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Modelling Grey seal Abundance in Canadian waters

Modélisation de l'abondance du phoque gris dans les eaux canadiennes

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ABSTRACT

The model used in this study to describe the population dynamics of the Northwest Atlantic grey seal is a two parameter model that uses information on age specific reproductive rates, ice-related mortality of young seals, removals and estimates of pup production. The model was fitted to the three grey seal herds: Sable Island, Eastern Shore and Gulf of St. Lawrence separately to obtain estimates of pup production and population size. Model outputs were also compared to two other models that have been used to describe the dynamics of the Northwest Atlantic grey seal population (Thomas et al. 2007,2008; Trzcinski et al. 2006) and population trajectories were similar when run under similar conditions. Pup production in the Gulf herd is quite variable and is likely associated with variable mortality due to fluctuating ice conditions. A significant relationship was observed between pup production on the ice and ice cover in the southern Gulf. The Northwest Atlantic grey seal population has increased substantially over the last 5 decades increasing from approximately 13,000 (SE=1,100) to 402,700 (SE=7,700) in 2010.

RÉSUMÉ

Le modèle utilisé dans cette étude pour décrire la dynamique des populations du phoques gris du nord-ouest Atlantique est un modèle à deux paramètres qui utilise les informations sur les taux de reproduction à l'âge, la mortalité attribuable à la glace de jeunes phoques, les retraits et les estimations de la production de petits. Le modèle a été ajusté aux trois troupeaux de phoques gris: l'île de Sable, Côte est et le golfe du Saint-Laurent séparément afin d'obtenir des estimations de la production de petits et de la taille de la population. Les résultats du modèle ont été comparées à deux autres modèles qui ont été utilisés pour décrire la dynamique de population de phoques gris (Thomas et al 2007, 2008; Trzcinski et al. 2006.) et les trajectoires de population étaient similaires lorsqu' exécuté dans des conditions semblables. La production de petits dans le troupeau du golfe est très variable et est probablement associée à une mortalité variable en raison des conditions de glace fluctuantes. Une relation significative a été observée entre la production de petits sur la glace et la couverture de glace dans le sud du golfe. La population de phoques gris a augmenté considérablement au cours des 5 dernières décennies passant d'environ 13 000 (SE = 1100) à 402 700 (SE =7700) en 2010.

INTRODUCTION

Northwest Atlantic ecosystems have undergone significant changes in recent decades (e.g., Savenkoff et al. 2007a,b). In the southern Gulf of St. Lawrence (Gulf) the biomass of large demersal fishes, notably Atlantic cod (*Gadus morhua*), collapsed in the late 1980s and early 1990s, mostly due to overfishing. Following this decline in large piscivorous fish, the abundance of small fish increased sharply (Benoît and Swain 2008). In addition to these changes in the fish community, there have been major increases in the abundance of two marine mammals, the harp seal (*Pagophilus groenlandicus*) and the much larger grey seal (*Halichoerus grypus*), (Hammill and Stenson 2008, Thomas et al. 2008) of which the Northwest Atlantic grey seal is considered the more important consumer of commercial fish in the Gulf of St. Lawrence and on the Scotian shelf (Hammill and Stenson 2000). This has led to concerns that grey seals may be affecting the recovery of commercial groundfish stocks.

Unlike the harp seals which has a long history of commercial harvesting with significant information on harvests that extend over the last two centuries, little is known of historical abundance of grey seals 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 as a result of declines in walrus and whale populations. In the late 1800s, Gilpin (1874) speaks of herds of only 20 or 30 seals on Sable Island and in the early 1950s, they are considered to be rare throughout eastern Canada (Lavigueur and Hammill 1993; Fisher 1955). Government sponsored culls and a bounty program may have contributed to limiting grey seal recovery in the 20th Century, but over the last five decades the Canadian grey seal population has increased from approximately 15 000 animals in the 1960s to over 300,000 in 2007 (Mohn and Bowen 1996; Thomas et al. 2007).

In the Northwest Atlantic, mitochondrial DNA work has shown that grey seals consist of a single population (Boskovic et al. 1996), but within Canadian waters the population is subdivided into three groups for management considerations based on the locations of concentrations (colonies or herds) of breeding animals: Sable Island, Gulf of St. Lawrence (Gulf), and Eastern shore components (Fig. 1). Outside of the breeding season, there is some overlap in the distribution of animals from the different colonies (eg Lavigueur and Hammill 1993; Harvey et al. 2008; Breed et al. 2006, 2009). The three regions are quite different physically, and have had very different population trajectories. Sable Island, Nova Scotia, Canada, is a sand island located approximately 300 km east of Halifax (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 group in Atlantic Canada occurs in the Gulf of St. Lawrence (Gulf), where grey seals have their young on the pack-ice in the southern Gulf or on small islands (Fig. 1). The trajectory of pup production in the Gulf has been much more variable than on Sable Island due to higher bounty, culling and scientific harvests (Hammill et al. 1998), and higher mortality rates associated with pupping on the pack-ice (Hammill et al. 2008; Thomas et al. 2007). Traditionally, a relatively small number of animals breed on isolated islands along the Nova Scotia Eastern shore (Mansfield and Beck 1977). Significant culling efforts, particularly in the Basque Island area limited pup production in this area to the low 100's, during the 1970s and significant commercial hunting has occurred on Hay Island over the last decade. In the last few years, small colonies have also appeared along the southwestern shore of Nova Scotia on Flat and Noddy Islands, but for the moment the estimates from the southwestern shore colonies are combined with the Eastern Shore. Grey seal pupping also occurs in the northeastern United States, with pup production of around 1000 animals in 2002 (Wood et al. 2007).

Total abundance of grey seals is estimated using a population model that incorporates information on fecundity, removals and estimates of pup production obtained from direct counts or surveys. Recent estimates of abundance have been obtained from two different models. Thomas et al (2007) presented a Bayesian model that has been used for the assessment. Briefly, this model assumes that pup survival is density dependent, and it estimates maximum pup and adult female survival rates that apply across all herds, but different carrying capacities for each herd separately. Reproductive rates are also assumed to be constant across herds and time. A second model, presented in Trzcinski et al (2006) considered the Gulf and Sable Island herds separately. Population growth in the Gulf was described using an exponential growth model, while the dynamics of the Sable Island herd were described with a theta-logistic model using several assumptions about the strength and timing of density dependence and the level of carrying capacity. In this model, adult mortality rates were fixed to published values, while pup mortality rates were estimated by fitting the model to the pup count data. Age specific reproductive rates were adjusted to take into account apparent changes in the dynamics of the Sable Island herd as reported by Bowen et al. (2007) (Trzcinski et al. 2006).

Here we apply a two parameter model similar to that developed for harp seals (Hammill and Stenson 2009) that uses information on age specific reproductive rates, ice-related mortality of young of the year seals (YOY) and human removals to predict population size. The model is fitted separately to independent estimates of pup production for each herd by adjusting the starting population size and adult mortality. Estimated pup production and total population size from the current model were compared to predictions from the two models described above (Thomas et al 2007, Trzcinski et al 2006). Comparisons were made for Sable Island, as this component is the best documented. The model was also fitted to the times series of pup counts/series to obtain estimates of pup production and total population size for each herd. These were combined to provide an estimate of the Canadian grey seal population.

MATERIALS AND METHODS

MODEL

The basic age structured model is the same as used for harp seals, but has been adapted to apply to Canadian grey seals based upon Mohn and Bowen (1996) and Hammill et al. (2009). The model assumes that there is no difference in mortality rates between males and females as found by Mansfield and Beck (1977).

