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Northwest Atlantic Grey Seal Population Trends, 1960-2012

Tendances de la population de phoques gris de l'Atlantique Nord-Ouest, 1960-2012

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ABSTRACT

A model of Northwest Atlantic grey seal population dynamics was fitted to available pup production data to provide estimates of the Canadian component of the Northwest Atlantic grey seal population from 1960-2012. In previous assessments, the population model estimated a common adult and juvenile mortality rate for the whole population and separate carrying capacities for each herd. For the 2012 assessment, the model was fit to each of the three breeding colonies separately, resulting in separate estimates of pup production, total population size, adult and juvenile mortality and environmental carrying capacity. The 2012 total population of each herd was 262,000 (95% CI 219,000 -332,000), 20,000 (95% CI=17,000-23,000), and 49,000 (95% CI=27,000-102,000), for the Sable, Coastal Nova Scotia and Gulf of St Lawrence herds respectively. In 2012, total pup production was estimated as 75,000 (95% CI=63,000-97,000) animals, with a total population of 331,000 (95% CI=263,000-458,000). Taking into account changes in modeling approaches the population has increased slightly. Total removals should not exceed 36,700 animals if YOY comprise 95% of the harvest or 19,900 animals if YOY comprised 50% of the harvest. Higher harvests are possible, but with increased risk of falling below the limit reference level and subsequent population collapse. Further work is needed on how reproductive rates are incorporated into the herd specific models, as well as the treatment of removals from each area, particularly on the Scotian Shelf area.

RÉSUMÉ

Un modèle de population dynamique pour le phoque gris de l'Atlantique Nord-Ouest a été adapté aux données disponibles de production de petits pour fournir des estimations de la composante canadienne de la population de phoque gris de l'Atlantique Nord-Ouest de 1960 à 2012. Dans les évaluations précédentes, le modèle de population estimait un taux de mortalité commun pour les adultes et les juvéniles pour la population entière et une capacité de charge distincts pour chaque troupeau. Pour l'évaluation de 2012, le modèle a été ajusté à chacune des trois colonies reproductrices séparément, ce qui entraîne des estimations distinctes de la production de petits, de la taille de la population totale, la mortalité adulte et juvénile et la capacité de charge environnementale. La population totale de chaque troupeau en 2012 était de 262 000 (IC 95 %, 219 000 – 332 000) 20 000 (IC 95 %, 17 000 – 23 000) et 49 000 (IC 95 %, 27 000 – 102 000), pour les troupeaux de l'île de Sable, du littoral de Nouvelle-Écosse et du Golfe du Saint-Laurent respectivement. En 2012, la production totale de petits a été estimée à 75 000 animaux (IC 95 %, 63 000 – 97 000), avec une population totale de 331 000 (IC 95 %, 263 000 – 458 000). En tenant compte des changements dans l'approche en modélisation, la population a légèrement augmenté. Le total des prélèvements ne devraient pas dépasser 36 700 animaux si les jeunes de l'année représentent 95 % de la récolte ou de 19 900 animaux si les jeunes de l'année composent 50 % de la récolte. Des niveaux de récoltes supérieurs sont possibles, mais avec un risque accru de tomber en dessous du niveau de référence limite et l'effondrement de la population ultérieurement. Des travaux complémentaires sont nécessaires pour déterminer comment les taux de reproduction sont intégrés dans les modèles spécifiques des troupeaux, ainsi que le traitement des prélèvements de chaque région, en particulier sur la zone du plateau néo-écossais.

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 longer-term major increases in the abundance of two marine mammal species, the harp seal (*Pagophilus groenlandicus*) and the much larger-bodied grey seal (*Halichoerus grypus*) (Hammill and Stenson 2008, Thomas et al. 2008).

Unlike the harp seal, for which there exists good information on population abundance and harvests that extend over the last two centuries, little is known of historical abundance or harvests 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. In the late 1800s, Gilpin (1874) speaks of herds of only 20 or 30 seals on Sable Island, and in the early 1950s, they were considered to be rare throughout eastern Canada (Lavigueur and Hammill 1993; Bowen 2011). Government sponsored culls and a bounty program may have slowed grey seal recovery in the 20th Century (Bowen and Lidgard 2012), but over the last five decades the Canadian grey seal population has increased from approximately 15,000 animals in the 1960s to over 350,000 in 2007 (Mohn and Bowen 1996; Thomas et al. 2007).

The Northwest Atlantic grey seal forms a single population (Boskovic et al. 1996; Wood et al. 2011). Within Canadian waters the population is subdivided into three groups for management considerations based on the locations of main breeding colonies: Sable Island (Sable), Gulf of St. Lawrence (Gulf), and Coastal Nova Scotia (Coastal) components (Fig. 1). Sable Island, Nova Scotia, Canada, is 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). A relatively small number of animals breed on isolated islands along coastal Nova Scotia. These have traditionally been primarily in the area known as the Eastern Shore (Mansfield and Beck 1977). In the last few years, small colonies have also appeared along the southwestern shore of Nova Scotia on Flat and Noddy Islands. Outside of the breeding season, there is overlap in the distribution of animals from the different colonies (e.g., Lavigueur and Hammill 1993; Harvey et al. 2008; Breed et al. 2006, 2009). Grey seal pupping also occurs in the northeastern United States, with pup production of around 1,000 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 assessments have used a Bayesian model that assumes that pup survival is density dependent, and that estimates the same maximum pup and adult female survival rates, but different carrying capacities for all three herds. Reproductive rates are also assumed to be constant across herds and time. Female migration is allowed to occur between colonies, but once females establish themselves at a new colony, they are assumed to remain there (Thomas et al. 2007)

The herds in the three regions have had very different population trajectories. Prior to 1997, pup production increased at a rate of 13% a year on Sable Island (Bowen et al. 2011). Between

2007 and 2010, the rate of increase slowed to about 4%, suggesting that the population may be facing resource limitation. 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 and Stenson 2011; Thomas et al. 2007). On the Eastern Shore, significant culling efforts, particularly in the Basque Island area limited pup production to the low 100's during the 1970s, and significant commercial hunting has occurred on Hay Island over the last decade.

Here we apply a three parameter model similar to that developed for harp seals (Hammill et al. 2013) that uses information on age-specific reproductive rates, pup production, 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, adult mortality and carrying capacity. Estimated pup production and total population size from the current model were compared to predictions from the assessment model described above (Thomas et al 2007). Comparisons between models were made for all herds up to the 2010 assessment. Since then new data have been obtained on reproductive rates and removals. These data were incorporated into the revised model to provide estimate total population size in Atlantic Canada as well as harvest advice.

MATERIALS AND METHODS

Modelling the dynamics of the Northwest Atlantic grey seal population occurs in two steps. In the first, using Monte Carlo sampling, the model is fitted to independent estimates of the total pup production, by adjusting initial population size (α), adult (i.e., one year old and older, referred to as 1+) mortality rates (M) and the carrying capacity (K). It is considered that the dynamics of the population can be described by assuming density-dependent mortality acting on juvenile survival. It is also assumed that the sex ratio is 1:1.

A second component of the model, referred to as the 'Projection Model', projects the population into the future to examine the impacts of different management options on the population. The projection model is based on the same equations as the fitting model.

