastern Newfoundland (Front) and in the Gulf of St. Lawrence (Gulf) (Fig. 1)(Sergeant 1991; Stenson and Hammill 2014). Harp seals require pack ice as a platform on which to haul out, to give birth, and to nurse their pup or young of the year (YOY). After weaning the YOY use the ice as a resting platform, for several weeks. The harp seal is the most abundant pinniped in the North Atlantic. They play an important role in structuring the North Atlantic ecosystem acting as both predator and prey (Morissette et al. 2006; Bundy 2001; Peacock et al. 2013; Hammill and Stenson 2014a). The Northwest Atlantic harp seal is harvested commercially in Atlantic Canada, for subsistence in Arctic Canada and Greenland, and is taken as bycatch in commercial fisheries.

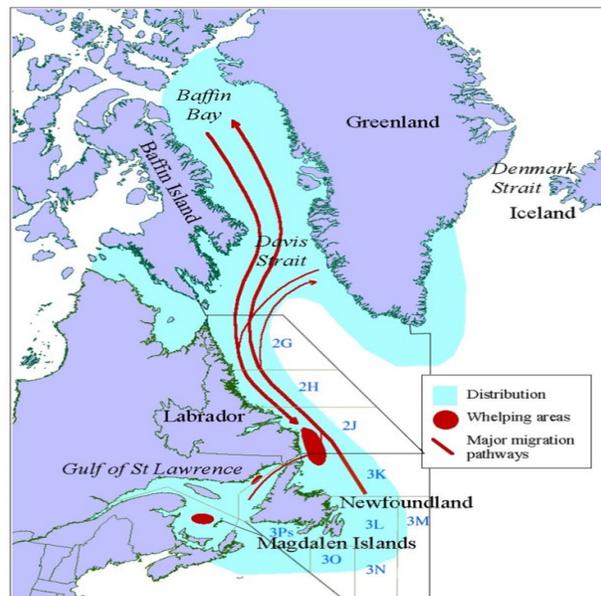


Figure 1. General locations of harp seal whelping patches in the Northwest Atlantic.

Estimated pup production of NWA harp seals increased from a minimum of 288,000 (SD=21300) animals in 1971, to a maximum of 1.58 (SD=0.137) million animals in 2008, then dropped to an estimated 797,000 (SD=69,700) animals in 2012. The most recent assessment concluded that the total population increased from a minimum of 1.15 (SD=0.090) million seals in 1971 to a maximum of 7.82 (SD=0.806) million animals in 2008, then declined to 7.45 (SD=0.698) million seals in 2012 (Fig. 2) (Hammill et al. 2015).

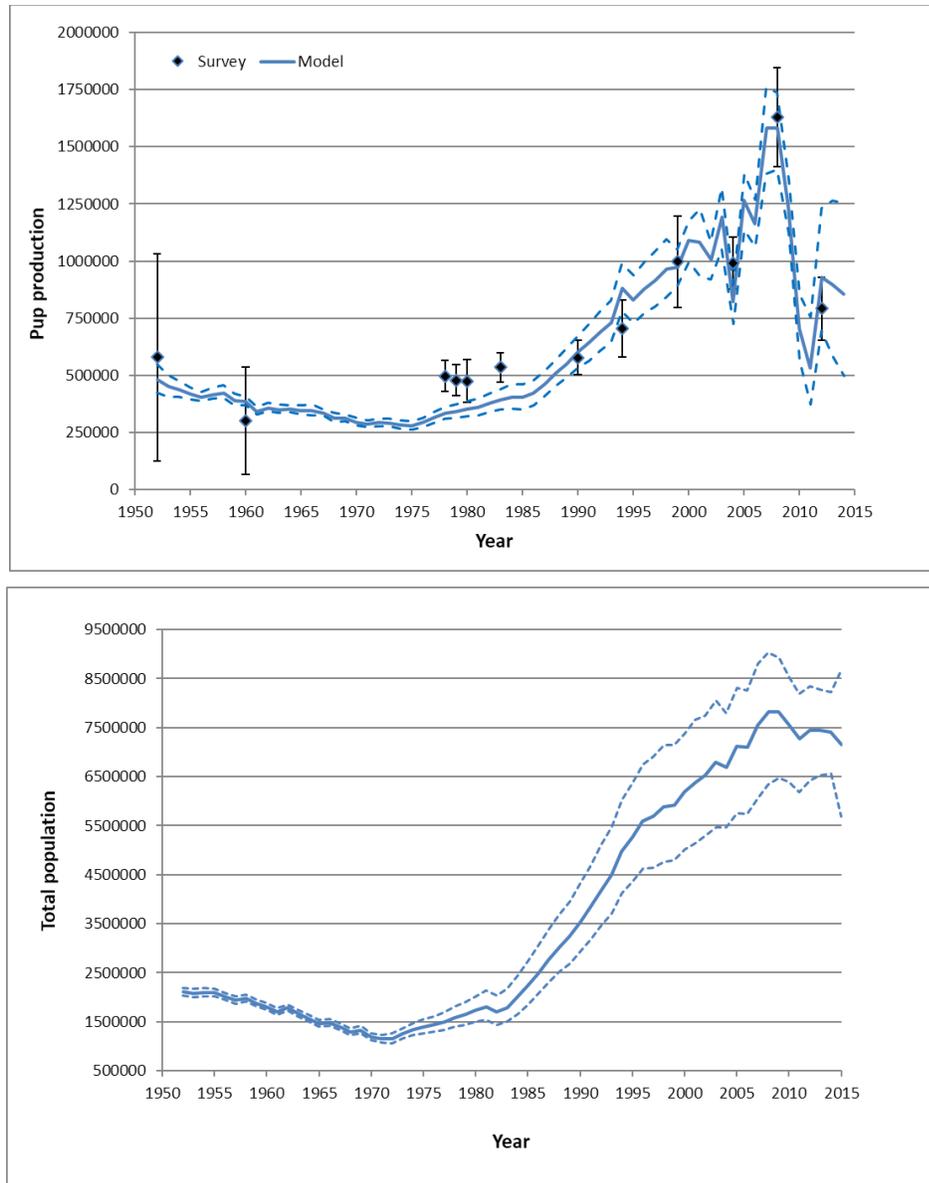


Figure 2. Estimate of pup production (top) and total abundance (bottom) of Northwest Atlantic harp seals (1952-2014)(mean  $\pm$ 95% CI). Symbols are aerial survey estimates of pup production (mean  $\pm$ 95% CI) (Hammill et al. 2015).

Climate change will induce temperature changes and associated modifications in ocean circulation, ice coverage and sea level (McCarthy et al. 2001). For harp seals, a lack of suitable or insufficient ice results in increased pup mortality (Sergeant 1991; Johnston et al. 2005; Stenson and Hammill 2014), while changes in the timing of ice breakup has cascading effects on food resources, body condition and reproduction (Buren et al. 2014; Stenson et al. 2016; Hammill and Sauvé 2017). Therefore, any attempt to model the population trend of NWA harp seals should consider the impact of a changing climate.

Several recent papers have described overall ice conditions in the NW Atlantic and have attempted to model ice cover in the Gulf and off the Front (Peterson et al. 2015; Long et al. 2015; Han et al. 2015, 2019). These exercises point to a significant reduction in overall ice cover with a decline in winter ice extent off Newfoundland and Labrador of 20-77% over the next

50 years, a delay in the timing of freeze-up, a shift in the onset of peak ice cover from the current situation of late January extending to March, to a short-lived March peak and a shortening of the overall ice cover season (Figs. 3, 4)(Han et al. 2015, 2019).

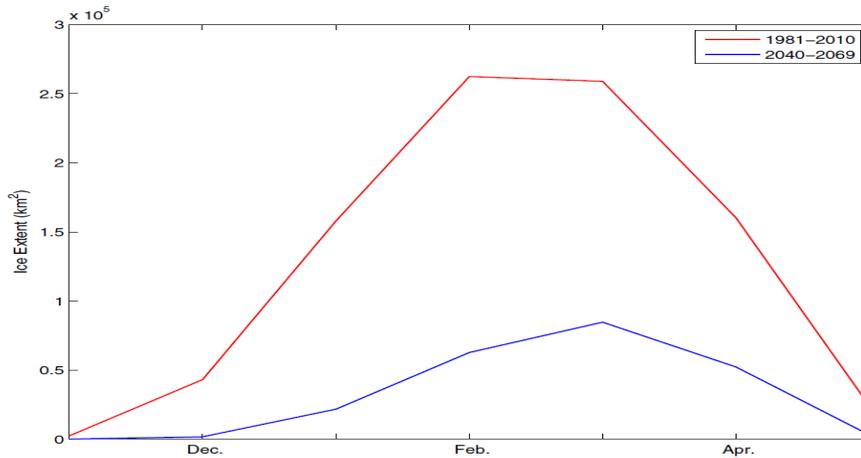


Figure 3. Simulated monthly sea-ice extent south of 55°N (Han et al. 2019)

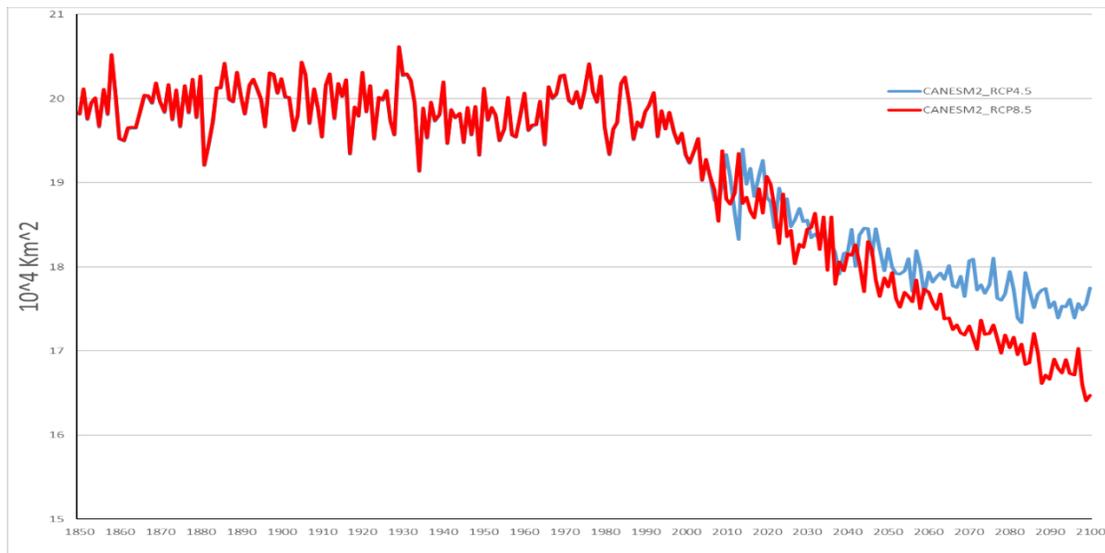


Figure 4. Simulated ice cover ( $10,000 \text{ km}^2$ ) and changes in ice cover (1850-2100) as modelled using the CANESM2\_RCP4.5 and 8.5 climate models (Han et al. 2015, 2019). Han et al. (2015) consider that the southern Labrador will be virtually ice free by 2100. For our analysis we used the 4.5 model.