The model is composed of 5 equations:

$$n_{a,t} = ((n_{a-1,t-1} - c_{a-1,t-1})\, e^{-\gamma M} \quad \text{for a=1,} \qquad (1)$$

$$n_{a,t} = ((n_{a-1,t-1} - c_{a-1,t-1})\, e^{-\gamma M}\, [1-(N_t/K)^{\Theta}] \quad \text{for a=}1_{\text{sable}}, \qquad (2)$$

$$n_{a,t} = (n_{a-1,t-1} e^{-M/2} - c_{a-1,t-1}) e^{-M/2} \quad \text{for } 1 < a < A, \qquad (3)$$

$$n_{A,t} = [(n_{a-1,t-1} + n_{A,t-1}) e^{-M/2} - c_{a-1,t-1}] e^{-M/2} \quad \text{for } a = A, \qquad (4)$$

$$n_{0,t} = \sum_{a-1}^{A} n_{a,t} P_{a,t} w \quad \text{for a=0.} \qquad (5)$$

where $n_{a,1}$ = population numbers-at-age *a* in year *t*,
N_t =total population size at time *t*
K = carrying capacity
Θ = theta, the degree of density dependence , set at 2.4 (Trzcinski et al. 2006)
$c_{a,t}$ = the numbers caught at age *a* in year *t*,
$P_{a,t}$ = per capita pregnancy rate of age *a* parents in year *t*, assuming a 1:1 sex ratio. P is expressed as a normally distributed variable, with mean and standard error taken from the reproductive data. Animals have their first pup at age 4.
M = the instantaneous rate of natural mortality.
γ = a multiplier to allow for higher mortality of first year seals. Initially, assumed to equal 3, as in harp seals.
w = is the proportion of pups surviving an unusual mortality event arising from poor ice conditions or weather.
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).

The model creates a population matrix with 26 age classes (0-24, 25+). This allows for cohort effects to be present in the population. Although some animals in their 30s have been observed, the majority of animals die before then. The model allows for some 25 year old animals to die during the year, then at the end of the year, all remaining animals in that age class die (Hammill and Stenson 2009). The model starts in 1960 and continues until the current year (2010). Data inputs included age specific pregnancy rates, human removals and ice-related mortality of YOY and estimates of pup production. Two parameters are estimated to maximise the fitting of the model to the pup production estimates; the instantaneous mortality rate (*M*) and the initial population factor (α). The latter parameter is used to estimate the initial population in 1960. An initial population vector (26 × 1) was created to which α is multiplied. This initial population vector can be interpreted as an initial population age structure and the initial population size is calculated using:

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

Where *P* is the total population, α the initial population parameter and l_i the initial population size for the i^{th} age class. The initial population size is a vector with an initial pup production on Sable Island of 500 animals in 1960, assuming first year mortality of 3 x adult mortality, then annual adult mortality rates for animals aged 1, 2,3, etc. In the Gulf, the initial pup production was assumed to be 5000, and a similar mortality schedule was assumed. For the Eastern shore, an initial pup production of 800 was assumed. During initial trials, all populations were run using the same initial population, but to see if changing the initial population vector had any impact, herd specific vectors were developed based approximately on available information on pup production in 1960 for each herd. The simulations did not identify any differences, other than the fitted alpha varied for each herd, but once separate files were developed, it was decided to continue using them.

In the model, α and M are adjusted by iterative methods to minimize the sum of square differences between the number of pups born, as predicted by the model and the number of pups estimated from the independent pup surveys. Pregnancy rates and the pup production estimates are resampled to incorporate uncertainty, assuming a normal distribution of known mean and standard error. For every year of the simulation (from 1960 until present day), 26 new pregnancy rates were sampled. However, it is likely that if one year class has a poor year, the other age classes are also likely to have a poor year. Therefore, a correlation factor between the reproductive rates of the females from each age within a year has been added and fixed at r=0.85.

DATA

Data inputs into the model include estimates of pup production from each herd, removals from each herd, reproductive rates and in the case of the Gulf herd, a factor to account for ice-related mortality. In the case of the Sable Island herd, the number of animals surviving in their first year is assumed to be density dependent. All other herds were assumed to have exponential growth.

Pup production estimates

Estimates of pup production for each herd are obtained from mark-recapture studies, total counts and aerial surveys (Table 1a). The methods used for early estimates (prior to 1977) likely under-estimate pup production in the area since numbers presented appear to be rough counts/guesstimates, the level of reconnaissance is not indicated and counts are not corrected for births. In these cases a standard error equal to the estimate has been applied. The initial age distributions were set up based loosely on approximate 1960 pup production in each region, assuming a YOY mortality rate of 3 times the adult rate and an adult rate of 0.06 (Table 1b).

In the Gulf, estimates of pup production during the 1980s were obtained using mark-recapture studies. In these studies, the Gulf and Eastern Shelf herds were often combined (Hammill et al. 1998). Since complete tagging was carried out along the Eastern shore, pup production estimates for this area are based on the numbers of tag deployed. The number of Eastern shore tags recovered were subtracted from the estimates of pup production for the Gulf. The Gulf numbers were not re-calculated .

Removals

Grey seals in Atlantic Canada have been killed during bounty programs, government sponsored kills, commercial harvests, scientific collections and as nuisance seals under special licence (Tables 2, 3. 4). Animals are also likely caught as bycatch in commercial fisheries, although we do not have any data on which to base an estimate and therefore is not included. Commercial harvests and culling programs were closely monitored and it is assumed that there was no loss associated with these programs. Estimates of struck and loss are available from scientific catches (20-50%), and we use 30% here for all age classes. Estimates of animals caught under the bounty program depend on submissions of jaws in turn for payment. There is no information on struck and loss from this system, but it was assumed to be 30% since often people participating in bounty programs were also hired for scientific collections.

Reports on the numbers of seals removed under the nuisance seal program are limited by the low number of license holders reporting. In 2008, 422 licenses were issued; 31 holders reported that 218 grey seals were killed for an average of 7 seals per report. In 2009, 428 licenses were issued, 14 holders reported killing 122 seals for an average of 8.7 seals per report. Together this results in an average of 7.9 seals (SE 0.6) per reporting holder in the two years. This removal rate was extrapolated to the total number of permits issued to derive an estimate of seals removed under the nuisance seal program. Since these permits have largely been issued by Maritimes region, removals were applied against the Sable herd which is the largest herd on the Scotian Shelf. The age structure of these catches was assumed to be proportional to that in the model.

Reproductive rates

Reproductive rate data have been collected during scientific collections in the Gulf since 1968 (Hammill and Gosselin 1995) and have continued at various levels of sampling up to 2008. These consist of samples collected between June and November. Hammill and Gosselin (1995) did not find any significant difference between reproductive rates obtained form animals collected in June and those from animals collected in the fall. Reproductive rates were assumed to be the same for all three herds. In some years there are no samples, samples are small, or age classes are missing. With changes in the population, reproductive rates may have changed over time. To examine possible changes in reproductive rates over time, and to obtain estimates of reproductive rates in years when samples are not available a Logistic Model was fit to the data with fixed effects where age was expressed as a quadratic and temporal changes were modeled using a first order Fourier transformation. This provided reproductive rate information during years when data are missing and allowed us to examine if there were changes over time.

Ice conditions

Grey seals in the Gulf give birth on the ice as well as on islands. In heavy ice years, the majority of animals are born on the ice, while in light ice years, more pups are born on the islands (Hammill and Stenson 2011). Pup mortality appears to be higher in the Gulf herd than on Sable and in poor ice years we have observed that pups are being lost during the surveys (e.g. 1997, 2010), although the numbers lost have been difficult to quantify. To examine the impact of ice on grey seal pup production, ice data for the week of 21-24 January 1969-2010 for an area of Northumberland Strait located between Amet island in the west, and Cape George in the east were obtained from the Canadian Ice Service. Data consisted of a 10km-spaced grid square database. Each 10km-spaced grid point contains information on the total ice concentration (in tenths) and the partial concentration for the thickest ice types among 4 different stages of development: new (the youngest stage), grey, grey-white and first-year ice (the oldest stage). To determine which ice variables and spatial scales are the best predictors of grey seal pup production, a series of models were built using linear regression and ranked using the second order Akaike's Information Criterion (AICc). Only one ice variable was included in the model at a time owing to multicollinearity. Parameter estimates, standard error and 95% confidence intervals were computed for each model (i.e. with the lowest AICc ($AICc_{min}$)) and in the models whose AICc differed less than 2 from $AICc_{min}$ ($\Delta AICc<2$). Ice variables were considered to influence pup production if the confidence interval excluded zero. Analyses were conducted for Gulf pup production on land, on ice and total Gulf pup production.