MODEL STRUCTURE

Initial population

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

Survival

For age 1:

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

with $M_1 = \gamma \times M$

For age a, with 1<a<A:

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

For age A

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

Reproduction

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

For age a, with 1<a<8

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

For age a, with a ≥ 8 (i.e. 8+)

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

also $Psim_{8+,t} = 0.9 \times (1 - N_t / K)^{\theta}$

where

P_{init}	= size of the total initial population,
α	= multiplying factor,
l_i	= initial population size for the i[th] age class,
$n_{a,t}$	= population numbers-at-age *a* in year *t*,
$c_{a,t}$	= the numbers caught at age *a* in year *t*,
$P_{a,t}$	= per capita pregnancy rate of age *a* parents in year *t*, assuming a 1:1 sex ratio,
$CorBin$	= multivariate distribution composed of binomial distributions which degree of correlation is controlled via an 8-dimension Gaussian copula (Hammill et al. 2013). Note: this function is only used during the fitting part (see below the point 4 of the projection part specifications),
$n_{a.reprod,t}$	= sample size used to obtain the observed pregnancy rate in year t,

$p_{a.reprod,t}$ = proportion of pregnancy in the observed group in year t,

$Psim_{8+,t}$ = per capita pregnancy rate of age 8+ parents estimated by its relation with the carrying capacity. The value of 0.9 corresponds to the maximum pregnancy rate observed when the population was low (i.e. far from the carrying capacity). This estimation is used to fit the model with observed pregnancy rates obtained during the same period.

M = the instantaneous rate of natural mortality,

γ = a multiplier to allow for higher mortality of first year seals. This was set to 6, (den Heyer et al. this meeting)

w = the proportion of pups surviving an unusual mortality event arising from poor ice conditions or weather prior to the start of harvesting,

A = the 'plus' age class (i.e., older ages are lumped into this age class and accounted for separately, taken as age 25 in this analysis),

N_t = total population size,

K = carrying capacity

θ = theta, set at 2.4 (Trzcinski et al. 2006).

The model creates a population matrix with 26 age classes from 1960 until the current year. The initial population vector (26 × 1) was created as an initial population age structure which size is controlled by a multiplying factor (α). The model integrates data on pregnancy rates, removals and ice-related mortality, and is fitted to pup production estimates. It minimizes the weighted sum-of-square differences between the pup production estimated by the model ($n_{0,t}$) and the observed production from surveys. The sums of squares are minimized by estimating three parameters; the initial population factor (α), the instantaneous mortality rate (*M*), and the carrying capacity (*K*).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), and pup production estimates are resampled assuming a normal distribution (with variance based on estimates of the survey errors). The three parameters (α, *M* and *K)* are optimized by iterative methods. For each Monte Carlo simulation, a new *M, K* and α were estimated and stored. The model is written using the programming language R.

DATA INPUT

Pup production estimates

The model was fit to independent estimates of pup production (Table 1) obtained at each herd. Not all herds have been assessed in the same year(s) and not all estimates have used the same methods.

Reproductive rates

Late-term pregnancy data are available from sampling programs (Hammill and Gosselin 1995). Samples were collected between late May and November. Fall samples represent late-term pregnancy rates since they were collected only a few months prior to pupping in December. It is assumed that there were no abortions after the samples were taken. The mean birthdate is assumed to be 1 January, and all animals advance one year on this date. Females enter the model at the age that they turn on 1 January of each year. There are gaps in the time series of reproductive data, and in some years sample sizes are small (Table 2). When sample sizes were <10, reproductive rates were estimated by smoothing the data using a local likelihood estimator (Hammill et al. 2013).

Catches

Catch data are available since 1960. There are four types of catches: the Canadian commercial harvest (Department of Fisheries and Oceans, Statistics Branch); those from nuisance seal licences, those from bounty kills and culls, and those from science sampling programs. The Canadian commercial hunt consists of 99% of young of the year. All harvests were corrected for estimates of seals struck and killed, but not landed or reported.

Ice-related mortality of YOY

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, whereas in years of light ice 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. Hammill and Stenson (2011) used an index based on the late January Northumberland Strait ice cover, where the index = 1/(mean ice cover-ice cover in year *t*). In years when ice cover was greater than the mean, the index was set to 1 (Hammill and Stenson 2011). In 2011 and 2012, there was very little ice-cover in the traditional whelping areas, and survey flights indicated that seals were not using what ice was available. Instead all seals in these years had their young on land. For these 2 years, the index was set to 1 (Table 3).

Sable Island

The reproductive data are obtained from animals collected in the Gulf of St. Lawrence and in Cabot Strait in late fall, when many Sable animals will have returned to the island. The recent reproductive data from these collections show a decline in age-specific reproductive rates since 2008, which would imply a decline in pup production on Sable Island. However, field observations at sable Island do not support this (Bowen unpublished). Mark- resighting of branded females on Sable Island show that mean age at first birth and average birth rate have not changed over time, so an alternative scenario was run assuming that there has been no change in reproductive rates since 2008.

Projection model

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

1. mortality from nuisance seal, culls, and science harvests remain constant. For Sable Island this described nuisance seal removals as a uniform distribution with limits of 3,000 to 3,500 animals. In the Gulf this was set at a uniform distribution that was allowed to vary between 100 and 400 animals. For CNS this was set to a uniform distribution with limits of 100-150,

2. ice-related mortality (actually expressed as survival in model) was set at 1 for all three herds,

3. reproductive rates were set as a vector to the age-specific rate for the last 5 years, with each year having an equal probability of being selected. A second approach assumed that the reproductive rates of 8+ animals could be related primarily to the population size by the equation (r=0.9 * $(1-(N/K)^{2.4})$. Pregnancy rates within ages (4 to 8+) were described by a logistic curve fitted on the observed rates. The rate for animals aged 8+ years being the asymptote. This was done for the projection model under the assumption that if the 8+ pregnancy rates can be predicted using a density-dependent relationship, then it is possible to evaluate pregnancy rates for other ages, keeping the correlation between values. Moreover, taking into account the error around the other parameters of the logistic curve, it allows for consideration of a certain source of "natural" variability around each pregnancy rate that is estimated, and

4. the dynamics of the population can be described assuming density-dependent mortality acting on juvenile survival by the relationship:

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

The model is projected forward to determine if the catches will respect the management plan (i.e. 80% likelihood of population remaining above the Precautionary Reference Level) for the next 15 years. This projection period is required to ensure that at a given level of harvest the population would have <5% chance of collapsing (Hammill and Stenson 2009a).

RESULTS

The smoother fitted to the reproductive data provide a means of interpolating for missing years and captured the variability in the data fairly well (Fig. 2). Overall, reproductive rates were high throughout most of the time-series. There appears to have been a decline in the early 2000s that lasted for 2-3 years, then a return to high rates from 2004 until 2009. Since 2009, there has been a decline in reproductive rates across all age-classes, but samples sizes are small for age classes 4-7 years old (Table 2).