A survey to estimate pup production of NWA harp seals was flown in 2017. Here we provide estimates of current abundance of NW Atlantic harp seals based upon the results of this pup production survey, and data on reproductive rates and removals up to 2019. In addition, we provide sustainable harvest advice that would maintain an 80% probability of remaining above the precautionary reference point ( $N_{70}$ ), over a period of 20 years, under age-structure catch scenarios of 5% adults/95% beaters, 10% adults/90% beaters, and 50% adults/ 50% beaters, as well as Potential Biological Removals. We examine this request within the context of predicted declining ice cover.

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## METHODS

The dynamics of the Northwest Atlantic harp seal population are described by fitting a model to independent estimates of the total pup production, and reproductive rates observed for seals 8 years of age and older (referred to as 8+)(Hammill et al. 2015). Density-dependent factors are assumed to affect reproductive rates and juvenile survival. It is also assumed that the sex ratio is 1:1. Here we present a modified model that integrates data on removals and ice-related mortality, and is fitted by adjusting initial population size ( $\alpha$ ), juvenile (i.e. less than 1 year old) mortality rates ( $M_0$ ) and the carrying capacity ( $K$ ) and includes environmental covariates for juvenile survival and reproductive rates. We compare these results to the previous version of this assessment model (Hammill et al. 2015).

We begin by presenting inputs to the population model, followed by an explanation of the model structure and fitting.

### DATA INPUT

#### Pup production estimates

The model is fit to 13 independent estimates of pup production using a combination of mark-recapture and aerial-survey methods (Table 1)(Sergeant and Fisher 1960; Roff and Bowen 1986; Stenson et al. 2014a, 2020b). A coefficient of variation of 50% has been assigned to the 1952 and 1960 surveys to account for uncertainty in methods used and survey coverage. The 1990-2017 aerial surveys have used the same basic sampling design (Stenson et al. 2020b).

#### Reproductive rates

The model is also fit to the reproductive rate data collected from 1954-2019 (Stenson et al. 2014b, 2020a). The data are smoothed by applying a local logistic regression (Hammill et al. 2015). The effect of sample size on the variability of reproductive rates has been examined and this analysis showed that the variance declined rapidly as sample size increases until reaching sample sizes of 40-50 seals, when the curve becomes asymptotic (Stenson et al. 2014b). In this study, the threshold was set at 49. If sample size exceeded the threshold, then the model used the raw data in the population model, otherwise the observed value was replaced with a value derived from the smoothing model.

The reproductive data are assumed to follow a binomial distribution. The variance around observed pregnancy rates is small (due to mostly large sample sizes), which constrains the model during fitting. Data on pregnancy rates were examined for signs of over-dispersion (i.e., variance in excess of that expected for a binomial distribution) that would justify the use of a larger variance. Four recent years of data with a sample size  $> 75$  (2009, 2010, 2011 and 2014) were selected and Monte-Carlo resampling was used to generate random subsets of increasing sizes (from 10 to 75, in increments of 5). For each year and sample size, 1000 iterations were performed. The empirical variance of these random samples was then compared to the theoretical binomial variance for that sample size  $p*(1-p)/n$  (where  $n$  is the sample size).

*Table 1. Pup production estimates (SE) from aerial surveys (1951, 1960, 1990-2012), and mark-recapture studies (1978-1983) used as input into the population model.*

Year	Southern Gulf	Northern Gulf	Front	Total	Method	Reference
1951	-	-	-	645,000 (322,500) <sup>1</sup>	Aerial survey	Sergeant and Fisher 1960
1960	-	-	-	235,000 (117,500) <sup>1</sup>	Aerial survey	Sergeant and Fisher 1960
1978	-	-	-	497,000 (34,000)	Mark-Recapture	Roff and Bowen 1986
1979	-	-	-	478,000 (35,000)	Mark-Recapture	Roff and Bowen 1986
1980	-	-	-	475,000 (47,000)	Mark-Recapture	Roff and Bowen 1986
1983	-	-	-	534,000 (33,000)	Mark-Recapture	Roff and Bowen 1986
1990	106,000 (23,000)	4400 (1,300)	467,000 (31,000)	577,900 (38,800)	Aerial survey	Stenson et al. 1993
1994	198,600 (24,200)	57,600 (13,700)	446,700 (57,200)	702,900 (63,600)	Aerial survey	Stenson et al. 2002
1999	176,200 (25,400)	82,600 (22,500)	739,100 (96,300)	997,900 (102,100)	Aerial survey	Stenson et al. 2003
2004	261,000 (25,700)	89,600 (22,500)	640,800 (46,900)	991,400 (58,200)	Aerial survey	Stenson et al. 2014b
2008	287,000 (27,600)	172,600 (22,300)	1,185,000 (112,000)	1,644,500 (117,900)	Aerial survey	Stenson et al. 2014b
2012	121,500 (15,300)	74,100 (12 400)	626,200 (66,700)	815,900 (69,500)	Aerial survey	Stenson et al. 2020b
2017	18,300 (1,500)	13,600 (3000)	714,600 (89,700)	746,500 (89,800)	Aerial survey	Stenson et al. 2020b

<sup>1</sup> Assumed a coefficient of variation of 50%.

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## Catches

Catch data available since 1952 (Fig. 5)(Stenson and Upward 2020). There is normally a two year delay in the collection of the Greenland harvest data. For 2018 and 2019, the average catch for the last five years was used.

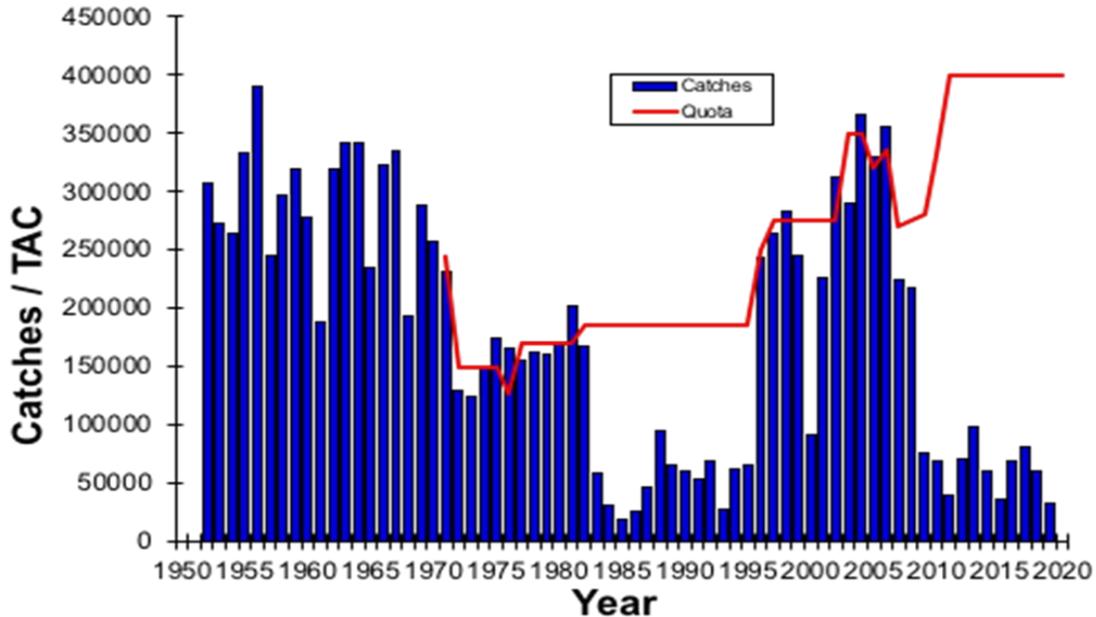


Figure 5. Reported catches of NW Atlantic harp seals (from Stenson and Upward 2020).

Corrections for struck and loss are incorporated into the model as the proportion of animals recovered (Sjare and Stenson 2002). For the whitecoat hunt prior to 1983, the struck and loss correction is only 1%. Since 1983, it is assumed that 95% of the YOY and 50% of the 1+ animals in the Canadian commercial hunt (Front and Gulf) are reported, while 50% of all animals killed in Greenland and the Canadian Arctic are assumed to have been recovered and/or reported (Sjare and Stenson 2002).

## Ice-related mortality of YOY

In some years, extremely poor ice conditions, result in increased mortality of YOY during their first month of life ( $M_{ice}$ ). This mortality is periodic and is not captured by the model estimate of mortality (Stenson and Hammill 2014). Harp seals do not use all of the available ice in the pupping areas and so minor positive or negative anomalies are unlikely to have an impact on pup survival. In some years large numbers of dead pups washed up on the beach, or were observed floating in the water, suggesting higher than usual mortality had occurred. We used these years to identify a threshold for the annual ice anomaly at -0.3 in the Gulf and -0.5 at the Front (Hammill and Stenson 2014b). The annual ice anomaly ( $A$ ) was calculated using the formula:  $A_t = (ice\ cover_t - ice\ cover_{mean\ 1969-2000}) / ice\ cover_{mean\ 1969-2000}$  where ice cover is in  $km^2$  in year  $t$ . The total extent of first year ice was taken from the Gulf of St Lawrence and southern Labrador ice charts for the weeks of 28 February and 5 March respectively from the [Canadian Ice Service of Environment Canada](#). In the last assessment the mean ice cover was estimated between 1969 (the first year we have data) and 2013. However, ice cover has declined since 2000, and there has been a marked increase in poor ice years in the Gulf. Therefore, in this assessment the period used to estimate the average ice cover was 1969-2000. No additional

mortality is assumed to occur if the ice-cover anomaly is above the threshold, but if the anomaly is below the threshold, higher than normal mortality is assumed to be proportional to the magnitude of the negative anomaly. Thus a 60% decline in ice cover is assumed to result in 60% mortality (or 40% survival).  $M_{ice}$  was calculated for the Front and the Gulf separately and then the two indices are combined, weighted assuming that 30% of pups were born in the Gulf and 70% at the Front. These are converted to a survival index ( $S_{ice}=1- M_{ice}$ ) that is included in the model as  $S_{ice}$  (Equation 2)(Appendix 1, Table 1).

## MODEL STRUCTURE

The initial population ( $Pop_{init}$ ) is entered as a vector of numbers of animals at age  $x$  ( $n_x$ ):

$$Pop_{init} = \sum_{x=1}^{26} (\alpha \times n_x) \quad (\text{Equation 1})$$

Where  $\alpha$  is a multiplier that is adjusted during the model fitting process.

In previous assessments, the model estimated adult mortality ( $M_{1+}$ ) (Equations 3,4) and fixed young of the year (YOY) mortality at three times adult mortality ( $M_0=3x M_{1+}$ )(Equation 2) (Hammill et al. 2015). In this assessment, model results using the same approach are presented, but the selected model fixed adult mortality at  $M_{1+}=0.03$ , and the model estimated  $M_0$  (Equation 2).