RESULTS

Reproductive rates

Pregnancy rate data were available from 772 females collected in the Gulf between 1969 and 2008, of which 532 animals were pregnant. Pregnancy rates change with age, but the Fourier transform term in the regression was not significant indicating no year effect in reproductive rates over the period examined. The logistic regression fitted to the pregnancy rate data was : z=0.54 (age)-0.37 (age^2) -17.24, where z is the pregnancy rate in logit, which can be transformed using p= exp(z)/(1+exp(z)) (Fig. 2). Pregnancy rates in the Gulf and Eastern shore models were assumed to not change with year (Table 5), but some adjustment was made in reproductive rates for the Sable Island herd (see below).

Model Fitting

During initial runs, the model was fitted (N=300 runs) to the Sable Island data assuming that there was no density dependence, and no change in reproductive rates. Estimated pup production and population size were compared with estimates from Trzcinski et al. (2006) and Thomas et al (2007)(Table 6). For comparisons with Trzcinski et al., the 2007 and 2010 survey estimates were excluded, while the 2010 survey was excluded to allow comparison with Thomas et al. (2007). Gamma, the multiplier on adult mortality (m) was initially set at 3, which means that pup mortality was set at 3 times adult mortality. The latter was estimated by the model. Although the model fit to the 2004 survey point was poor (Fig 3), it estimated an adult mortality rate (M_a) of 0.056, a 2004 pup production of 54,000 and a total population of 304,000. This is much higher than the estimates obtained by Trzcinski etl al (2006) who set M= 0.03-0.05 , and estimated M_{juv} = 0.307, a pup production of 42,000 and a total population of 200,000. However, Trzcinski et al. (2006), delayed the age at first reproduction to age 6 years, based on observations from Bowen et al. (2007), and included a density dependent term with K=400,000. To improve the comparison of our model to that of Trzcinski et al (2006), we adjusted γ to allow M_a to decline to close to 0.03 (which is within the range of values observed by Manske et al. (2002) and Schwarz and Stobo 2000) and beginning in 2001, altered the age specific reproductive rates by setting the age specific reproductive rate at age 4 to 0, and replacing the age specific reproductive rates at age 5 and age 6 with the rates observed ages 4 and 5 from Table 5. We also included a density-dependent term, with K=400,000 (Trzcinski et al. 2006). Under these conditions and for M_a =0.03, γ increases to 14, pup production declines to 42,000 and the total population declines to 233,00 in 2004, which is similar to Trzcinski et al. (2006). Much of the remaining difference for total population would be due to the assumption by Trzcinski et al. (2006) that males had higher mortality rates after age 9, where as in our model male and female M are assumed to be the same.

Thomas et al (2007) fitted to data that included the 2007 survey points, but did not include any changes in reproductive rates for the Sable herd. Using these conditions, we estimated Sable pup production in 2007 to be 59,000 and a total population of 275,000 which is comparable to that of Thomas et al. (54,600 pups and a total population of 242,200). Assuming a shift in the age of first reproduction beginning in 2001 and fitting to the 2007 pup production estimate results in Ma of 0.032, a pup production estimate of 55,499 and a total population of 281, 000 (Fig. 3).

Fitting the model to the new survey estimate from 2010 resulted in a model estimate of M=0.03, with γ=12. In 1960, pup production was 355 (SE=20.2) increasing to 65,200 (SE=2,800) in

2010. Total Sable population size was estimated to be 1,442 (SE=73.8), increasing to 318,400 (SE=6,300) in 2010.

Fitting the new model to the Gulf data, up to 2004, resulted in M_a of 0.06, pup production of 12,100 and a total population of 54,700. Trzcinski et al (2006) reported a slightly higher M_a of 0.1, M_{pup}=1.06 (SE=0.06), a pup production of about 11,200 and a total population of 50,000 . The model was refit to include more recent pup production estimates up to 2010 (Table 6). γ was set at 22, to obtain an estimated M_a = 0.05 (Se=0.001). However, the fit to the data is very poor (Fig. 4). Total pup production was 2,536 (SE=264) in 1960 increasing to 14,800 (SE=1,000) in 2010. In 1960, the total population size was 10,556 (SE=1,094), increasing to 64,300 (SE=4,200) in 2010.

Fitting the new model to the Eastern Shore data up to 2010, resulted in a total pup production estimate of 251 (SE=35) in 1960, increasing to 4,200 (SE=300) in 2010. In 1960, the estimated 1,045 (SE=146) increasing to 20,000 (SE=1,500) in 2010. M was estimated to be 0.04, and γ=12.

Combining estimates from the different herds, total pup production has increased from 3,100 (SE=300) in 1960 to 84,200 (SE=3,000) in 2010. Over the same period the total population has increased from 13,000 (SE=1,100) in 1960 to 402,700 (SE=7,700) in 2010.

Ice analysis

Pup production on the ice, on land and total pup production were regressed on total ice cover and cover of different ice types in Northumberland Strait and the Gulf of St. Lawrence. The only model that was retained included total ice cover in Northumberland Strait (Table 7),

We then examined how the estimates of pups counted on the ice changed with ice conditions by comparing ice anomalies ((ice cover-mean ice cover)/mean ice cover) with pups born on ice anomalies ((pup_{ice} count-mean pup_{ice} count)/mean pup_{ice} count) (Fig 5). In years where the ice anomaly was above average, the pups born on the ice anomaly was high, whereas for years when the ice anomaly was below average the pups born on the ice anomaly was also low (Fig. 5).

DISCUSSION

The grey seal population in Atlantic Canada has increased remarkably over the last 50 years from around 13,000 animals in 1960 to around 400,000 in 2010. Additional Grey seals also occur in the northeastern United States where they have established new colonies. Northeast Atlantic grey seal populations have also shown remarkable signs of recovery over the last 5 decades and could, from one perspective, be considered a conservation success story (Lamb 2002). The reasons for such a recovery are not understood, but likely result from several factors. Possible explanations include an improvement in breeding habitat conditions, and a reduction in removals. A reduction in predator numbers (sharks) may also have played some role in this recovery.

Improvements in breeding conditions likely result from 2 factors. Beginning in the mid-1950s, the Cape Breton Causeway was built which linked the island of Cape Breton to the Nova Scotia mainland. Prior to the causeway, ice drifted through the channel past Port Hawkesbury into the Atlantic where ice destruction would have been rapid and mortality among young would have been high. Construction of the Causeway blocked the exit of ice from the Gulf forcing ice to move north and around the Cape Breton Island coast. This would have allowed a buildup of ice in the Canso Strait and St. George's Bay areas, increasing the availability of pupping habitat for grey seals. This would also have allowed earlier formation of stable ice in these southern Gulf areas. During the 1980's and 1990's much of the tagging of grey seals occurred in the Bay and along the western coast of Cape Breton Island.

Over the last decade, however, there has been a general decline in the quality and quantity of ice cover in the Northumberland Strait area. In response to poor ice conditions, an increasing proportion of pupping now occurs on islands. Throughout the year, grey seals tend to occupy the outermost islands and pupping colonies occur in these islands, in areas where there are few inhabitants, and/or animals are rarely disturbed (e.g. Anticosti Island, Deadman Island), or where disturbance is benign (Sable Island, Pictou Island). In the United Kingdom, the abandonment of isolated islands by humans created new pupping habitat for grey seals (J. Harwood, personal communication) and in Atlantic Canada a reduction of harvesting in areas like Sable Island (compared to historical records) has opened up considerable new breeding habitat. Interestingly enough, much of the southern Gulf, with its long beaches and relatively shallow water, resembles the Sable Island area, was occupied by grey seals historically (Lavigueur and Hammill 1993), but harvesting reduced their numbers and today the main haulout areas occur in park/protected areas or in areas where traffic is benign (e.g. Miramichi). Generally, a reduction in cull and bounty efforts, limited commercial harvesting and a change in human behaviour (less overall shooting) has also likely favoured grey seal recovery.