COMPARISON OF MODELS

The model was fitted to the pup production estimates from each herd and compared to the estimates obtained by Thomas et al. (2011). Thomas et al. fitted their model to the period 1970-2010 using pup production estimates available from 1977 to 2010, and using the 1970 to 2008 reproductive rate data (i.e., when reproductive rates were high). The best fit was obtained fitting the model to the Sable Island data, which is also the most extensive and consistent dataset (Fig. 3). The pup production estimate from the 2010 survey was 62,000 (Table 1). The model estimated a pup production of 62,000 (95% CI=57,000-65000). The total population estimate was 276,000 (95% CI=230,000 to 311,000), compared to Thomas et al (2011) who estimated a 2010 population of 277,000 (95% CI=250,000 to 308,000). Adult mortality (M) was estimated to be .051 (SE=.006), and carrying capacity (K) was estimated to be 465,000 (SE=155,000). For the CNS herd, there is a long series of observations, dating back to the 1960s. These observations represent approximate numbers of pups on small islands, primarily on Basque Island off the east coast of Cape Breton Island. A new colony of animals was discovered at Hay Island in 1994, and estimates of pup production increased rapidly, then appear to have leveled off at about 2500 pups. Over time, the number of pups at other small colonies (Flat, Noddy, and White Islands) may become more important, but for the moment Hay Island remains the single largest colony in coastal Nova Scotia. Estimates from the Thomas et al (2011) and the new model were similar, but the new model suggested a more gradual leveling off of the population (Fig. 4). The 2010 total population was estimated to be 10,000 (95% CI=9600-13,000). Adult mortality was estimated to be 0.029 (SE=.013) and K=10,800 (SE=2,500). In the Gulf, overall model fit is poor, although the new model appears to provide a better fit to the pup production data. There was considerable overlap between the two models with the new model suggesting a leveling off in the population in recent years, whereas the Thomas et al. (2011) model indicating that the population continued to increase (Fig. 5). In 2012, the total estimate population was 44,000 (95% CI=29,000-68,000), M=0.046 (SE=0.033), and K=76,000 (SE=89,000).

NEW MODEL ESTIMATES

For the Sable Island herd, fitting the model to the pup production data, using updated age-specific reproductive rate data to include the years 1969-2011, predicted that pup production and the population increased until 2010, but then declined with a 2012 pup production estimate of 36,000, which is approximately 40% of the pup production observed in 2010. However, there is evidence that does not support such a decline suggesting that updating the reproductive rates to 2012 was not appropriate for Sable Island (see above). Refitting the model, assuming no change in reproductive rates since 2008, resulted in a pup production and total population that continue to increase, although more slowly in recent years (Fig. 6). The 2012 pup production estimate is 67,000 (95% CI=56,000 to 85,000), the total population size estimate of 262,000 (95% CI 219,000 -332,000), M=0.049 (SE=0.003), K=332,000 (SE=58,000). This resulted in a juvenile mortality estimate of 0.64.

Fitting the model to the Coastal Nova Scotia estimates of pup production with the updated age specific reproductive rate data from the Gulf results in a 2012 pup production estimate of 2,300 (95% CI =1,100-3,800), and a total population of 20,000 (95% CI=17,000-23,000), with M=0.04 (SE=.002) and K=29,000 (SE=2,500)(Fig. 7).

Fitting the model to the Gulf pup estimates with the updated reproductive data resulted in a 2012 pup production estimate of 5,500 (95%CI=1,700-11,800) and a total population of 64,000 (95% CI=43,000-101,000), M=0.08 (SE=0.01), K=125,000 (SE=16,000)(Fig. 8). We also fitted the model to the Gulf pup production estimates assuming that poor ice conditions increased early pup mortality. Taking into account ice conditions resulted in a smaller population but appeared to improve the fit to the pup survey estimates (Fig 9). However, the differences were not significant (Fig 9). Pup production in 2012 was estimated to be 7,000 (95% CI=2,900-15,200). Total population size in the Gulf was estimated to be 49,000 (95% CI=27,000-102,000), M=0.06 (SE=0.008), K=45,000 (SE=5,000), which is fewer animals than estimated from the model with no ice-related mortality, but the differences were not significant. However, the ice-related mortality model suggests that population size in the Gulf may be near carrying capacity rather than at about 50% of K as suggested by the model without ice-related mortality.

Combining all three herds and assuming an ice effect in the Gulf , grey seal pup production in 2012 is estimated to be 76,300 (95% CI=60,000-105,000) animals, with a total population of 331,000 (95% CI=262,000-458,000)(Fig. 9). Sable Island production accounts for about 88% of the estimated total number of pups born in 2012.

SUSTAINABLE HARVEST LEVELS

For the Sable Island herd, assuming that future reproductive rates are fixed, a two year TAC with an annual harvest of up to 30,000 animals assuming YOY comprise 95% of the catch, would respect the management objective of remaining above N70. A harvest of 37,000 would have a 95% probability of remaining above N30, but only a 49% probability of remaining above N70. If YOY only comprised 50% of the catch, then a harvest of 16,000 would continue to respect the management objective of N70, while a harvest of 20,000 would have a 95% probability of remaining above N30 and only a 30% chance of remaining above N70 (Fig. 10).

For the Coastal Nova Scotia herd, assuming that future reproductive rates are fixed, a two year TAC with an annual harvest of up to 3,200 animals assuming YOY comprise 95% of the catch, would respect the management objective of remaining above N70. A harvest of 4,000 would have a 95% probability of remaining above N30. If YOY only comprised 50% of the catch, then a harvest of 1,900 would continue to respect the management objective of N70, while a harvest of 2,100 would have a 95% probability of remaining above N30. Assuming that future reproductive rates were density dependent resulted in similar harvest levels (Fig. 11).

For the Gulf herd, assuming that future reproductive rates are fixed, a two year TAC with an annual harvest of up to 3,500 animals assuming YOY comprise 95% of the catch, would respect the management objective of remaining above N70. A harvest of 5,500 would have a 95% probability of remaining above N30. If YOY only comprised 50% of the catch, then a harvest of 2,000 would continue to respect the management objective of N70, while a harvest of 3,000 would have a 95% probability of remaining above N30. Assuming that future reproductive rates were density-dependent resulted in annual harvests that respected the plan declining to 2,500 if the harvest was 95% YOY and 2,100 if the harvest was comprised of 50%YOY (Fig. 12).

DISCUSSION

The last two assessments of grey seals in Atlantic Canada have applied a population model that was developed and applied to the management of grey seals in the United Kingdom. The model was statistically complex and computationally intensive. As outlined in Thomas et al. (2007), the results reported were based on 150 runs of 1 million particles. This represents approximately 150 hours of computer time, although in practice runs were made in parallel on up to 8 processors so results were available in 1-2 days. The Thomas et al. (2007) model estimates a single adult and juvenile mortality rate and separate carrying capacities for each herd. Consequently, the Sable Island herd, as the largest herd, has a considerable influence on the overall estimates of adult and juvenile M. Although it is tempting to argue that adult mortality rates (M_{adult}) might be similar between herds, this may not be the case owing to different levels of unreported removals through bycatch and nuisance seal takes as well as ecological differences experienced by each herd. Similarly, juvenile mortality is also likely to differ between herds, particularly within the Gulf where animals pup on the ice. Finally, although the Thomas model does provide an estimate of movement between herds, there is little information available regarding this parameter.

Fitting the new model to each herd separately resulted in similar estimates, but wider confidence limits, to those produced by the Thomas et al. (2007, 2011) of pup production and population size, particularly for the Sable Island herd where we have the longest time-series of data. The wider confidence limits are due to differences in the way that the reproductive data were incorporated into the two models. The new model takes into account more of the uncertainty associated with the reproductive rate data. The fits to the 2010 survey data, presented in Thomas et al. (2011) incorporated reproductive rate data up to and including 2008. Although reproductive rates did vary with age, no temporal trend in reproductive rates was observed. New reproductive data collected between 2008 and 2011 suggest that overall reproductive rates are declining, which may indicate a density-dependent response to population size.