The model estimate of Young of the Year (YOY) mortality (as indicated above) was also assumed to be subject to density-dependent factors related to total population size  $N$ , the estimated carrying capacity ( $K$ ) and theta ( $\theta$ : set at 2.4; Trczinski et al. 2006) (Equation 2):

$$n_{1,t} = ((n_{0,t-1} \times S_{ice,t-1}) - c_{0,t-1}) \times e^{-M_0} \times (1 - (N_t/K)^\theta) \quad (\text{Equation 2})$$

The number of animals age  $x$ , with  $1 < x < X$  was related to mortality and catches:

$$n_{a,t} = \left( n_{a-1,t-1} \times e^{\frac{-M_{1+}}{2}} - c_{a-1,t-1} \right) \times e^{\frac{-M_{1+}}{2}} \quad (\text{Equation 3})$$

while numbers for the terminal age class  $n_x$  is

$$n_{A,t} = [(n_{A-1,t-1} + n_{A,t-1}) \times e^{-M_{1+}/2} - (C_{A-1,t-1} + C_{A,t-1})] \times e^{-M_{1+}/2} \quad (\text{Equation 4})$$

The number of pups born in year  $t$  is described by the number of females ( $n_{x,t} \times 0.5$  considering a sex ratio of 1:1) at age ( $x$ ) and age specific reproductive rates ( $P_{x,t}$ ) in year  $t$ :

$$n_{0,t} = \sum_{x=1}^x n_{x,t} \times P_{x,t} \times 0.5 \quad (\text{Equation 5})$$

$$n_{0,t} = \left( \sum_{x=1}^x (n_{0,t} \cdot P_{x,t} \cdot 0.5) \right) \cdot S_{ice} \quad (\text{Equation 6})$$

It was felt that in years where good environmental conditions were encountered that these conditions would likely be experienced across all the age classes and *vice versa* in poor years. We incorporated this feature of synchrony into the model using the function *Corbin*, a multivariate distribution composed of binomial distributions where the degree of correlation is controlled via an 8-dimension Gaussian copula (Hammill et al. 2015). In this function,  $n_{x.reprod,t}$  corresponded to the sample size used to obtain the observed pregnancy rate for females at age  $x$  in year  $t$ , and  $p_{x.preg,t}$  was the proportion pregnant in the observed group in year  $t$ .

For age  $x$ , with  $1 < x < 8$ :

$$P_{x,t} \sim CorBin(n_{x.reprod,t}, P_{x.preg,t}) \quad (\text{Equation 7})$$

For age  $x$ , with  $x \geq 8$  (i.e. 8+):

$$P_{x,t} = P_{8,t} \sim CorBin(n_{8+,reprod,t}, P_{8+,preg,t}) \quad (\text{Equation 8})$$

During the model fitting, the model samples from the distribution of pregnancy rates for the 8+ age class. If the reproductive rate is high, then the correlation ensures that higher values (depending on the strength of the correlation) for the other age classes will also be chosen. This synchrony increased uncertainty, since the model tends to show a mix of good and bad years for pregnancy. The model also assumes that pregnancy rates undergo density-dependent changes as the population nears carrying capacity. The predicted reproductive rates ( $P_{sim}$ ) for animals aged 8+ years in year  $t$  is:

$$P_{sim_{8+,t}} = 0.88 \times (1 - N_t / (K \times CEI))^\theta \quad (\text{Equation 9})$$

Where 0.88 is the maximum reproductive rate observed for animals aged 8+;  $N$ ,  $K$  and  $\theta$  are defined as above (equation 2) and CEI is the Composite Environmental Index. The CEI provides a measure of the overall state of environment conditions. The index is a mosaic of a time series including meteorological, sea temperature, salinity, ice and cold intermediate layer measurements from sites in the Northwest Atlantic. It is calculated annually as the sum of the standardized anomalies of 28 environmental indices (Colbourne et al. 2016).

## MONTE CARLO RESAMPLING AND PARAMETER ESTIMATION

The model creates a population matrix with 26 age classes from 1952 until the current year (Appendix 1, Table 2). It was created as an initial population age structure, with first year mortality assumed to be three times (Roff and Bowen 1986) the adult mortality rate of 0.06. The size of the initial population is adjusted by a multiplying factor ( $\alpha$ ) (Equation 1). 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 iteration of the model, pregnancy rates are resampled for each year assuming a binomial distribution (correlated among age classes). Parameters of the binomial distributions were estimated directly from reproductive rate data when the number of reproductive samples exceeds a threshold of 49 (see section 2.1.2) or based on the smoothed estimate of pregnancy rates if the number of samples is <50. Pup production estimates from the surveys are resampled assuming a normal distribution (with variance based on estimates of the survey errors). For each iteration, the model minimizes the sum of squares (MSS) of two objective functions:

$$MSS = \left[ \frac{\sum (Pup_{model} - Pup_{survey})^2}{variance_{Pup\ survey}} \right] + \left[ \frac{\sum (P_{sim_{8+,t}} - P_{8+,t})^2}{variance_{P_{8+}}} \right] \quad (\text{Equation 9})$$

by estimating three parameters; the initial population factor ( $\alpha$ ), the instantaneous mortality rate ( $M$ ), and the carrying capacity ( $K$ ). The three parameters ( $\alpha$ ,  $M$  and  $K$ ) are optimized by iterative methods (N=10,000 iterations). For each Monte Carlo iteration, new  $M$ ,  $K$  and  $\alpha$  are estimated and stored. The model runs in the programming language *R* (R Core Team 2014). Results are specified as mean ( $\pm$ SE) unless stated otherwise; 95% confidence limits are presented as 0.0275 and 0.975 quantiles, except for the 1951 and 1960 surveys which are estimated as  $\pm 1.96 * SE$ .

## PROJECTION MODEL

The projection model structure mirrors that of the fitting model. It predicts the impact of future catch scenarios based upon estimates of current population (abundance at age), carrying capacity and natural mortality, assuming the following:

1. Struck and loss do not change;

- 
2. Annual catches in Greenland followed a uniform distribution between 45,000 and 55,000; Canadian Arctic catches of 1,000 seals; and bycatch varies between 1,000 and 3,000 animals;
  3. Ice-related mortality (expressed as survival in model), is assumed to vary with the proportional change in ice cover when it falls below a threshold of 0.7. The proportion is generated by comparing the forecast ice cover divided by ice cover in 2000 (Han et al. 2015). The change in ice cover follows the Han (2015, 2019) scenario corresponding to moderate emissions of CO<sub>2</sub> as indicated under the Representative Concentration Pathway (RCP) 4.5 (Fig. 4). This pattern was recreated by fitting a logistic regression to the changes in winter ice-cover reported by Han et al. (2015, 2019), with the southeast Labrador Sea area being virtually ice-free by 2100. Two other time series were created assuming the median value  $\pm$  a random normal error (SD=1.5).
  4. Reproductive rates for 8+ year old animals were assumed to be fixed in the projection model to the values observed during the last 10 years, with each year having an equal probability of being selected.
  5. The model is projected forward to determine what level of catches will respect the management plan (i.e. 80% likelihood of population remaining above the Precautionary Reference Level) for a period of 20 years as recommended by Hammill and Stenson (2009) to account for lag effects.

### Potential Biological Removal

Potential Biological Removals (PBR), was developed in response to the United States Marine Mammal Protection Act (Wade 1998). The management objective is to prevent populations from becoming depleted, where depletion is considered to have occurred if a population falls below its maximum net productivity level (defined as being between 50% and 85% of carrying capacity) (Taylor and DeMaster 1993). The PBR approach has been subjected to extensive simulation testing to examine how it behaves under different scenarios, with the objective that the population must have a 95% probability that it will not become depleted.

PBR is calculated as:

$$PBR = 0.5 \cdot R_{max} \cdot f \cdot N_{min}, \quad (\text{Equation 10})$$

where  $R_{max}$  is the maximum rate of population increase,  $f$  is a recovery factor (between 0.1 and 1.0) and  $N_{min}$  is the estimated population size using the 20-percentile of the log-normal distribution of the most recent population estimate (Wade and Angliss 1997, Wade 1998). Within the Atlantic Seal Management Strategy (ASMS),  $f$  is set at 1.0, unless there is an obvious serious conservation concern. In the absence of data,  $R_{max}$  is assumed to be 12% for pinnipeds (Wade and Angliss 1997).

## RESULTS

Results from the re-sampling did not show any sign of over-dispersion in the data, and therefore little justification to increase the variance around pregnancy rates in the absence of other information (Fig. 6).

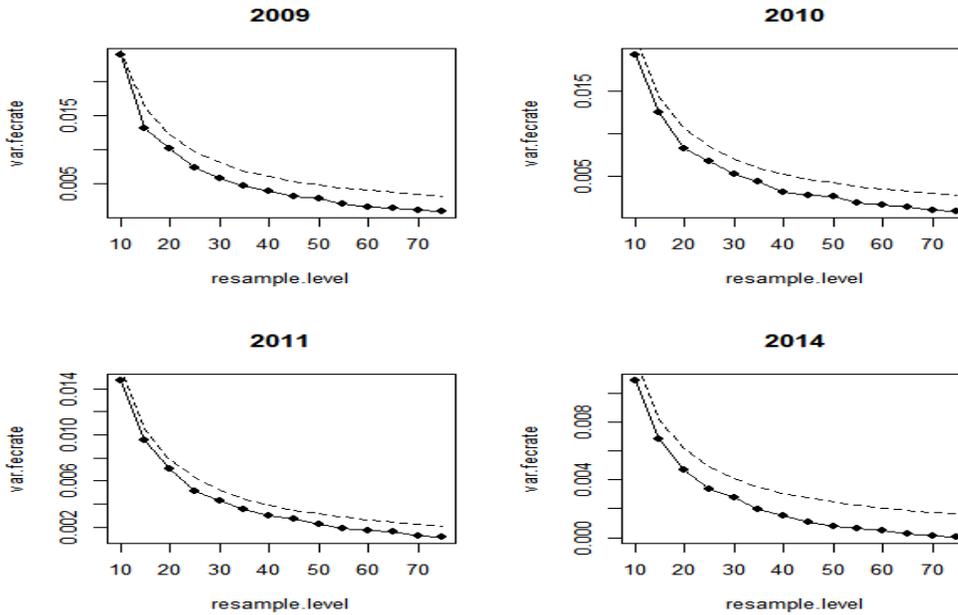


Figure 6. Results from bootstrap resampling of reproductive rate data to examine if the variance (y-axis) (solid line) was greater than expected from a binomial distribution (dotted line) for increasing sample sizes (x-axis).

The smoother fitted to the reproductive data provided a means of interpolating for missing years and captured some of the variability in the data (Fig. 7; Appendix 1, Fig. 1). The greatest number of samples was available for the 8+ year class, which also accounts for the majority of reproduction.