Our estimates of population size depend on several assumptions. In developing these estimates we have assumed that the age-specific reproductive rates observed in the Gulf can be applied to the Eastern shore component and the Sable Island component as well. Although this is likely to be correct for much of the time series, in recent years Bowen et al. (2007) observed that the age of first reproduction in the Sable Island herd had increased, and making assumptions about this change (shifting in age specific reproductive rates) improved the fit of the model to the survey estimates. In the current model, these changes were incorporated as a knife-edge change, although they were likely more gradual over time. Assumptions were also made about density-dependent changes in first year mortality. We assumed that juvenile mortality was density-dependent with a K value of 400,000 (Trzcinski et al. 2006). This improved the fit of the model to the survey data, but in this study K was imposed. Overall, our understanding of the density dependent relationship is very poor and if K is in fact lower, then the overall Sable population will also be lower. Reproductive rate data from the Sable Island would also allow us to understand more fully how density-dependent factors are operating on this herd.

We have also assumed that males and females have a similar mortality schedules. This is supported by the earlier work of Mansfield and Beck (1977), and more recent mark-resighting data (Schwarz and Stobo 2000; Manske et al. 2002), although research in the United Kingdom suggests that male grey seals may have a higher mortality rate than females. If males do have higher mortality rates, then the overall population will be less than we have indicated here.

The Eastern Shore herd is currently relatively small, compared to the other components of the Northwest Atlantic grey seal population, but it is expanding and new colonies are appearing. The commercial hunt may be affecting the growth of this herd. We assumed that it was appropriate to describe the dynamics of this herd using the age-specific reproductive rates from the Gulf herd and an exponential model, but the limited change in abundance between the last two surveys of Hay Island may also indicate that density-dependent factors, possibly through space limitations are limiting the growth of the herd on this island. If this is the case, then incorporating density-dependent regulation into the population model would be a more appropriate manner to describe the dynamics of this herd and the resulting estimated population may also be smaller than presented here.

The dynamics of the Gulf herd are more complicated. Early in the time series, much of the Northwest Atlantic grey seal population occurred in the Gulf (Mohn and Bowen 1996), but high natural mortality among animals born on the ice, high levels of removals (Hammill et al. 2007; this study) and some emigration to Sable Island and the Eastern Shore have likely contributed to the low rates of population growth observed in this area. In contrast to Trzcinski et al (2006), we assumed that adult mortality rates changed little between the Sable Island and Gulf components of the population. We believe that this is a reasonable assumption, but should be explored further. However, it is likely that YOY mortality is much higher among Gulf animals and this mortality is probably related to variability in ice cover and ice stability.

The model fit to the Gulf survey data was very poor. Surveys of this herd are complicated by the long pupping season and the apparent poor ability of grey seal mother-pup pairs to adjust to breaking ice (Hammill and Stenson 2011). Grey seals also appear to be poorly adapted to cold-water exposure at the beater stage (Worthy 1991), suggesting that pupping on ice is an indication of their flexibility in adjusting to environmental conditions, rather than evidence of long term evolution in this environment. We observed a positive relationship between the occurrence of ice anomalies and the occurrence of pup production anomalies for the numbers of pups born on the ice. We explored this further by incorporating the effects of ice-related mortality into the model. If we use the ice anomaly value as the coefficient for w in equation 5 and only use negative anomalies, (expressed as 1-the anomaly in the model) setting positive anomalies to 0 (Table 8), the fit of the model to the pup survey data improves substantially, reducing the sum of squares from 84.6×10^6 to 42.4×10^6 (Fig. 6). For 2010, this resulted in a pup production estimate of 11,586 (SE=1,172) and a total population of 70,890 (SE=7,303) (Fig. 6). This suggests that the Gulf grey seal population could be about 10% higher than the initial run of the model estimates, ie closer to 71,000 animals instead of the 64,000 animals. However, the observed relationship occurs between numbers of pups born on the ice, but no relationship was observed between total pup counts or numbers of pups born on the land. Until this can be explored further, we prefer to consider this somewhat exploratory and suggest it as a possible bound for the population.

In this study we modified the assessment model currently used for harp seals to apply it to modelling the dynamics of the Northwest Atlantic grey seal population. The model provides similar estimates to those obtained from other models used to evaluate seal-cod interactions (eg Trzcinski et al. 2006) and the model used in the grey seal assessment (Thomas et al. 2007), when similar assumptions are applied.[1]

The grey seal population in Atlantic Canada has likely increased by 30 fold since the 1960s. At an estimated population of around 400,000 animals, the current population is the highest observed since work began on this species in Canada during the 1960s. Some components of the population, such as Sable Island and possibly Hay Island are showing signs of density-dependent changes in their dynamics, but this relationship is not well-understood with the

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[1] The estimates obtained from this study were used for other work that examined the impact of grey seals on cod in the southern Gulf at this meeting. A more complete assessment of the grey seal population held later in the fall, resulted in a final estimate of 349,000 (95% Bayesian credibility limits 291,000 to 415,000)(Thomas et al. 2011), which is not significantly different from the estimates presented here.

information available to us at this time. Here we set K_{Sable} =400,000 (Kurtis Trzcinski pers. Comm.), but changes to this value will affect our estimates of the population on Sable Island, particularly if it is lower than the value indicated above. Additional assessments, as well as information on factors such as age –specific reproductive rates are needed, particularly for Sable Island and coastal Nova Scotia. Since grey seals also reproduce on the ice in the Gulf of St. Lawrence, climate change and associated changes in ice cover, may result in increased mortality among grey seal YOY in the southern Gulf. At the same time, it may also increase opportunities for grey seals to occupy new or expand current breeding habitat, particularly in the northern Gulf of St. Lawrence (eg Anticosti Island), where animals are also unlikely to be disturbed.

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Table 1a. Estimates of pup production in the Gulf of St. Lawrence. Sable Island and Eastern Shore herds. [1] *In early studies there is no estimate of the standard error, this was assigned as equal to the estimate. Estimates are compiled from: Bowen et al. 2003, 2007; Hammill et al. 2007; Mansfield 1966; Mansfield and Beck 1977; Thomas et al. 2007.*

	Gulf		Sable Island		Eastern Shore	
	Estimate	SE	Estimate	SE	Estimate	SE
1962					130	200[1]
1963			400	400[1]	180	200[1]
1964			550	550[1]	190	200[1]
1965			660	660[1]	230	200[1]
1966	900	500[1]			180	200[1]
1967			580	580[1]	270	200[1]
1968			700	700[1]		
1969			800	800[1]		
1970			800	800[1]	100	200[1]
1971			1000	1000[1]	130	200[1]
1972			950	950[1]		
1973			1200	1200[1]		
1974			1250	1250[1]	135	200[1]
1975	3800	3800[1]			180	200[1]
1976			2000	2000[1]	130	200[1]
1977	3900	3900[1]	2181	173		
1978			2687	192		
1979			2933	201		
1980			3344	214		
1981			3143	208		
1982			4489	248		
1983			5435	273		
1984	7169	911	5856	283	142	200[1]
1985	6706	795	5606	277	135	200[1]
1986	5588	679	6301	294	151	200[1]
1987			7391	318	179	200[1]
1988			8593	343		
1989	9352	1756	9712	365	179	200[1]
1990	9176	649	10451	575		
1993			15500	463		
1996	10717	1306			395	74
1997	6839	800	25400	750	1061	121
2000	5260	910			799	105
2004	14210	1200	41100	4381	2469	76
2007	11413	1077	54482	1288	3017	40
2010	11329	6442	62,054	587	2,960	236

[1] *In early studies there is no estimate of the standard error, this was assigned as equal to the estimate.*

Table 1b. Initial age structures used in the models for each herd.

Age	Sable Island Number	Eastern Shore Number	Gulf Number
0	500	800	5000
1	372	656	4100
2	360.84	616.64	3854
3	350.0148	579.6416	3623
4	339.5144	544.8631	3405
5	329.3289	512.1713	3201
6	319.4491	481.441	3009
7	309.8656	452.5546	2828
8	300.5696	425.4013	2659
9	291.5525	399.8772	2499
10	282.806	375.8846	2349
11	274.3218	353.3315	2208
12	266.0921	332.1316	2076
13	258.1094	312.2037	1951
14	250.3661	293.4715	1834
15	242.8551	275.8632	1724
16	235.5694	259.3114	1621
17	228.5024	243.7527	1523
18	221.6473	229.1276	1432
19	214.9979	215.3799	1346
20	208.5479	202.4571	1265
21	202.2915	190.3097	1189
22	196.2228	178.8911	1118
23	190.3361	168.1576	1051
24	184.626	158.0682	988
25	179.0872	148.5841	929

Table 2. Removals of grey seals from the Gulf of St. Lawrence.