Although we have fitted to the herds separately, the reproductive rate data used in the fitting are from animals collected in the Gulf and Cabot Strait areas. Some Sable Island animals do summer in the Gulf and presumably some will have been collected in our sampling, but the majority of animals that contribute to the dynamics of the Sable herd remain on the Scotian shelf, where different ecosystem conditions might be expected. Fitting the model to the Sable Island pup production data with updated reproductive rate data resulted in a continuous drastic drop in pup production on the island from an estimated 62,000 in 2010 to approximately 36,000 in 2012. Field observations do not support such a decline (Bowen unpublished). Furthermore, mark-recapture/resight data from Sable Island indicate that minimum average birth rates of ~75% and these data have not detected any change in adult survival or average age at first birth over time, but changes have been observed in juvenile survival rates (den Heyer et al. 2013). These observations and data indicate that it is not appropriate to apply the recent reproductive rate data obtained from the Gulf of St. Lawrence to the Sable Island herd.

We examined an alternative scenario, where age-specific reproductive rates have remained high, which is consistent with the Sable Island observations. This resulted in pup production and total population estimates that continue to increase at a rate of about 2.8% since 2010. This is slightly lower than a rate of 3.3% observed during the period 2007-2010. Model estimates for M_{adult} and $M_{juvenile}$ are also in line with estimates from mark-recapture/resighting estimates on Sable Island of 0.03-0.05 and 0.65, although $M_{juvenile}$ in the model and the resighting studies are not identical (den Heyer et al. 2013). Application of the Gulf reproductive rate data to the CNS herd may also not be appropriate and the use of different rates might affect estimated harvest impacts. This remains to be investigated.

Grey seals along CNS have received less attention than in the Gulf and on Sable. This is because the main colony is relatively new and all coastal colonies combined still contribute little to the overall Canadian grey seal population. Historically, small colonies have persisted in spite of repeated harvesting activity, particularly around Basque Island off the east coast of Cape Breton Island. Erosion has altered the island so that currently little remains of it to serve as a pupping site, but small numbers are still observed (approximately 12 pups in 2012; MOH pers obs.), and based on bounty and science collections during the 1960s-1970s the Gaborus/Fourchu area appears to have been an area where grey seals were locally abundant . Currently, the CNS herd is dominated by pupping activity on Hay Island, a relatively new colony discovered in 1994. The new model was able to fit to CNS herd and provided a similar impression of the herd when fitted to the same data as the Thomas et al (2011) model. However, to do so, the new model estimated a very low adult M for the CNS herd of only 0.02, which seems unrealistically low. Fitting the new model to the estimates of pup abundance, using reproductive rates updated to 2011, resulted in a more realistic, although still low estimate (compared to the other herds) of M_{adult} of 0.04. The Thomas et al. (2011) model used in the last assessment also suggested that the CNS population had leveled off. This was due to the dominance of the Hay Island colony in the CNS abundance surveys, where pup counts from this colony had shown no change over the last two assessments. Overall, the adult to pup ratio for the CNS colony was approximately 5:1when the model was fitted to the pup estimates and the reproductive data that was limited to up to 2008. In contrast, fitting the new model to the CNS survey data with the new reproductive rates (up to 2011) suggest that the CNS herd has continued to grow, although this rate of growth has slowed. The adult to pup ratio from this fitting is approximately 9:1, which is extraordinarily high (Wickens and Shelton 1992). This may result from the use of inappropriate reproductive rate data to the CNS herd; instability in the dynamics of this herd, which may be due for example to continued harvesting activity on the small islands where animals from this herd have their young, or factors associated with the survey. Surveys typically involve only a single count, although in the case of Hay Island, staging surveys are also undertaken to correct counts for pups born after the surveys are flown. Emigration of pups from the island prior to the surveys being completed is not considered. Overall, it appears that the CNS herd is becoming more important in the dynamics of the Canadian grey seal population. In 2012, an unusual mortality of approximately 400 grey seals was documented on Hay Island. Almost all animals were weaned, fully moulted YOY. The cause of death has been linked to a parasitic infection, but has not been identified to species (P.-Y. Daoust, Atlantic Veterinary College, pers. com.). This mortality was treated as natural mortality, and no special adjustments in the model were made.

Variable ice conditions, particularly since the early 1990s have complicated attempts to assess grey seals in the Gulf. Attempts to correct estimates for variable pup mortality prior to the assessment provide a better fit overall to the survey data, and this model is recommended. In some years, when some ice forms, limiting access to the islands, animals pup on the ice and mortality can be high if this ice breaks up before animals are weaned. In recent years, suitable ice has not formed in the Gulf, which has allowed access to islands that were not available for pupping before, e.g., Brion Island, Pictou Island, and Anticosti Island (Hammill and Stenson 2011). These conditions are likely more favourable to grey seals, although human disturbance and storm surges may offset the advantages of pupping on these islands. Continued high levels of removal in the Gulf have also had an impact on the dynamics of this herd.

The total Northwest Atlantic grey seal population in 2012 is estimated to be 331,000 (95% CI=263,000-458,000) animals. Using the current model, the 2010 population estimate is 318,000 (95% CI=266,000-405,000), indicating that there has been some limited growth (approximately 2% per year) in the population since 2010, owing to a decline in the rate of increase in the Sable Island herd and uncertainties in the dynamics of the Gulf and CNS herds. Nevertheless, this is less than the Thomas et al. (2011) estimate of 348,900 (95% CI 291,300-414,900) for 2010. The modeling approaches are much different, and this underlines the point in Hammill and Stenson (2012), that often model revisions can result in important changes in our perception of the population, while the underlying status of the population may not have changed.

To respect the current management objective of maintaining an 80% probability of staying above N70, total removals should not exceed 36,700 animals if YOY comprise 95% of the harvest or 19,900 animals if YOY comprised 50% of the harvest. These estimates are much lower than recommendations from Thomas et al. (2011) of 70,000 and 30,000 for 95%YOY and 50% YOY respectively. These differences result from differences between the two studies in estimates of M_{adult}, $M_{juvenile}$, the higher level of uncertainty associated with the reproductive rates that is incorporated into the models, as well as possible differences in the way that harvests were calculated. Thomas et al. (2011) estimated a common M_{adult} and $M_{juvenile}$ of 0.039 and 0.23 for adults and juveniles respectively (expressed as survival in Thomas et al. 2011) and for their projections used an average reproductive rate of 0.88 for animals aged 8+ years. In the current study, the mortality rates were generally higher for each herd, with $M_{juvenile}$ set at 6 times M_{adult} and M_{adult} estimated separately for each herd with estimates of 0.049-0.08. Thomas et al. (2011) provided harvest levels that would respect the management objective if maintained over a period of 3, 5 and 20 years; the latter (20 years) was similar to the approach used here. This concept takes into account that seals are relatively long-lived and that high harvests are unlikely to have much impact over a period of 3-5 years, but can result in population collapse over longer time frames (Hammill and Stenson 2009a).

We have presented these harvest levels as annual harvests for a two year management plan. Variable harvest rates including carryover from year one to the second year would also respect the management framework as long as the two year take did not exceed the sum of the recommended TAC level, as shown for harp seals (Hammill et al. 2013). We have also included harvest levels that would have a high probability (<95%) of not falling below N30 if changes in management objectives were to occur, but the higher the risk that is accepted to fall below 30, the greater the risk of population collapse. This is particularly important given that population models only represent a perception of the population, which can change markedly as model formulation and new data are included. Failure to consider this uncertainty has resulted in population collapses throughout several fisheries.

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Table 1. Pup production estimates used as input into the population model.