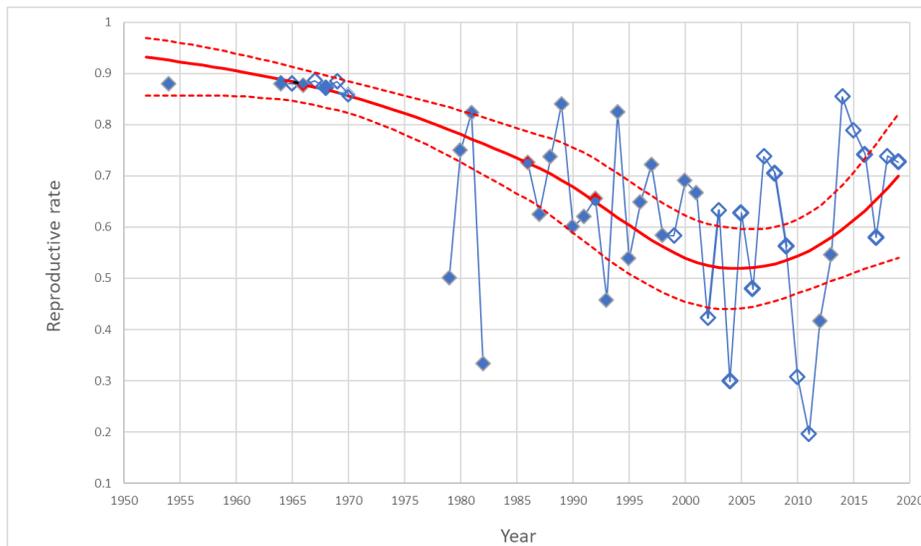


Figure 7. Reproductive rates for females 8 years of age and older (symbols) and smoothed data. Empty symbols represent samples sizes of  $\geq 50$ . Solid symbols represent sample sizes  $< 50$ . Smoothed line (1952-2019) ( $\pm 95\%$  CI) is in red.

There is considerable inter-annual variability in ice cover in Atlantic Canada, but overall, ice cover has declined by about 7% per decade since 1969 when monitoring by Environment

Canada began (Fig. 8). The decline in ice cover can be broken down into 6% per decade in the Gulf of St Lawrence, 7% per decade off the southeast coast of Labrador and 10% off northeast Newfoundland (Appendix 1, Fig. 2). The limited ice cover available in the Gulf of St Lawrence has resulted in a greater number of years where there was additional neonate mortality, although high mortality may occasionally occur at the Front as well, such as in 1981, 2010 and 2011 (Fig. 9).

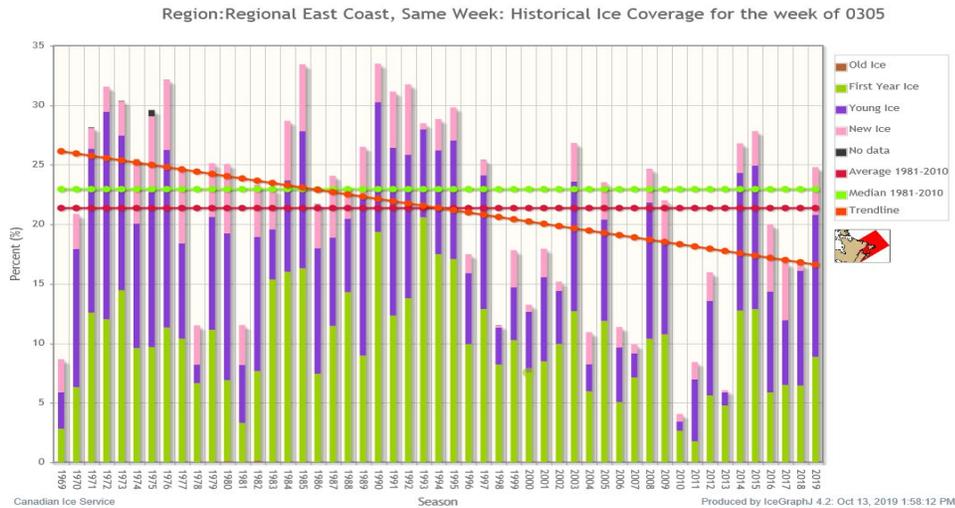


Figure 8. Ice cover (%) showing total ice concentration and concentration of first-year ice (30-120 cm thick), young ice (10-30 cm thick), and new ice (10 cm thick) in Atlantic Canada for March 5, 1969-2019.

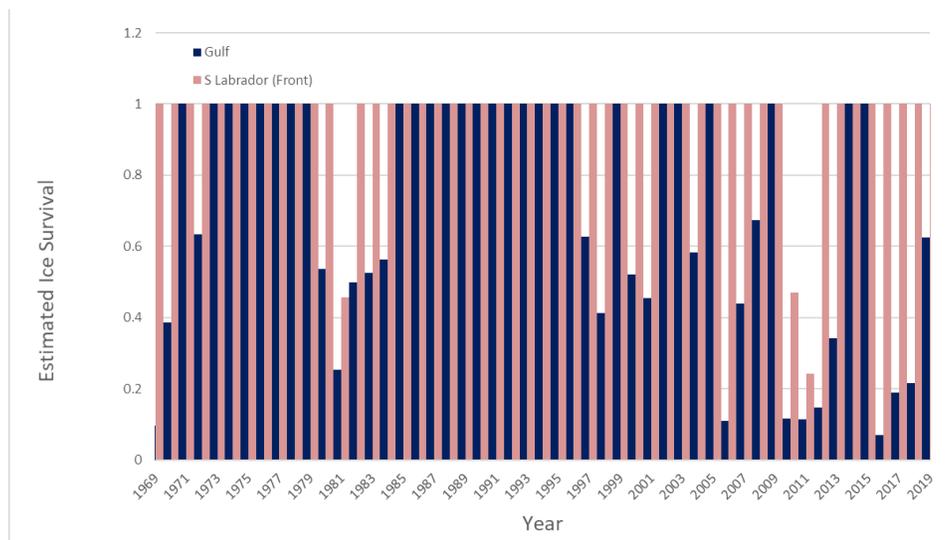


Figure 9. Estimated ice related survival of pups. The index is calculated from the standardized negative anomaly between the mean ice cover and ice cover in year  $x$ , divided by the mean.

We first ran the model formulation used in previous assessments, where the model estimated adult mortality and juvenile mortality was fixed at three times adult mortality. The model which included harvest and ice-related mortality data (1952- 2019) was fitted to the pup production estimates (1952-2017), and reproductive data (1952-2019). The estimated 2017 pup production was 952,396 (SD=45,269), which is higher than the aerial survey estimate of 746,515 (SD=89,576) pups, but there was some overlap with the 95% confidence intervals (Fig. 10). Total estimated abundance was 6.377 (SE=0.376) million seals. Estimates for  $K$  and  $M_{1+}$  were

9.585 (SE=0.437) million and 0.042 (SE=0.008) respectively (Table 2). The model fitted well to the 1978-1983 mark-recapture estimates of pup production, but was unable to capture the 1990, 1994 and 2008 surveys. The highest pup production estimate in the series was an estimated 1.38 (SD=0.091) million animals born in 2014. The model also indicated that the population peaked at around 6 million animals in 1996, remained stable until 2001, then declined to a minimum of 5.1 million seals in 2011 before recovering to an estimated 6.38 (SD=0.376) million animals in 2017 (Fig. 9). Compared to the last assessment, adult mortality increased, while the estimated K and total abundance estimate declined (Table 2).

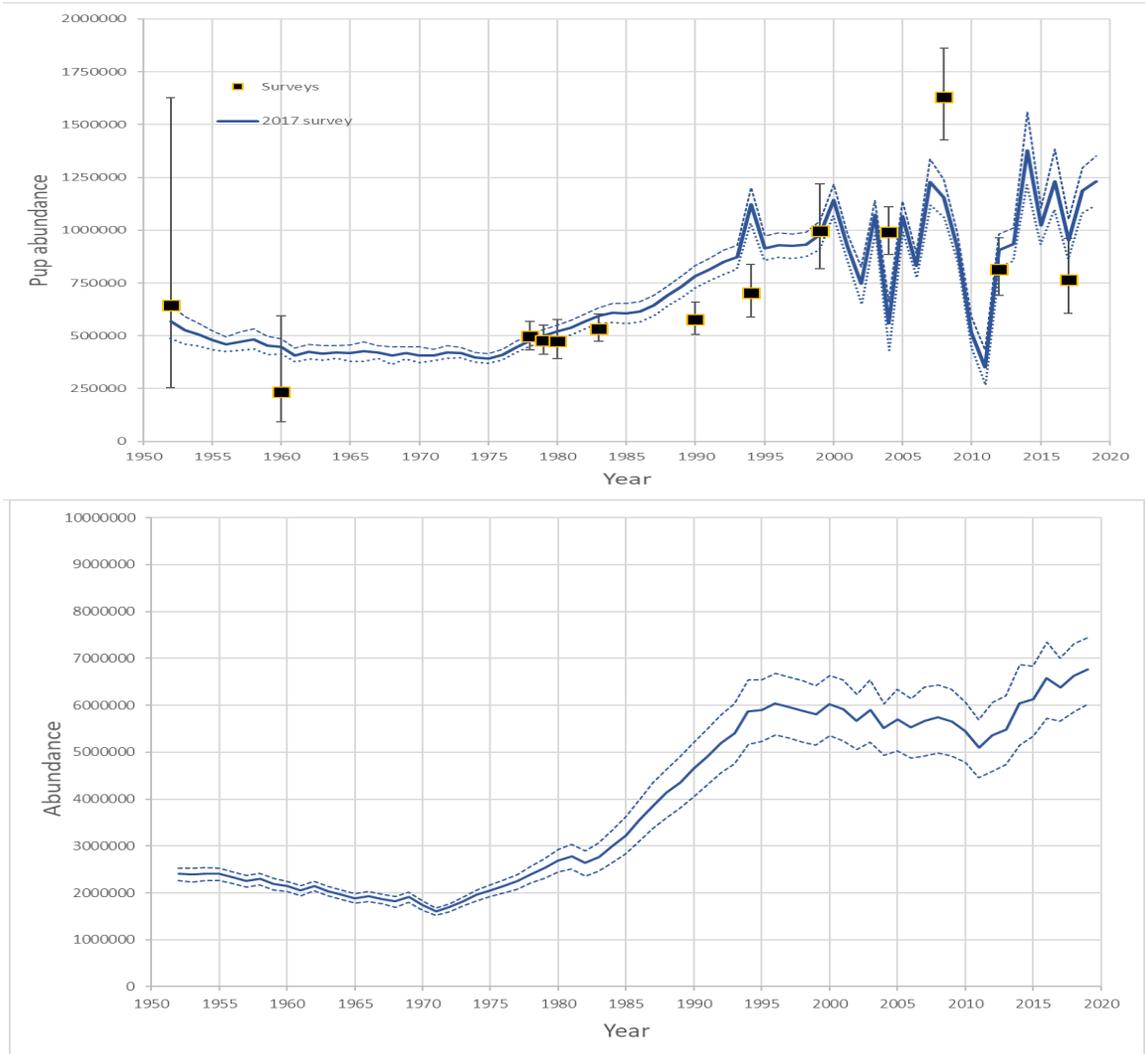


Figure 10. Estimated pup production (top) and total abundance trends from the population model using the formulation from the last (2013) assessment (bottom) ( $\pm 95\%$  CI) fitted to reproductive rate data and aerial survey estimates of pup production (1952-2019) ( $\pm 95\%$  CI). The squares represent the survey estimates of pup production ( $\pm 95\%$  CI).

Table 2. Estimates of pup production, total population, carrying capacity ( $K$ ), YOY mortality ( $M_0$ ), and adult mortality ( $M_{1+}$ ). The Standard error (in brackets), and the 95% Confidence Intervals (in curly brackets) from different model runs are also reported. The current assessment model runs fixed juvenile mortality ( $M_0$ ) and estimated adult mortality ( $M_{1+}$ ). The final model runs fixed  $M_{1+}$  and estimated  $M_0$ .