YEAR	Nuisance	Science	Commercial harvest: 0+	Commercial harvest: 1+:	Cull 1+	Cull 0+
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	0	210	0	0	0
2009	0	0	0	0	0	0
2010	0	0	58	25	0	0

Table 3. Removal of grey seals from the Eastern Shore.

YEAR	Nuisance	Science	Commercial harvest: 0+	Commercial harvest: 1+:	Cull 1+	Cull 0+
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	0	0	0	0

Table 4. Removal of grey seals from the Sable herd.

YEAR	Nuisance	Science	Commercial harvest: 0+	Commercial harvest: 1+:	Cull 1+	Cull 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	1,849	0	0	0	0	0
2000	1,967	0	0	0	0	0
2001	2,054	0	0	0	0	0
2002	2,204	0	0	0	0	0
2003	2,346	0	0	0	0	0
2004	3,002	0	0	0	0	0
2005	3,105	0	0	0	0	0
2006	3,437	0	0	0	0	0
2007	3,373	0	0	0	0	0
2008	3,334	0	0	0	0	0
2009	3,381	0	0	0	0	0
2010	2,933	0	0	0	0	0

Table 5. Age specific reproductive rates from Gulf grey seals used in the model (SE=standard error), unless stated otherwise (Top).

Age	Estimate	SE
4	0.167	0.051
5	0.607	0.082
6	0.849	0.037
7	0.906	0.018
8	0.888	0.021

Table 6. Outputs from fitting of model to estimates of pup production on Sable Island up to and included 2004 (Trzcinski et al 2006) and 2007 (Thomas et al 2007).

	Trzcinski et al	Current study	Current study	Thomas et al
		γ=3	γ=14; shift rpd rates, density dependence for 2004	
Year	2004	2004	2004	2007
Sable Island				
M_{adult}	0.03-0.05	0.056 (0.002)	0.032 (0.001)	0.036 (0.001)
M_{pup}	0.307 (.03)	0.169	0.443	0.504
Pup production	42000	54000 (3,100)	42,000 (2,300)	59,000(1,400)
Total population	200000	304,000 (15,000)	233,000 (10,000)	275,000 (6,500)

Table 7. The relationship between pup production and ice cover in the Northumberland Strait area was examined using total pup production, numbers of pups born on land and numbers of pups born on the ice. C_n is the concentration of each ice type (new, grey, grey-white, first-year or total cover). The different models examined are presented for the effects of ice on numbers of pups born on the ice only. The table below includes the best models from each analysis (pups born on ice, pups born on land and total pup production).

Candidate models	K	log likelihood	AIC	AICc	Min(AICc)	Delta AICc	Exp (-Delta/2)	Sum (exp)	Akaike weight
ice_surf_northumb	2	189.637	193.637	190.479	190.479	0.000	1.000	1.268	0.789
C_{new}_northumb	2	192.519	196.519	193.362	190.479	2.883	0.237	1.268	0.187
$C_{first\ year}$_northumb	2	197.970	201.970	198.812	190.479	8.333	0.016	1.268	0.012
$C_{grey\ white}$_northumb	2	200.275	204.275	201.117	190.479	10.638	0.005	1.268	0.004
C_{new}_GSL	2	200.744	204.744	201.586	190.479	11.107	0.004	1.268	0.003
C_{Grey}_northumb	2	201.234	205.234	202.076	190.479	11.597	0.003	1.268	0.002
ice_surf_GSL	2	202.961	206.961	203.803	190.479	13.324	0.001	1.268	0.001
$C_{first\ year}$_GSL	2	203.248	207.248	204.090	190.479	13.611	0.001	1.268	0.001
$C_{grey\ white}$_northumb	2	204.786	208.786	205.629	190.479	15.150	0.001	1.268	0.000
nul	1	205.440	207.440	205.740	190.479	15.262	0.000	1.268	0.000
C_{Grey}_GSL	2	205.315	209.315	206.157	190.479	15.678	0.000	1.268	0.000

Best Models

Model	Estimates	SE	"Model averaged" estimates	Erreur-type "Unconditional SE"	2.5%CI	97.5%CI
Ice pup production						
ice_surf_northumb	0.99	0.17	0.78	0.21	0.37	1.19
Land pup production						
ice_surf_GSL	-.032	0.008	-0.016	0.009	-0.034	0.002
Total pup production						
C1_surf_northumb	0.996	0.564	0.211	0.20451781	-0.191	0.612

Table 8. Annual ice anomaly calculated using (annual ice cover-mean ice cover)/mean ice cover (km^2), where the mean is the mean 1969-2010 ice cover. Runs of the model assumed that M_{ice} was equal to the anomaly, which is incorporated into the model as ($1\text{-}M_{ice}$).

Year	Ice cover anomaly	$1\text{-}M_{ice}$	Year	% ice coverage anomaly	$1\text{-}M_{ice}$
1969	-17.2	0.8	1990	39.6	1.0
1970	45.6	1.0	1991	-8.3	0.9
1971	51.0	1.0	1992	53.2	1.0
1972	-12.8	0.9	1993	-15.1	0.8
1973	42.1	1.0	1994	49.3	1.0
1974	44.5	1.0	1995	-83.7	0.2
1975	-57.2	0.4	1996	51.8	1.0
1976	-21.7	0.8	1997	-32.6	0.7
1977	44.8	1.0	1998	-34.6	0.7
1978	-40.0	0.6	1999	-80.8	0.2
1979	33.1	1.0	2000	-26.8	0.7
1980	-23.5	0.8	2001	-27.0	0.7
1981	49.7	1.0	2002	-57.5	0.4
1982	38.3	1.0	2003	30.1	1.0
1983	-48.6	0.5	2004	53.3	1.0
1984	23.6	1.0	2005	-25.5	0.7
1985	32.2	1.0	2006	-91.1	0.1
1986	-4.2	1.0	2007	-47.0	0.5
1987	7.2	1.0	2008	-39.2	0.6
1988	55.3	1.0	2009	45.7	1.0
1989	45.0	1.0	2010	-41.1	0.6