Year	Sable Island		Coastal Nova Scotia		Gulf	
	Estimate	se	Estimate	SE	Estimate	SE
1960						
1961						
1962			130	400		
1963	400	400	180	400		
1964	550	550	190	400		
1965	660	660	230	400		
1966			180	400	900	500
1967	580	580	270	400		
1968	700	700				
1969	800	800				
1970	800	800	100	400		
1971	1000	1000	130	400		
1972	950	950				
1973	1200	1200				
1974	1250	1250	135	400		
1975			180	400	3800	3800
1976	2000	2000	130	400		
1977	2181	173			3900	3900
1978	2687	192				
1979	2933	201				
1980	3344	214				
1981	3143	208				
1982	4489	248				
1983	5435	273				
1984	5856	283	142	400	7169	911
1985	5606	277	135	400	6706	795
1986	6301	294	151	400	5588	679
1987	7391	318	179	400		
1988	8593	343				
1989	9712	365	179	400	9352	1756
1990	10451	575			9176	649
1991						
1992						
1993	15500	463				
1994			900			
1995						
1996			395	148	10717	1306
1997	25400	750	1061	242	6839	800
1998						
1999						

Table 1. Suite.

Year	Sable Island		Coastal Nova Scotia		Gulf	
	Estimate	se	Estimate	SE	Estimate	SE
2000			799	210	5260	910
2001						
2002						
2003						
2004	41500	4381	2469	152	14210	1200
2005						
2006						
2007	54482	1288	3017	80	11413	1077
2008						
2009						
2010	62054	587	2960	272	11228	6442

Table 2. Year, Age (years), number of females collected between 1969 and 2012 (n) and number of females pregnant (n_preg)

Year	Age	n	n_preg	Age	n	n_preg	Age	n	n_preg
1969	4	12	3	5	7	5	6	9	9
1982	4	4	0	5	4	3	6	8	7
1986	4	4	1	5	2	2	6	4	3
1987	4	7	1	5	10	5	6	8	5
1988	4	7	2	5	14	10	6	10	9
1992	4	16	1	5	16	12	6	15	13
1994	4	1	0	5	3	0	6	1	1
1998	4	0		5	0		6	1	0
1999	4	0		5	2	0	6	2	2
2000	4	5	2	5	2	1	6	4	3
2001	4	1	0	5	0		6	1	1
2002	4	7	2	5	4	1	6	3	3
2003	4	2	0	5	4	2	6	3	2
2004	4	5	0	5	7	6	6	3	1
2006	4	1	1	5	0		6	0	NA
2007	4	1	0	5	3	2	6	3	3
2008	4	0		5	0		6	5	5
2009	4	0		5	0		6	1	1
2010	4	2	0	5	5	1	6	4	2
2011	4	3	0	5	7	0	6	8	3

Table 2. Suite.

Year	Age	n	n_preg	Age	n	n_preg
1969	7	6	6	8	36	29
1982	7	1	1	8	48	43
1986	7	7	6	8	34	32
1987	7	9	6	8	71	67
1988	7	5	4	8	57	51
1992	7	7	6	8	36	32
1994	7	2	2	8		
1998	7	1	1	8	10	8
1999	7	2	2	8	12	12
2000	7	2	2	8	10	7
2001	7	0		8	7	5
2002	7	8	7	8	21	17
2003	7	0		8	8	5
2004	7	3	2	8	28	28
2007	7	0		8	10	9
2008	7	1	1	8	11	11
2009	7	0		8	14	13
2010	7	4	2	8	66	40
2011	7	5	3	8	85	42

Table 3. Survival coefficient used to account for pups drowning before surveys are completed in the Gulf.

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

Table 4. Catches of grey seals. YOY represents young of the year, 1+ animals are seals aged 1 year and older.

Sable

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0
1969	0	0	0	0	0	0
1970	43	2	0	0	0	0
1971	1	12	0	0	0	0
1972	0	0	0	0	0	0
1973	0	0	0	0	0	0
1974	0	2	0	0	0	0
1975	22	0	0	0	0	0
1976	0	9	0	0	0	0
1977	0	69	0	0	0	0
1978	0	0	0	0	0	0
1979	0	0	0	0	0	0
1980	0	0	0	0	0	0
1981	0	69	0	0	0	0
1982	0	0	0	0	0	0
1983	0	214	0	0	0	0
1984	0	20	0	0	0	0
1985	0	0	0	0	0	0
1986	0	0	0	0	0	0
1987	0	0	0	0	0	0
1988	0	46	0	0	0	0
1989	0	477	0	0	0	0
1990	0	197	0	0	0	0
1991	0	0	0	0	0	0
1992	0	6	0	0	0	0
1993	0	0	0	0	0	0
1994	0	0	0	0	0	0
1995	0	0	0	0	0	0
1996	0	24	0	0	0	0
1997	0	7	0	0	0	0
1998	0	0	0	0	0	0
1999	1638	0	0	0	0	0
2000	1743	0	0	0	0	0
2001	1820	0	0	0	0	0
2002	1953	0	0	0	0	0

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
2003	2079	0	0	0	0	0
2004	2660	0	0	0	0	0
2005	2751	0	0	0	0	0
2006	3437	0	0	0	0	0
2007	3373	0	0	0	0	0
2008	3334	0	0	0	0	0
2009	3381	0	0	0	0	0
2010	2933	0	0	0	0	0
2011	3000	0	0	0	0	0
2012	3000	0	0	0	0	0

Coastal Nova Scotia

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

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1987	0	0	0	0	0	0
1988	0	0	0	0	0	0
1989	0	24	0	0	0	0
1990	0	9	0	0	0	0
1991	0	0	0	0	0	0
1992	0	0	0	0	0	0
1993	0	0	0	0	0	0
1994	0	0	0	0	0	0
1995	0	0	0	0	0	0
1996	0	0	6	0	0	0
1997	0	0	0	0	0	0
1998	0	0	0	0	0	0
1999	0	0	0	0	0	0
2000	0	0	82	0	0	0
2001	0	0	1301	0	0	0
2002	0	0	0	0	0	0
2003	0	0	0	0	0	0
2004	0	0	0	0	0	0
2005	0	0	494	0	0	0
2006	0	0	830	0	0	0
2007	0	0	868	0	0	0
2008	0	0	1261	0	0	0
2009	0	0	263	0	0	0
2010	0	0	50	0	0	0
2011	0	0	0	0	0	0
2012	0	0	0	0	0	0

Gulf

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
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

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
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
2011	0	0	200	18	0	0
2012	0	0	200	18	0	0