Run	2017 Pup production (thousand)	2017 Total population (million)	K (million)	$M_0$	$M_{1+}$	Alpha (initial population multiplier)
Last assessment	-	-	10.8 (0.6) {9.7-11.8}	$3 * M_{1+}$	0.025 (0.007) {0.015-0.039}	0.189 (0.011) {0.179-0.200}
Previous assessment model	952 (45.2) {865-1041}	6.383 (0.386) {5.671-7.164}	9.59 (0.439) {8.81-10.56}	$3 * M_{1+}$	0.043 (0.008) {0.037-0.058}	0.214 (0.004) {0.206-0.222}
Modified model	1 039 (55.2) {927-1139}	6.828 (0.569) {5.832-7.975}	11.9 (0.476) {11.0=12.9}	0.316 (0.079) {0.156-0.464}	0.03 (fixed)	0.212 (0.003) {0.205-0.218}

The modified model, which includes a new survey, and additional reproductive, ice mortality and catch data, resulted in a very different pattern and trend compared to previous evaluations, and differences in  $K$  and  $M_{1+}$  were also observed (Figs 2, 9; Table 2).

We modified the model to fix adult mortality at an assumed value of 0.03 and estimate  $M_0$  instead. The Comprehensive Environmental Index was also incorporated into the model to allow  $K$  to vary and the model was fitted to the aerial survey and reproductive rate data. This resulted in a 2017 pup production estimate of 1.04 (SD=0.055) million pups and a total population estimate of 6.83 (SD=0.569) million seals (Fig. 11). Juvenile mortality and the long-term average of  $K$  estimates were 0.0316 (SE=0.079) and 11.93 (SD=0.476) million animals respectively (Table 2). This formulation resulted in an improved fit to the 1990, 1994 and 2008 data (Fig. 11). The model also indicated that the population increased to 5.5 million by 1996, then showed little change until 2011, when the population dipped during the following two years with high ice mortality. Beginning in 2013, the population was estimated to then begin to increase again (Fig. 11). Estimated pup production in 2019 was 1.35 (95% CI=1.20-1.50) million seals. The total estimated 2019 abundance is 7.60 (95% CI=6.60-8.80) million harp seals.



Figure 11. Estimated pup production (top) and total abundance trends from the population model (bottom) ( $\pm 95\%$  CI) fitted to reproductive rate data and aerial survey estimates of pup production (1952-2019) ( $\pm 95\%$  CI). The model fixed adult mortality rates at  $M_{1+}=0.03$ , estimated juvenile mortality ( $M_0$ ), and incorporated a Comprehensive Environmental Index into carrying capacity ( $K$ ). The squares represent the survey estimates of pup production ( $\pm 95\%$  CI).

## HARVEST PROJECTIONS

Harvest levels that respected the management objectives (i.e. maintain an 80% probability of remaining above  $N_{70}$  for 20 years), were estimated from the model and take into account struck and loss. The harvest levels varied with model assumptions, age structure of the harvest and assumptions on the response of the population to a decline in ice cover as per Han et al (2015, 2019). We assumed that the ice declined as shown in Fig. 4. The southern Labrador coast area is considered to be ice-free in winter by 2100 (Han et al. 2015, 2019). The current  $N_{\max}$ ,  $N_{70}$ ,  $N_{50}$  and  $N_{30}$  lie at 7.6, 5.3, 3.8 and 2.3 million animals respectively.

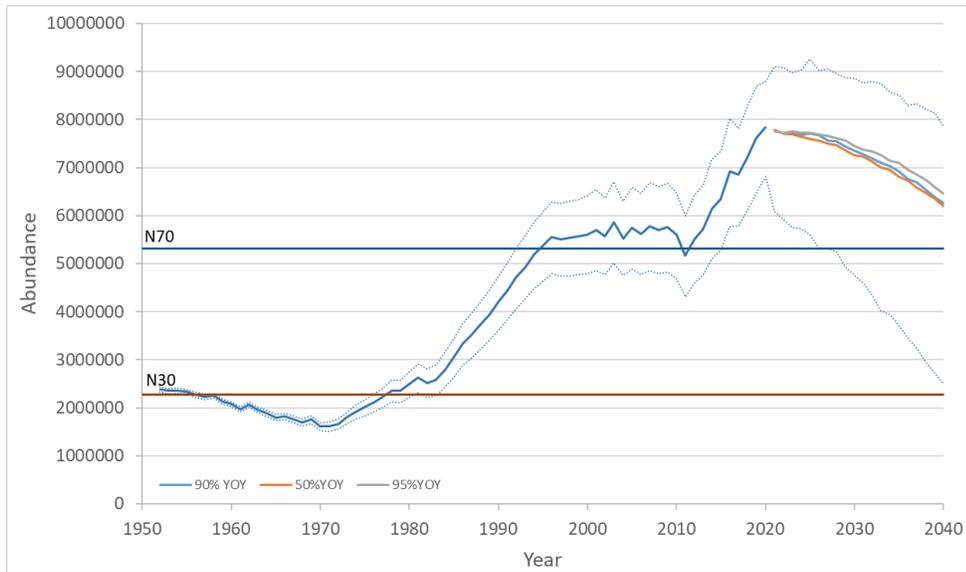


Figure 12. Population trend (1952-2019) and projected abundance using the modified model that estimated juvenile mortality. The three harvest strategies presented allow for maximum harvest that respects the management objective. The harvest levels, assume an age structure of 95% YOY/5% aged 1+ years, 90% YOY/10% aged 1+, and 50%YOY/ 50% aged 1+, for catches of 425, 375 and 175 thousand respectively (Table 3). The management objective is to have an 80% probability of the population staying above the precautionary level ( $N_{70}$ ) where,  $N_{70}$  is 70% of the largest population size observed or estimated ( $N_{Max}=7.6$  million).  $N_{30}$  is the limit reference level and is set at 30% of  $N_{Max}$ .

Table 3. Maximum harvest levels (,000s) that can be allowed to respect the management objective of an 80% probability of the population staying above  $N_{70}$  where, is 70% of the largest population size observed or estimated. Different harvest levels are presented from the different models (ie original and modified models) assuming an age structure of the harvest of 5%, 10% or 50% adults. The original model fixed juvenile mortality and estimated adult mortality. The revised model fixed adult mortality and estimated juvenile mortality.

Scenario	$N_{70}$
<b>5% adults</b>	<b>(‘000s)</b>
Original (Estimate Adult M) model	325
Modified (Estimate Juvenile M) model	425
<b>10% adults</b>	
Original (Estimate Adult M) model	280
Modified (Estimate Juvenile M) model	375
<b>50% adults</b>	
Original (Estimate Adult M) model	150
Modified (Estimate Juvenile M) model	175

Allowable removals were also estimated using PBR. PBR assumes that there is no age or gender selectivity in the harvest. It estimates all removals and so Canadian quotas must be lower to account for struck and loss, and catches in Greenland and the Canadian Arctic. PBR also does not explicitly account for the decline in ice cover in Atlantic Canada which will result in increased mortality.

*Table 4. Estimated 2019 population size, SD,  $N_{min}$  and Potential Biological Removals (PBR) for Northwest Atlantic harp seals assuming a recovery factor of 1. The previous assessment model estimated adult mortality (assuming a fixed juvenile mortality rate) and a fixed K. The new model fixes adult mortality, allows K to vary (Equation 9) and estimates juvenile mortality. PBR is a total catch, so reported catches should be lower to account for struck and loss. PBR does not explicitly consider future deterioration in habitat conditions.*

<b>Model</b>	<b>Estimate population</b>	<b>SE</b>	<b>95% CI</b>	<b><math>N_{min}</math></b>	<b>PBR</b>
Previous model	6,800,000	407,000	6,000,000-7,600,000	6,400,000	386,000
Modified model	7,600,000	643,700	6,400,000-9,000,000	7,100,000	425,600

## DISCUSSION

The assessment model used to describe the dynamics of the Northwest Atlantic harp seal population is a density-dependent, three parameter model that incorporates all known sources of human induced mortality (harvest, bycatch, struck and lost), environmentally-mediated mortality due to poor ice conditions, and annual reproductive rates. It assumes that density-dependent factors affect reproductive rates and juvenile survival. Prior to 2017, the model fitted very well to the observed changes in estimated pup production from the different surveys and provided a framework to evaluate the impacts of future catches and possible environmental changes on the population. However, with this update, which included a new survey, reproductive, catch and ice data, the fit of the model is poor and in particular, our perception of the population has changed. After the last assessment, our perception was that the population continued to increase after 1995, albeit at a slower rate, reaching a peak at around 7.8 million animals in 2008 and then stabilized at around 7.5 million animals (Fig. 2). In this new assessment, the model indicates that the population stabilized at around 5.5 million animals in 1995, and remained at these levels until 2010. It then declined to as low as 5.1 million animals in 2011, but has increased since, surpassing 7 million animals by 2019 (Table 4, Figs 10, 11). This change in population trend may result from the variable dynamics of high mortality due to varying harvest levels, ice-related mortality acting on juveniles and fluctuating environmental conditions including food resources (capelin), as their impacts work through the population (Hammill et al. 2015; Stenson et al. 2016).

Hammill and Stenson (2009) observed that a deterioration in the model fit to the survey data pointed to underlying problems relating to model assumptions, such as failure to consider ice-related mortality and its impact on juveniles. In this assessment, the poor fit of the assessment model to the 1990, 1994, 2008 and 2017 aerial survey estimates points to some feature that is not being captured. It is unclear what this might be, although it has generated some discussion among the authors. The three most plausible reasons include: an unknown change in the dynamics of the population that the model is not capturing; the recent reproductive data overestimate true pregnancy rates; the aerial survey is an underestimate due to missed pups or animals disappearing/dying prior to the survey being completed.

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The age-structured population model minimizes the sum of square differences between model and survey estimates of pup production and reproductive rates by adjusting the starting population, adult mortality and carrying capacity ( $K$ ). The catch is incorporated into the model as animals aged 0 and 1+, where the age structure of the 1+ animals is assumed proportional to their abundance in the population. For much of the time series, young of the year (YOY) have dominated the catch (99%), but since the end of the large harvests, 1+ animals have become increasingly important, although they have rarely exceeded 10% of the Canadian harvest. The previous model formulation, used in past assessments, assumed that base juvenile mortality rate ( $M_0$ ) is three times the adult mortality ( $M_{1+}$ ) and that  $M_0$  is also affected by density-dependent factors. The end of the large hunts a decade ago would have had the effect of a sudden increase of juveniles in the population. The model may not be able to adjust for this change in numbers because the signal is too sudden, very recent and likely transitional.