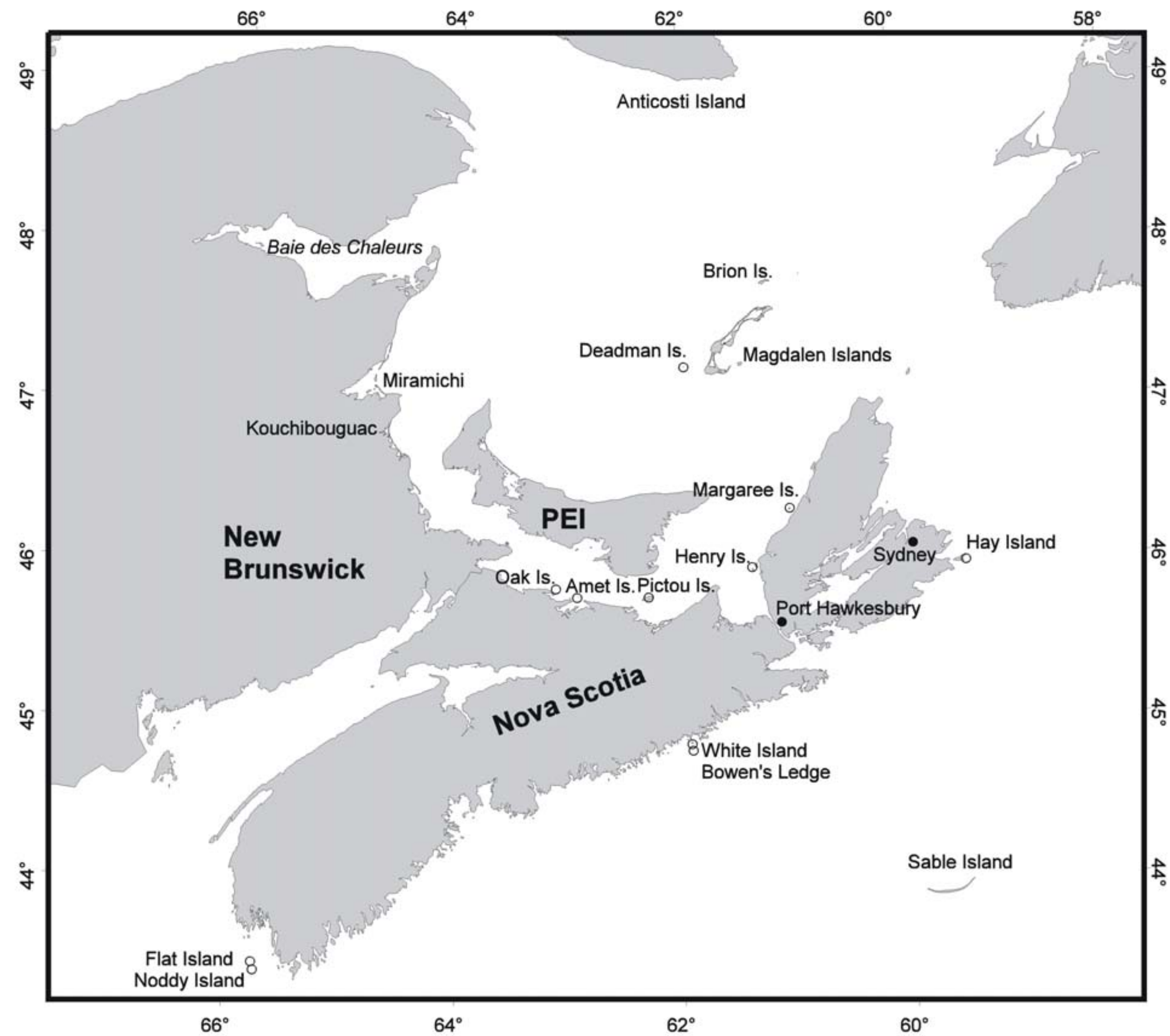


Figure 1. Map showing locations of main pupping colonies in Atlantic Canada.

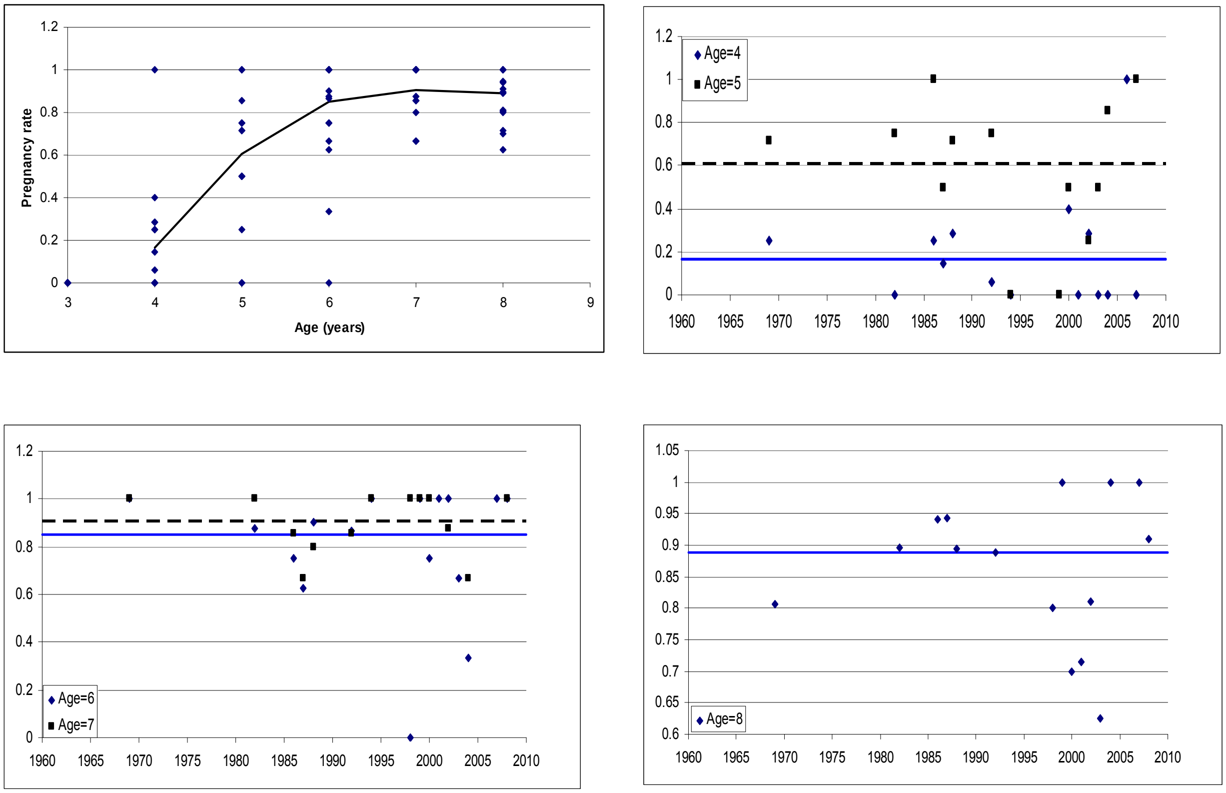


Figure 2. Changes in age-specific pregnancy rates of females aged 4 to 8+ at the time that pups are born over time. Data are from the Gulf of St. Lawrence. The top figure shows the change in pregnancy rates with age, while subsequent figures show no trend in pregnancy rates over time.