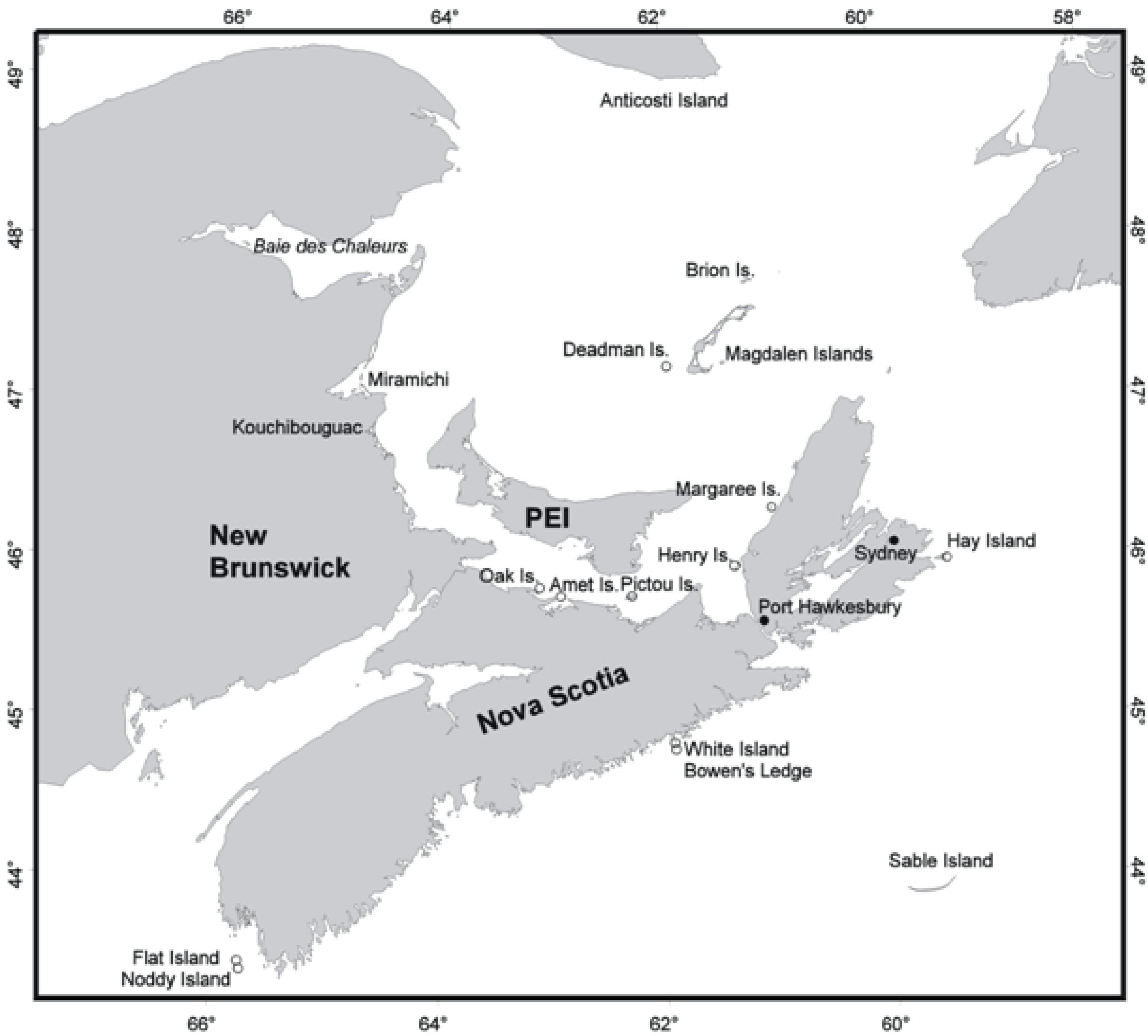


Figure 1. Map showing locations of main pupping colonies in Atlantic Canada. Sable Island is the largest colony. The remaining colonies are identified by open circles.

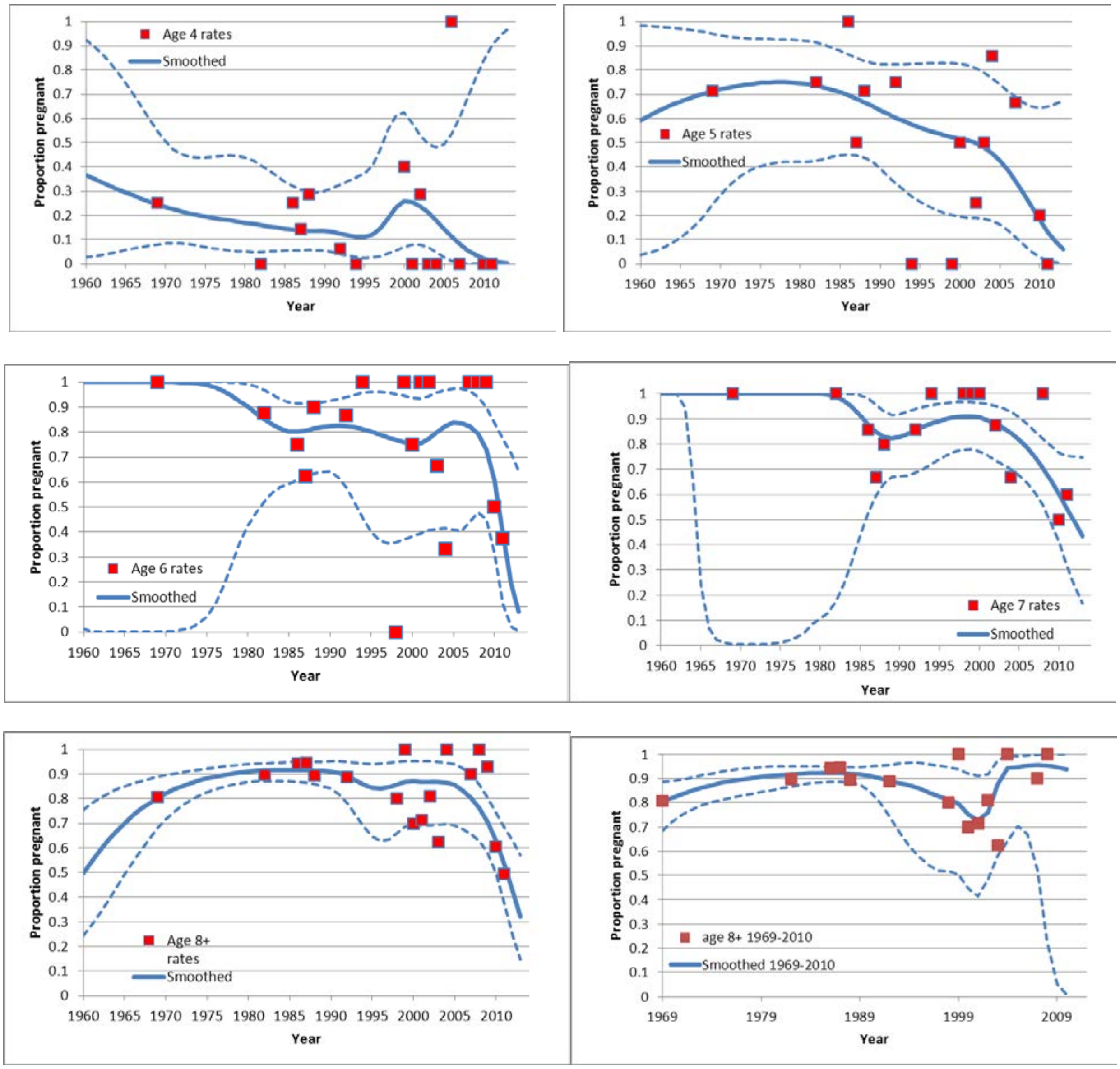


Figure 2. Age specific reproductive rates and non-parametric smoothed rates for the period 1969-2011 for ages 4-8+ years. The bottom right panel shows the smoothed rates for animals aged 8+ years for reproductive rate data from 1969-2008. Dotted lines represent 95% CI.