In wild mammal populations with limited human interference, annual adult female survival should be at least 0.94, and quite likely 0.99 or better (Eberhardt 2002). When resources are abundant, rates of juvenile survival to reproductive maturity are also high, and may approach adult rates. However, as the population increases, density-dependent changes are expected to occur as a population approaches carrying-capacity ( $K$ ), which is manifested as changes in growth, followed by an increase in juvenile mortality, then a decline in reproductive rates and finally an increase in adult mortality (Eberhardt 2002; Eberhardt and Siniff 1977; Fowler 1987; Gaillard et al. 1998). While conceptually simple, data to support this paradigm are difficult to obtain due to challenges in measuring the attributes of large long-lived mammals showing delayed maturity and low productivity, combined with the challenges of separating density-dependent effects from the complex interaction with environmental and habitat attributes, predation, and time-lagged effects (Owen-Smith 2006; Owen-Smith and Mills 2006; Bradshaw et al. 2006; Chamaillé-Jammes et al. 2008).

For harp seals, the removal of large numbers of YOY in the various hunts would have compensated to some extent for the density-dependent factors affecting  $M_0$ . After a decade of high harvests and high ice-related mortality, the sudden declines in the commercial and subsistence hunts will have released a large number of YOY into the population, which may be difficult for the model. To work around this, the model was updated, fixing  $M_{1+} = 0.03$ , which is similar to our  $M_{1+}$  estimate of 0.025, (95% CI= 0.015–0.039) from the last assessment, and a value of 0.02 for female northwest Atlantic grey seals (Hammill et al. 2014, 2015; den Heyer and Bowen 2017). The model was then allowed to estimate  $M_0$ . This improved the fit of the model to the pup production estimates.

In the model, reproductive rates are assumed to vary in a density-dependent manner determined by the relationship between current abundance and  $K$  (Equation 9). Over the last 60 years there has been a decline in size at length and mass of harp seals as well as considerable inter-annual changes in body condition, supporting the underlying hypothesis that density-dependent factors mediated by environmental conditions, most likely related to fluctuations in the abundance of their primary prey capelin, and changes in ice breakup conditions, are affecting the dynamics of this population (Buren et al. 2014; Stenson et al. 2016; Hammill and Sauv e 2017). Since the 2012 survey, reproductive rates have been higher than what would be expected if driven primarily by density-dependent factors (Fig. 6). There have been no changes in collection methods, and sample sizes are reasonable ( $N=69-110$ ), with the exception of 2015, when only 19 samples were obtained. Similarly, the variance does not appear to differ from that expected of a binomial distribution. The samples continue to be dominated by animals aged 8 years and older, while few samples are collected from younger animals, but there does not appear to be any clumping associated with the sampling. Therefore, unless there has been a

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change in behaviour between pregnant and non-pregnant animals, there does not appear to be a problem with the reproductive rate data.

Overall, capelin biomass remains low, but reproductive rates continue to mirror changes in capelin biomass which show increases from 2010 to 2015, then decline between 2015 and 2017, then increase again to 2019 (Stenson et al. 2020b). The continued strong association between capelin biomass and reproductive rates suggests that the observed rates are real and that fluctuations in reproductive rates reflect environmental variability. The original assessment model assumes that  $K$  is fixed, which in terrestrial ecosystems is overly simplistic (e.g. Chamaillé-Jammes et al. 2008) and is equally true in marine systems, as shown by the fluctuations in capelin biomass. A simple density-dependent relationship to a fixed  $K$  cannot handle the widely varying reproductive rates observed since 2010. A large-scale environmental index operating on the  $K$  parameter was included in the model to capture some of this variability. This improved the fit to the 1990 and 1994 survey data, and to a lesser extent the 2008 survey data (Fig 10, 11).

Overall, the basic model estimated a pup production of 1,039,000 animals (Table 2). This compares to an aerial survey estimate of 746,000 pups. Aerial surveys are one of the most commonly used methods to estimate abundance of marine mammals. They may be biased if seals are present but not detected, if a segment of the population is not available when the survey is flown, or if concentrations of animals are not detected. Myers and Bowen (1989) attempted to quantify this bias and concluded that failure to locate all concentrations of pups was the greatest source of potential bias for surveys of ice breeding seals, followed by failure to detect pups on the photographs and lastly, failure to correct for pups born or having left the ice after the survey was completed. The current surveys are characterized by extensive surveillance flights of the Gulf and Front areas to detect all concentrations, corrections for missed detections on the imagery and corrections for births that occurred after the surveys were completed. In recent years, the use of digital imagery has reduced the size of the correction that must be applied to adjust reader counts compared to earlier surveys, and the surveys are timed to fly after most pups have been born, but before animals enter the water (Stenson et al. 2020b).

The 2017 aerial survey was characterized by an absence of ice in the Gulf and survey estimates were less than 20,000 pups, compared to the roughly 100,000 to 200,000 pups estimated in previous surveys. The low numbers in the Gulf suggests that: Gulf females did not give birth (possibly aborted) in the absence of ice; females shifted to the Front to have their pups or mortality was high, due to the very poor Gulf ice conditions. Aerial surveillance was temporally and spatially extensive in the southern Gulf. There were no reports of births on land, which is consistent with what we know about this species (Stenson and Hammill 2014). However, there may have been some higher than normal mortality due to the very poor ice conditions. On 5 March a concentration of pups was located approximately 100 km to the north of Prince Edward Island in ice with 9/10 cover consisting of 3/5 first year ice, the rest comprising grey-white and new ice in small pans and slush. This concentration had not been detected prior to March 5<sup>th</sup>, and was not seen after this date. Pups were later located along the north shore of Prince Edward Island during photographic surveys the 6 and 7 March. If the patch of animals mentioned above drifted to the PEI coast, then mortality could have been high, due to high winds (gusts of over 80km/h) recorded at the time. These conditions could have broken up the ice and cast the pups into the water where they would have drowned prior to the survey being flown.

Surveillance was also extensive at the Front, and any northern patches would have been expected to have been detected as they drifted south over the surveillance period. Pupping at the Front started early compared to previous years, which is consistent with the movement of

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some females from the Gulf to the Front. In conclusion there is evidence to suggest that there may have been some higher than normal mortality of pups in the Gulf and some females also appear to have adapted to the poor ice conditions in the Gulf by pupping at the Front.

Harp seals use only a fraction of the available seasonal ice (e.g. Stenson et al 1993, 2003) and so it would be expected that overall ice-cover would not have a major impact on harp seals until total cover fell below some critical threshold (Stenson and Hammill 2014). We have attempted to develop quantitative measures, but outside of extreme conditions, it is difficult to evaluate the accuracy of this metric. Currently, when the ice cover falls below the threshold, ice-related mortality of YOY increases linearly. However, we cannot ignore the possibility that as ice cover declines, ice-related mortality accelerates i.e. increases non-linearly. Poor ice conditions in 1969, and especially in 1981 (Appendix 1, Fig. 1), combined with a large hunt resulted in the 1981 cohort disappearing from the population (Sergeant 1991). The winters of 2010 and 2011 were also extremely poor ice years, and mortality was considered to be high in both years, although the response of harp seals to these poor conditions differed (Stenson and Hammill 2014). In 2010, there was very little ice-formation in the Gulf and few animals gave birth there. At the Front, there was no ice present early in the pupping period and a significant shift northward in the location of the herd to more suitable ice occurred. In contrast, thin ice formed in the traditional whelping areas prior to pupping in 2011. Females pupped on the ice which subsequently broke up, resulting in high YOY mortality. Reproductive rates were low in 2010 and particularly low 2011, and it is expected that few animals survived due to a combination of lower pup production, high YOY mortality and harvesting. The poor Gulf ice conditions observed in 2017 indicate that YOY mortality in the Gulf could be high. However, it is more difficult to evaluate YOY mortality when ice quality deteriorates, but not in a way that is sufficient to identify a major mortality. Thus, mortality that exceeds background levels may occur, but will not be detected. In the Gulf we assumed that if first year ice cover fell below a threshold of 30%, then mortality would increase proportionally by the magnitude of the decline. At the Front, because there is more first-year ice and more options for suitable ice for pupping we set the threshold at 50%. However, ice-cover at the Front has declined by 20-30% over the last two decades and it has become increasingly difficult to find ice suitable for aircraft to land near the seals (Appendix 1, Fig. 2). This does not indicate that harp seal pups require pans suitable for landing a helicopter, but it points to an overall deterioration in ice conditions, where pans are now smaller and more open water is present which increases their vulnerability to ice destruction and drowning of pups during storms. If YOY mortality is increasing at the Front as well, then perhaps setting the Front threshold at 0.5 needs to be revisited. Similarly, in our projections evaluating the impact of harvesting on the population we assumed a threshold 0.7, which assumes that there is no ice mortality until there is a 30% decline in ice cover. Suggested harvests and how seal mortality might respond are very sensitive to this threshold.

The harvest removes primarily YOY, but since not all animals are mature until they are 8-10 years old, the impact of any harvest will not be observed until a harvested cohort is recruited into the breeding population. Harp seals are long-lived, with females continuing to reproduce well into their 20's. Consequently, a sharp reduction in a single cohort will have little impact on future pup production, but the sharp reduction in several cohorts will be reflected in future pup production for many years to come. On top of this, aerial surveys to estimate pup production are only flown every five years. The cumulative impact of these factors is that there will be a lag between when a given harvests or mortalities occur and when the effects will be reflected in the number of pups born. Since the pup surveys are the only tool available to monitor abundance and surveys are infrequent, it may be several years before a change in abundance is detected. To accommodate the impacts of these lags, Hammill and Stenson (2009) recommended that the impact of any harvest be evaluated over a minimum of 10-15 years. However, in order to identify a Total Allowable Catch over a 5 year management plan, its impact on the population is

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evaluated over the next 20 years, i.e. an additional 15 years after the management plan ends. This results in a more conservative TAC, but also avoids a risk of collapse in the population, which is not detected until a significant decline may have occurred for the reasons outlined above (Hammill and Stenson 2009). Harvest levels that respected the management objectives were sensitive to the types of models applied and the assumed threshold for ice-related mortality in the projections (Table 3). Under DFO's Atlantic Seal Management Strategy, the management objective is that a TAC will be set to maintain an 80% probability that the population will remain above  $N_{70}$ . Depending on where the population is relative to the  $N_{70}$  level the TAC could result in the population declining, as long as the probability of the population remaining above  $N_{70}$  is at least 80%. The rate at which the population may approach  $N_{70}$  will be affected by harvest rates, age structure of the harvest, changes in reproductive rates in response to density-dependent and environmental factors, and changes in ice conditions. In our catch scenarios we have made assumptions about how these factors may vary in the near future. In contrast, PBR assumes that there is no selectivity in the harvest, and does not explicitly consider environmental change, although adjusting the recovery factor provides a blunt approach to account declining environmental conditions. PBR also includes all sources of removals, and therefore to set the Total Allowable Catch, must be adjusted for catches in Greenland and the Canadian Arctic, struck and loss, and bycatch, (Table 4).