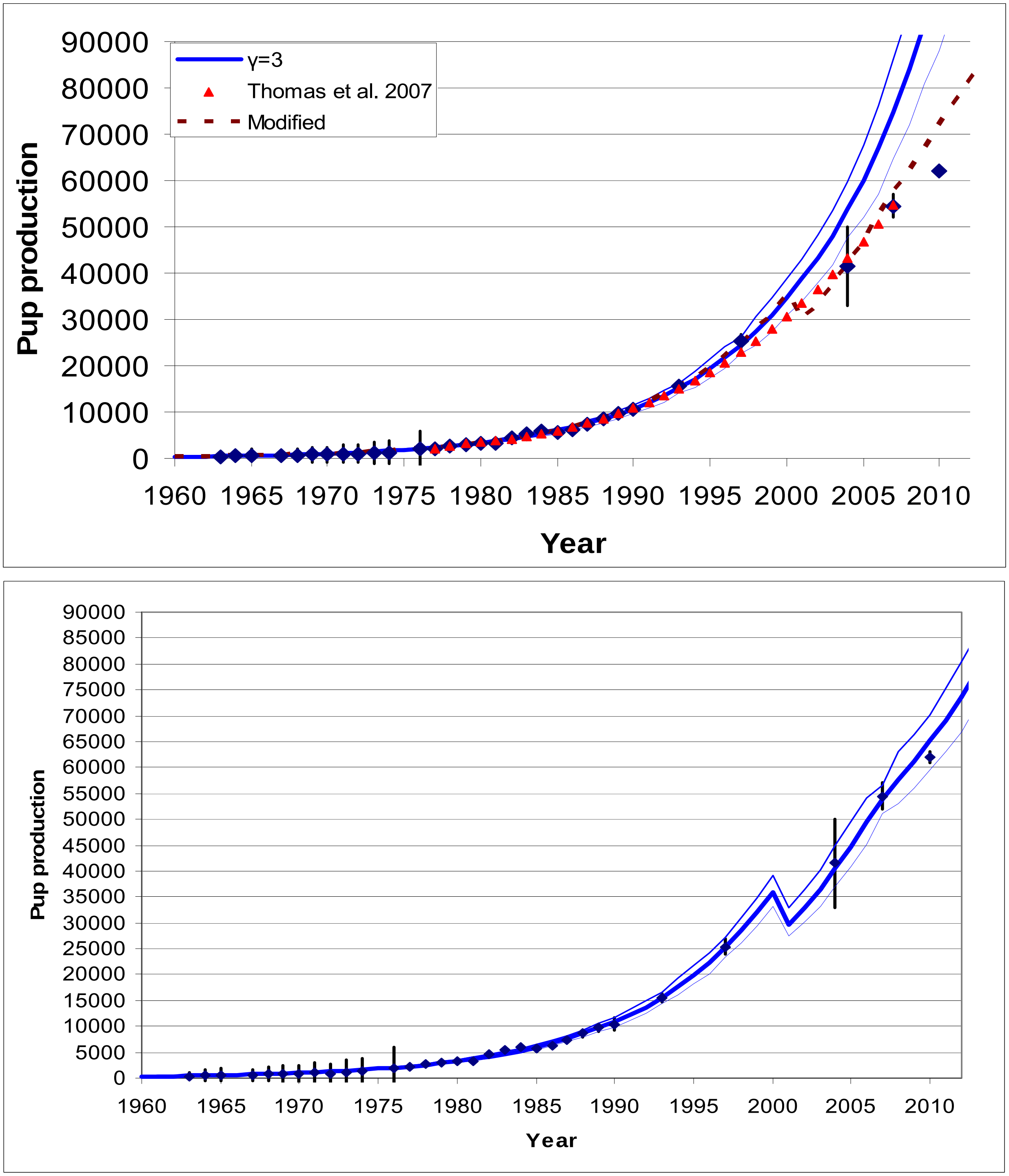
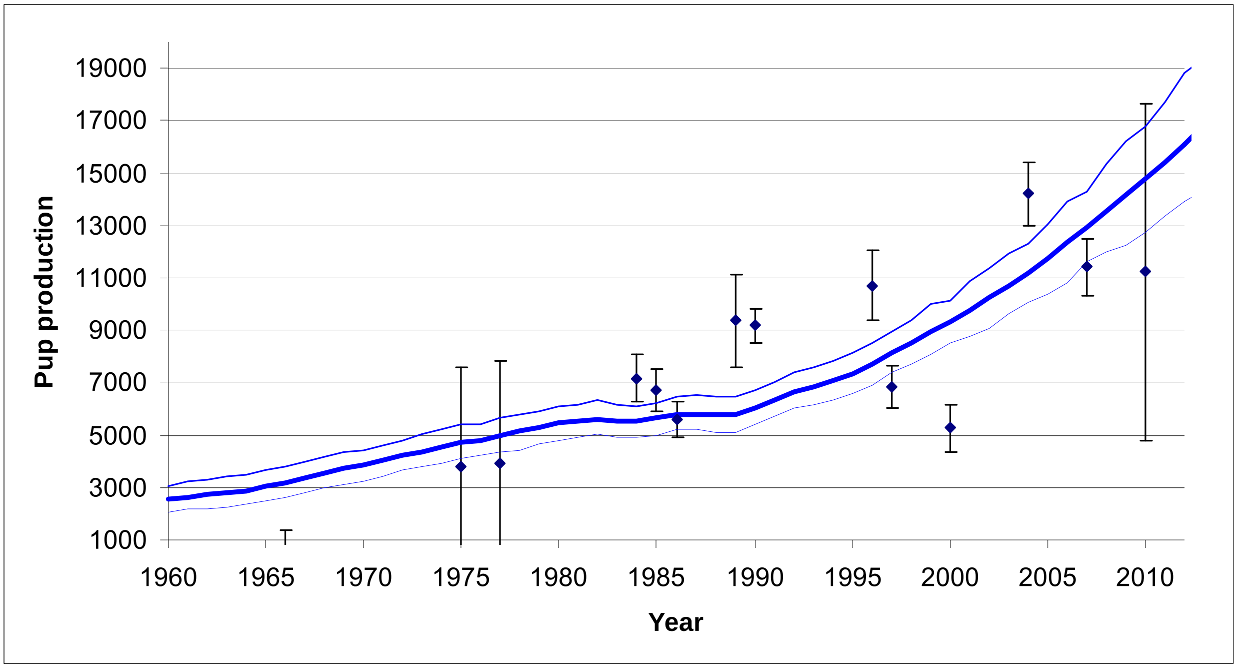


Figure 3. Estimated Pup production trajectory of Sable Island colony using a new model fitted to the pup survey data (top). The initial run fixed pup mortality (γ) to 3 x adult mortality. In a subsequent run, γ=15, age specific reproductive rates decline beginning in 2001, and density dependent mortality (K_{Sable}=400,000) is assumed. This is modified further by assuming a knife edge decline in age at first birth and subsequent shift in age specific reproductive rates and fitting to the new survey data (bottom).



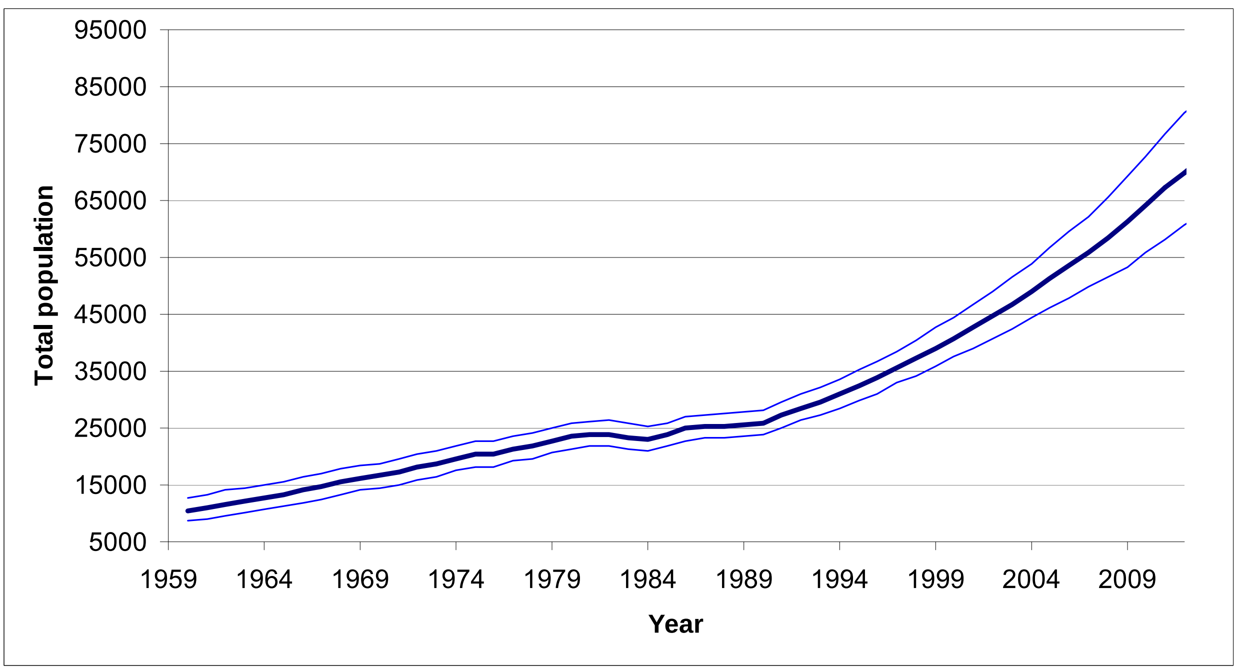


Figure 4. Estimates (±95% C.I.) of pup production (top) and total population (bottom) for the Gulf of St. Lawerence from a model of grey seal population dynamics fit to pup production estimates.
Eastern Shore graphs?