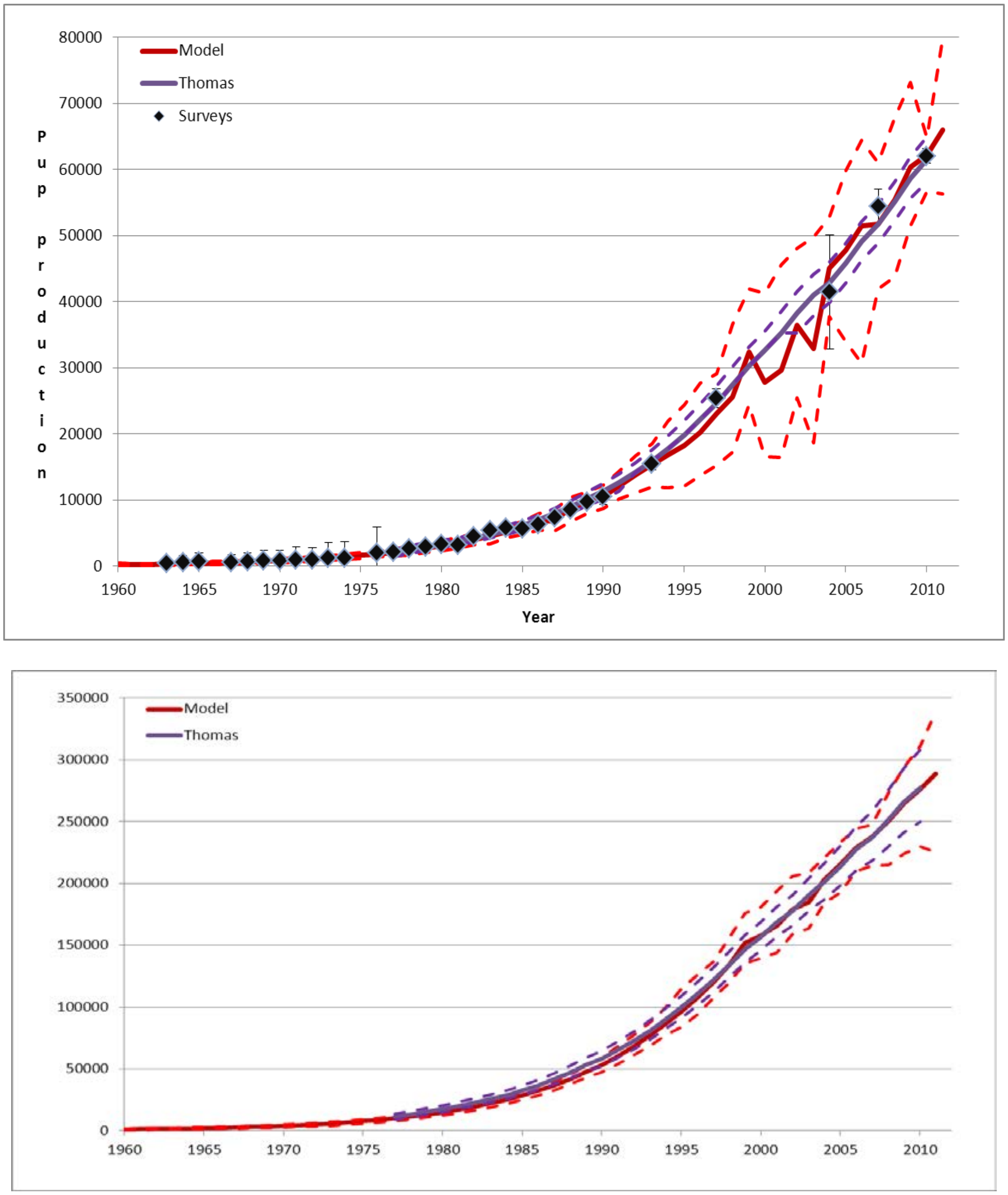


Figure 3. Plot of Sable Island pup survey estimates, model fit from the model used by Thomas et al. (2010) and using the 'harp seal model (top) and for total population size (bottom). Dotted lines represent 95% CI.

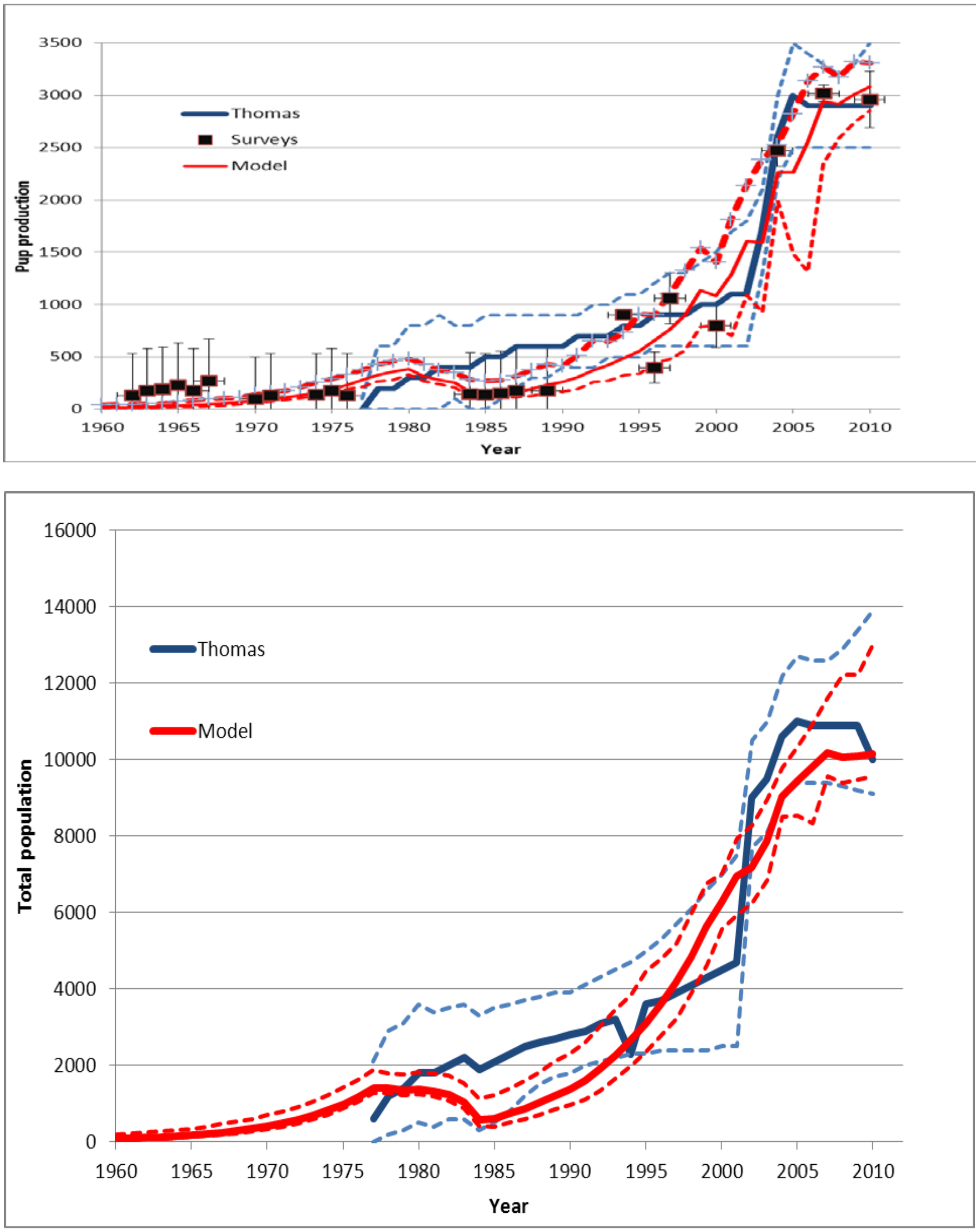
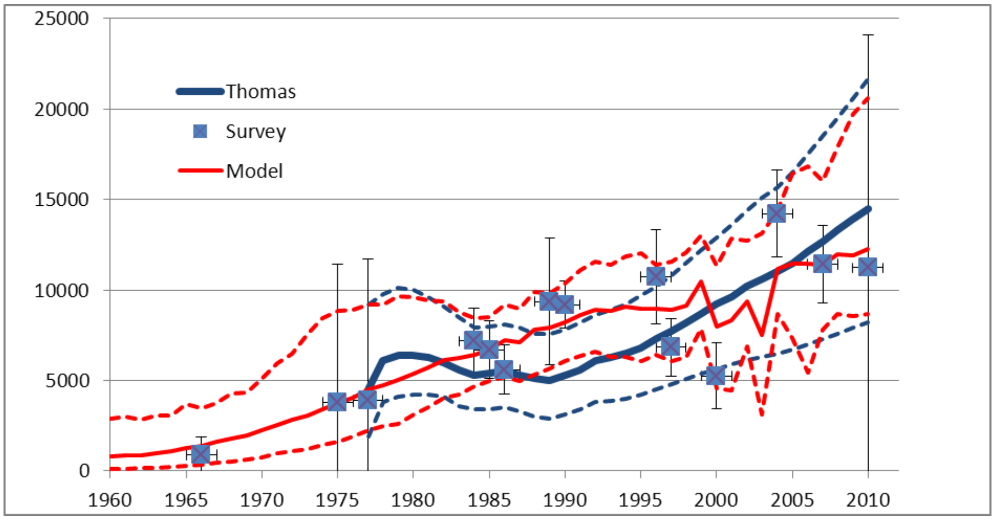