## OUTLOOK

The NW Atlantic harp seal is the largest of the three harp seal herds in the North Atlantic with an estimated population of 7.6 million animals. This compares to current estimated abundance of 1.5 million harp seals in the Barents/White Sea and 434,000 seals in the Greenland Sea herd (Biuw et al. 2019). Harp seals require stable pack-ice for breeding and although currently abundant, the decline in ice cover will have negative impacts on population trends in the short to medium term. Climate change will lead to a reduction in ice cover in the North Atlantic and its effects on harp seals are being felt in all areas with a decline in pack-ice in the Barents Sea and off the east Greenland coast, an increase in frequency of poor ice years in the Gulf, and the decline in ice cover at the Front. Han et al. (2015, 2019) predict a decline in overall ice cover, with the southeastern Labrador Sea being virtually ice free by 2100 (Fig. 4). Although not modeled explicitly, the Gulf will likely be ice-free well before then. At current low levels of harvest (approximately 60,000 animals in each of Canada and Greenland), the NW Atlantic harp seal population are expected to continue to increase until the middle of the century. However, the decline in ice cover is expected to become an increasingly important factor driving the dynamics of this population (Figs. 4, 13). One possible scenario is that harp seals may disappear from the Gulf and then, the southern Labrador Sea, and overall the population will decline unless they are able to find new areas for pupping further north (e.g. Stenson and Hammill 2014). This will require new considerations to manage for these changes.

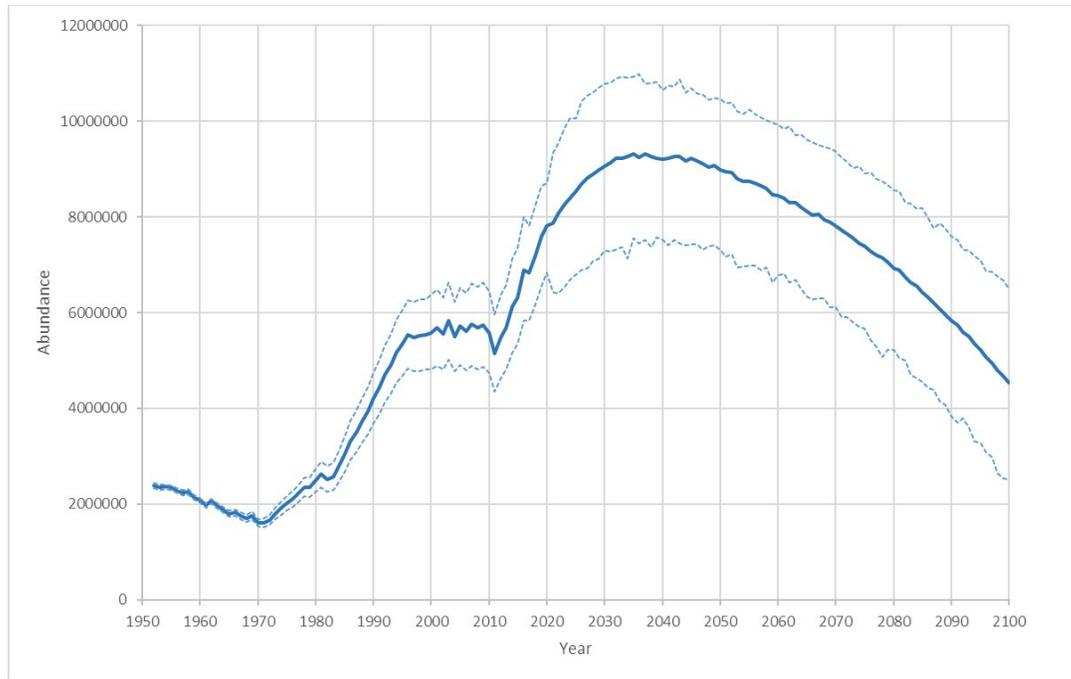


Figure 13. Projected trends in abundance ( $\pm$  95% CI) of the NW Atlantic harp seal population, with an annual Canadian harvest of 60,000 seals and assuming the decline in ice resembles the predictions of CANESM2\_RCP4.5 climate models (Han et al. 2015, 2019).

In the meantime, as ice cover declines, it is predicted that the timing and duration of peak ice will also change with a shift in peak ice to later dates and earlier breakup. In the Gulf the appearance of first births has advanced by one week, from 28 to 21 February, over the last decade (Hammill unpublished). It will be interesting to see if pupping at the Front also advances as the ice declines in that area as well.

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## APPENDICES

*Appendix 1, Table 1. Estimates of ice-related survival. The parameter is initially estimated as a mortality by the standardized difference in ice cover from the 1969-2000 mean ice cover. A threshold of -0.3 is used in the Gulf and -0.5 for the Front. If the ice anomaly is above the threshold, ice related mortality is set to 0. If it is below the anomaly, it is equal to the anomaly. Mortality is converted to survival by adding 1. The mortality estimates for the two regions are weighted using a weight of 0.3 for the Gulf and 0.7 for the Front.*

Year	Survival	Year	Survival	Year	Survival	Year	Survival
1952	1	1972	1.00	1992	1.00	2012	0.76
1953	1	1973	1.00	1993	1.00	2013	0.51
1954	1	1974	1.00	1994	1.00	2014	1.00
1955	1	1975	1.00	1995	1.00	2015	1.00
1956	1	1976	1.00	1996	0.93	2016	0.78
1957	1	1977	1.00	1997	1.00	2017	0.79
1958	1	1978	0.64	1998	0.92	2018	1.00
1959	1	1979	1.00	1999	1.00	2019	0.76
1960	1	1980	1.00	2000	0.92	-	-
1961	1	1981	0.45	2001	0.93	-	-
1962	1.00	1982	0.78	2002	1.00	-	-
1963	1.00	1983	0.91	2003	1.00	-	-
1964	1.00	1984	1.00	2004	0.52	-	-
1965	1.00	1985	1.00	2005	1.00	-	-
1966	1.00	1986	0.78	2006	0.59	-	-
1967	1.00	1987	0.93	2007	0.56	-	-
1968	1.00	1988	1.00	2008	1.00	-	-
1969	0.45	1989	1.00	2009	1.00	-	-
1970	1.00	1990	1.00	2010	0.35	-	-
1971	1.00	1991	1.00	2011	0.25	-	-

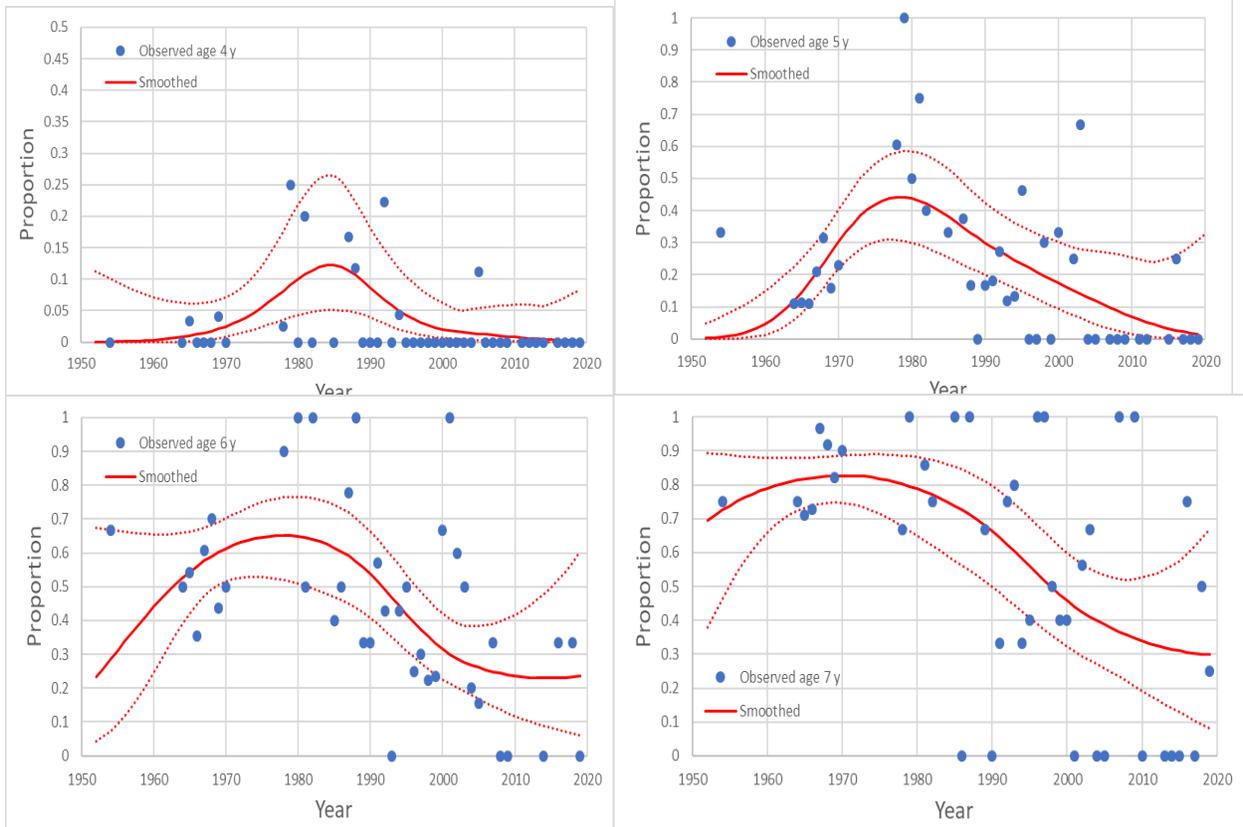
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*Appendix 1. Table 2. Age vector used when initiating the model.*

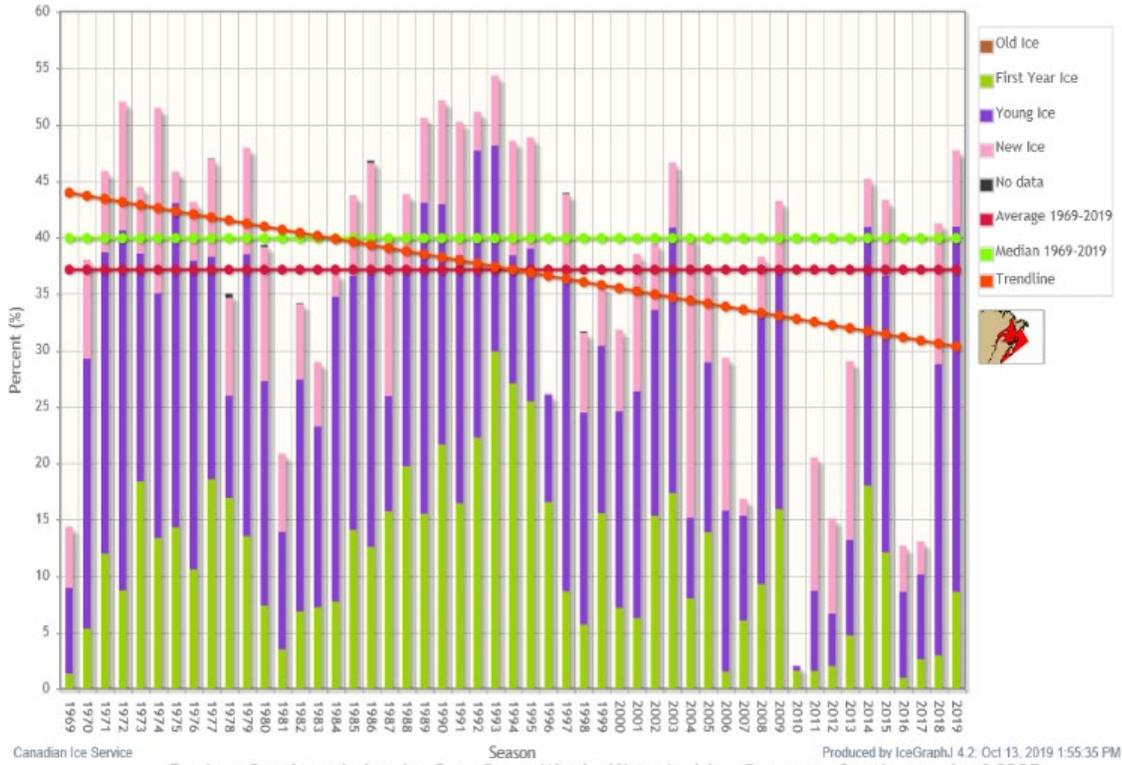
Age (years)	Initial abundance	Age (years, cont'd)	Initial abundance (cont'd)
0	800,000	13	312,204
1	656,000	14	293,472
2	616,640	15	275,863
3	579,642	16	259,311
4	544,863	17	243,753
5	512,171	18	229,128
6	481,441	19	215,380
7	452,555	20	202,457
8	425,401	21	190,310
9	399,877	22	178,891
10	375,885	23	168,158
11	353,332	24	158,068
12	332,132	25	148,584