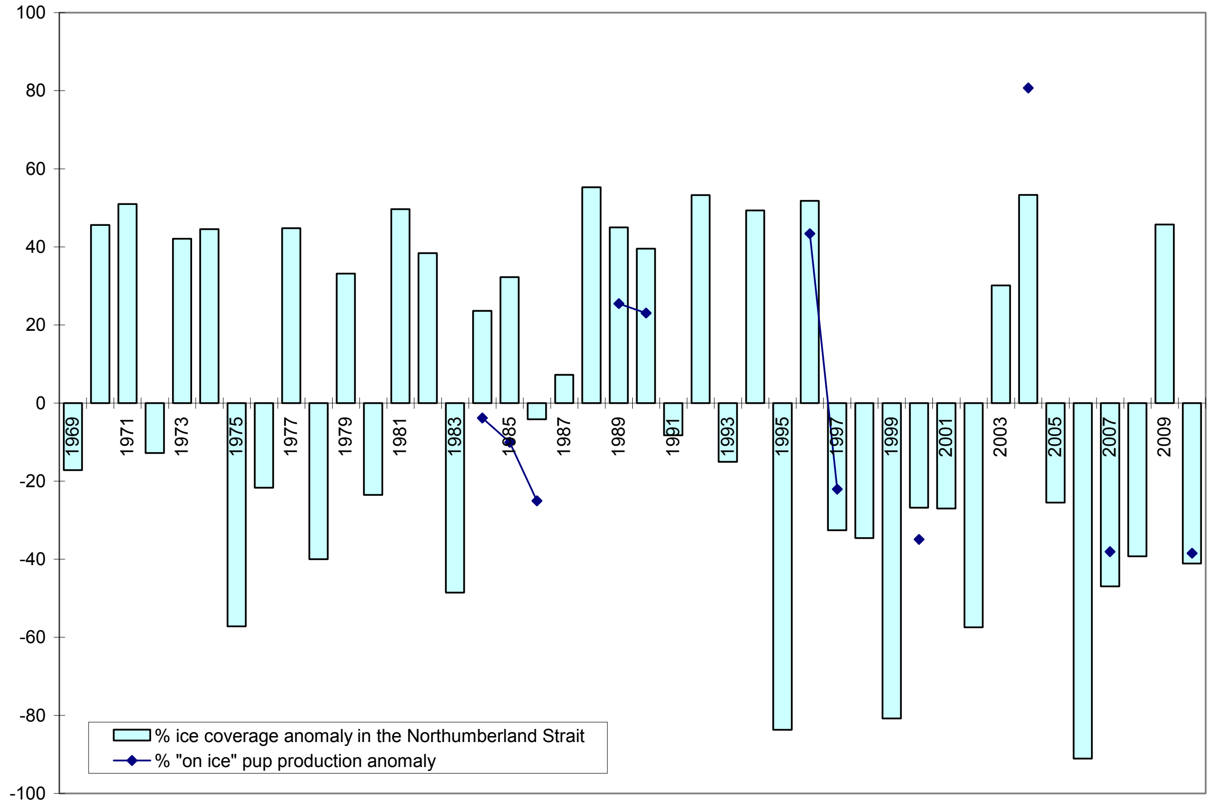
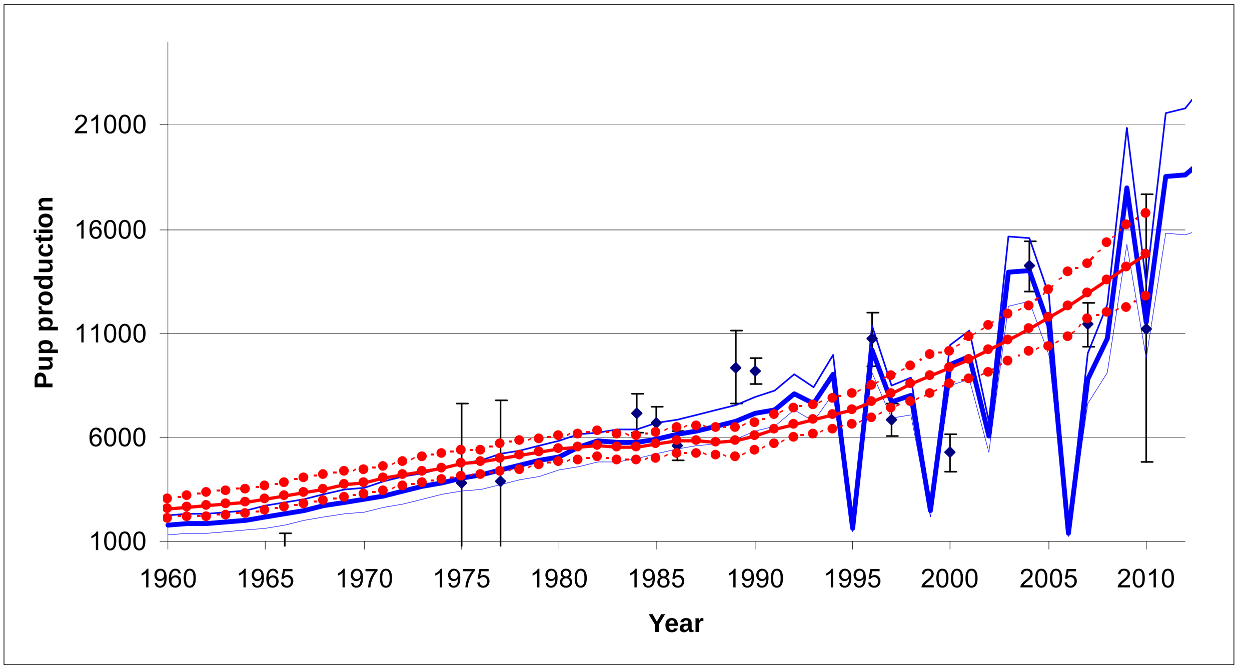


Figure 5. Plot of standardized estimates of pup production on the ice ((estimate-mean)/mean) and standardized ice cover ((surface cover-mean cover/mean cover)). The ice data are from 1969-2010, the pup production estimates are from 1984 to 2010.



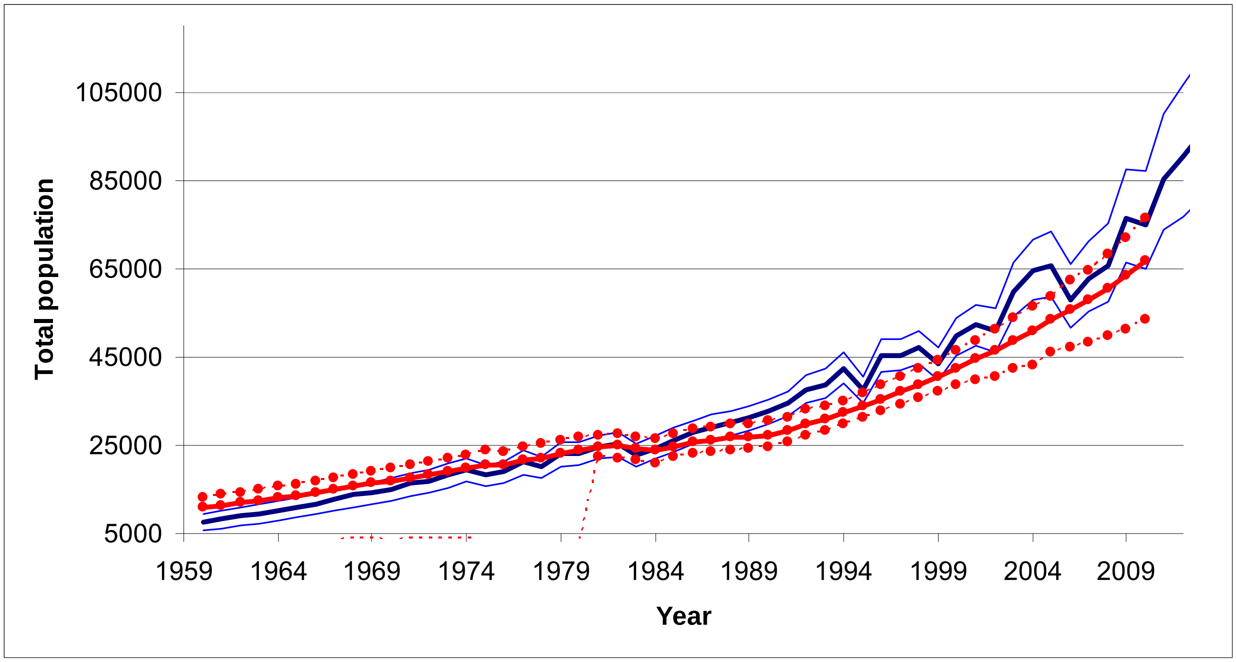


Figure 6. Estimates (±95% C.I.) of pup production (top) and total population (bottom) from a model of grey seal population dynamics fit to pup production estimates and incorporating a factor for ice related mortality (blue solid) and without incorporating a factor for ice-related mortality (red, dotted).