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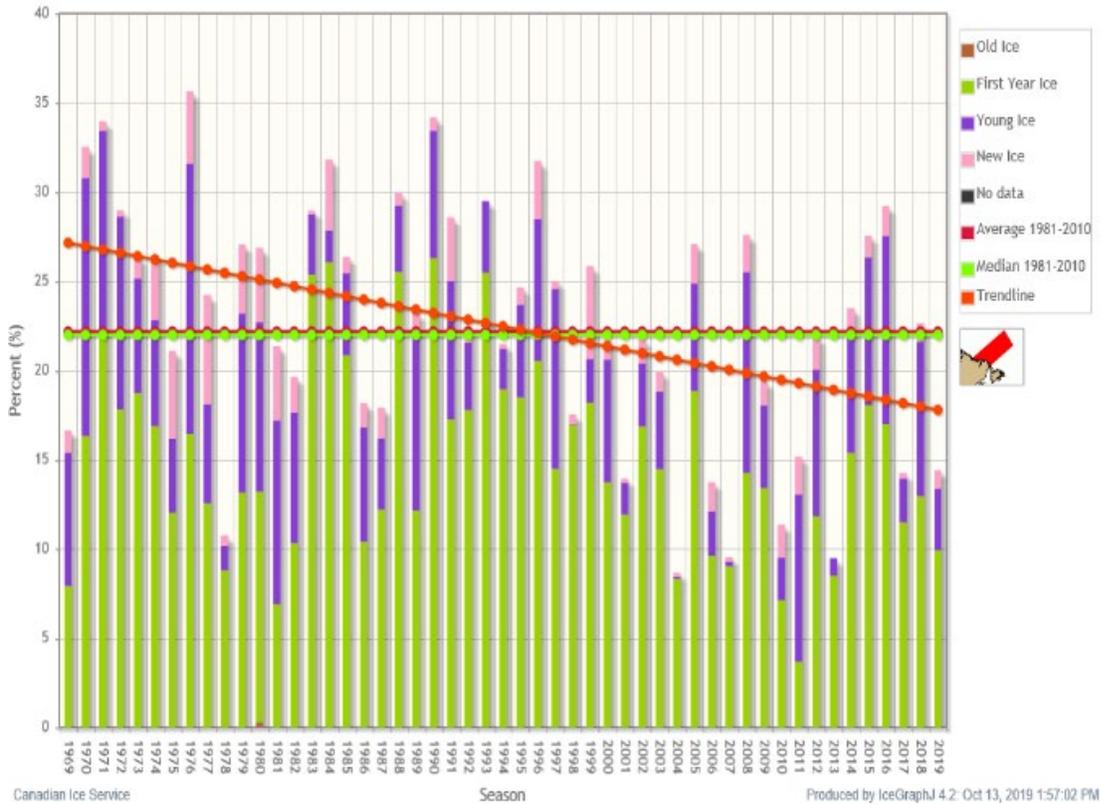


Appendix 1. Figure 1. Reproductive rates of females 4-7 years of age (circles). Smoothed data  $\pm 95\%$  confidence interval (red).

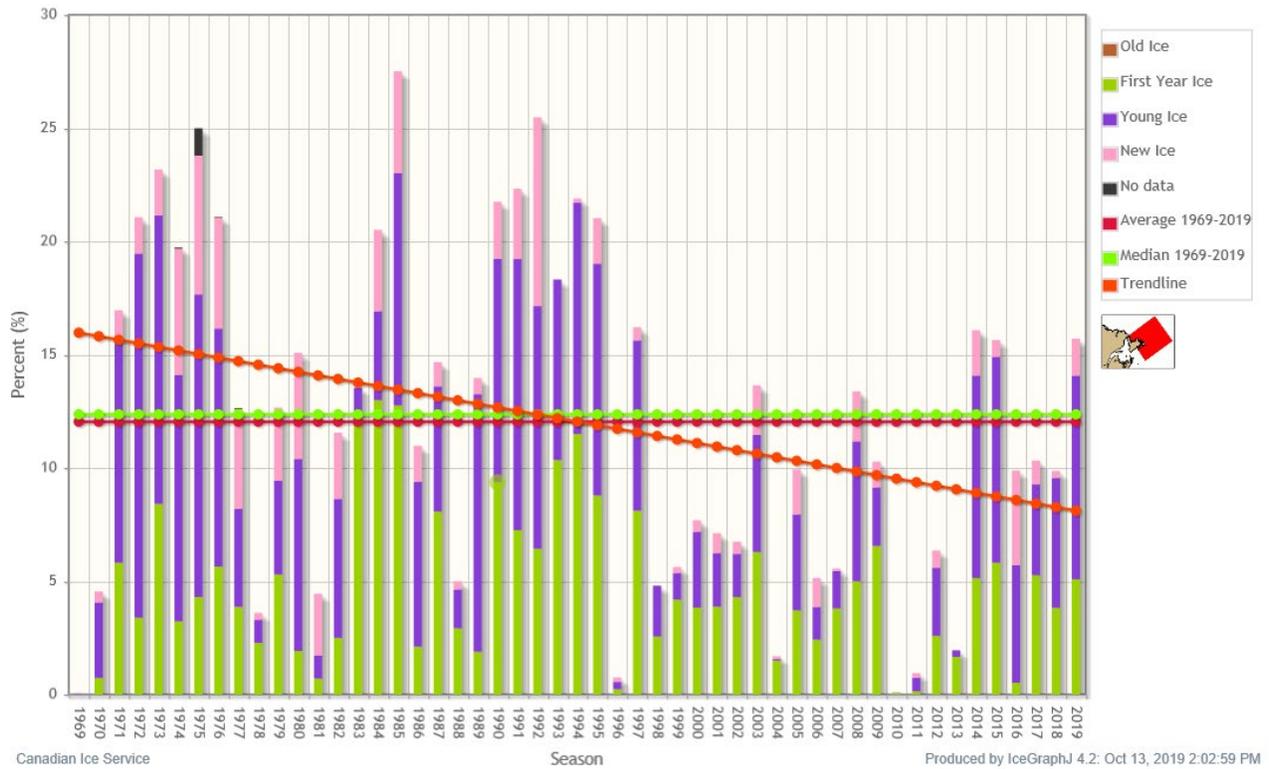
Region: Gulf of St. Lawrence, Same Week: Historical Ice Coverage for the week of 0226



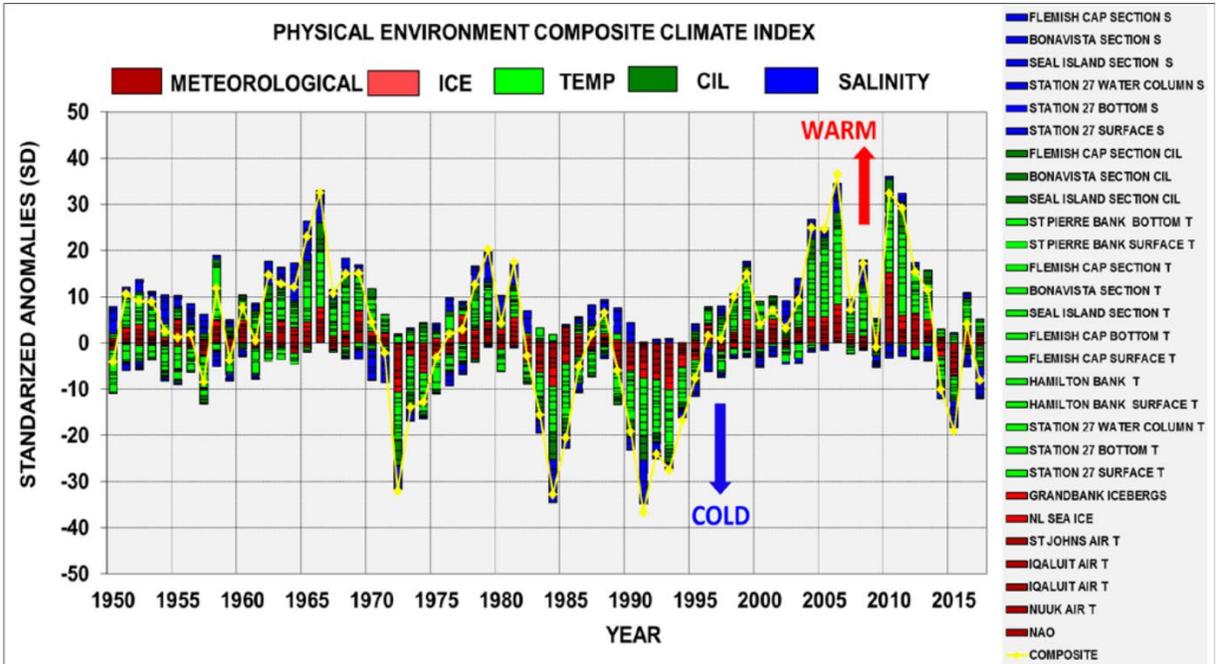
Region: Southern Labrador Sea, Same Week: Historical Ice Coverage for the week of 0305



Region: East Newfoundland Waters, Same Week: Historical Ice Coverage for the week of 0305



Appendix 1. Figure 2. Total ice cover and concentration of different ice types of ice in the Gulf of St Lawrence (February 26 1969-2019), off the southeast coast of Labrador where the Front patch usually forms (March 3 1969-2019) and northeast Newfoundland where the Front seals drift (March 5 1969-2019). Ice cover (%) expressed as total concentration and concentration of first-year ice (30-120 cm thick), young ice (10-30 cm thick), and new ice (10 cm thick). (from [Environment Canada](#)).



Appendix 1. Figure 3. Variability in the Comprehensive Environmental Index between 1950 and 2018. The Composite environmental Index (CEI) derived by summing the standardized anomalies of 28 environmental factors including the NAO, air temperature, ice, water temperature and salinity and CIL areas from several locations in the Northwest Atlantic colour-coded according to Figure 3. The anomalies are normalized with respect to their standard deviations<sup>10</sup>. incorporates 28 different environmental factors including meteorological conditions, ice cover, temperature, the cold intermediate layer (CIL) and salinity (Colbourne et al. 2016).