Figure 4. Plot of Coastal Nova Scotia pup survey estimates (top) and for total population size (bottom); model fits from the model used by Thomas et al. (2010) and using the new grey seal model. Dotted lines represent 95% CI.



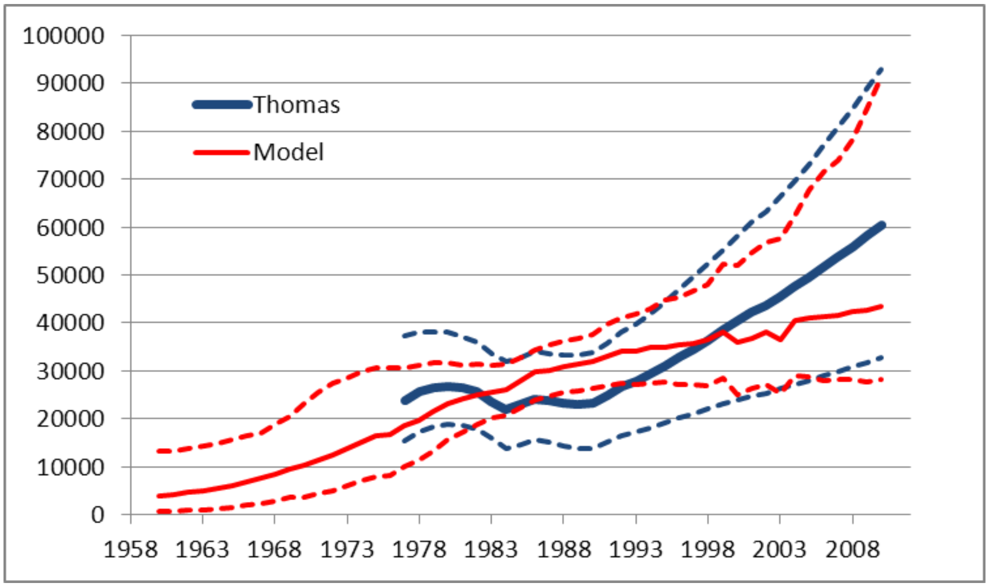


Figure 5. Plot of Gulf of St. Lawrence pup survey estimates (top) and for total population size (bottom) model fits from the model used by Thomas et al. (2010) and using the new grey seal model. Dotted lines represent 95% CI.

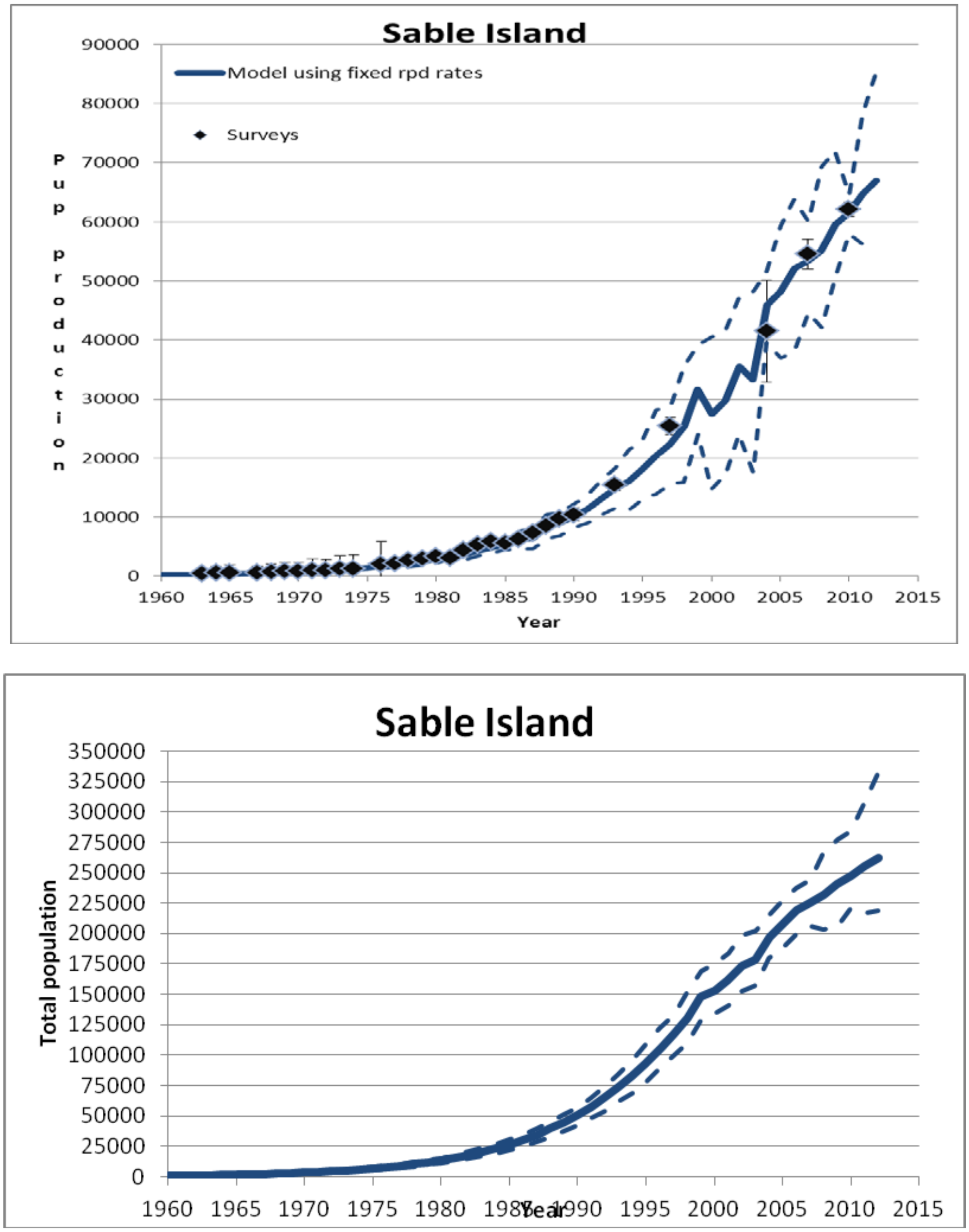


Figure 6. Sable Island pup production estimates (top) and total population size (bottom) through 2012 using reproductive data through 2011. Dotted lines represent 95% CI.

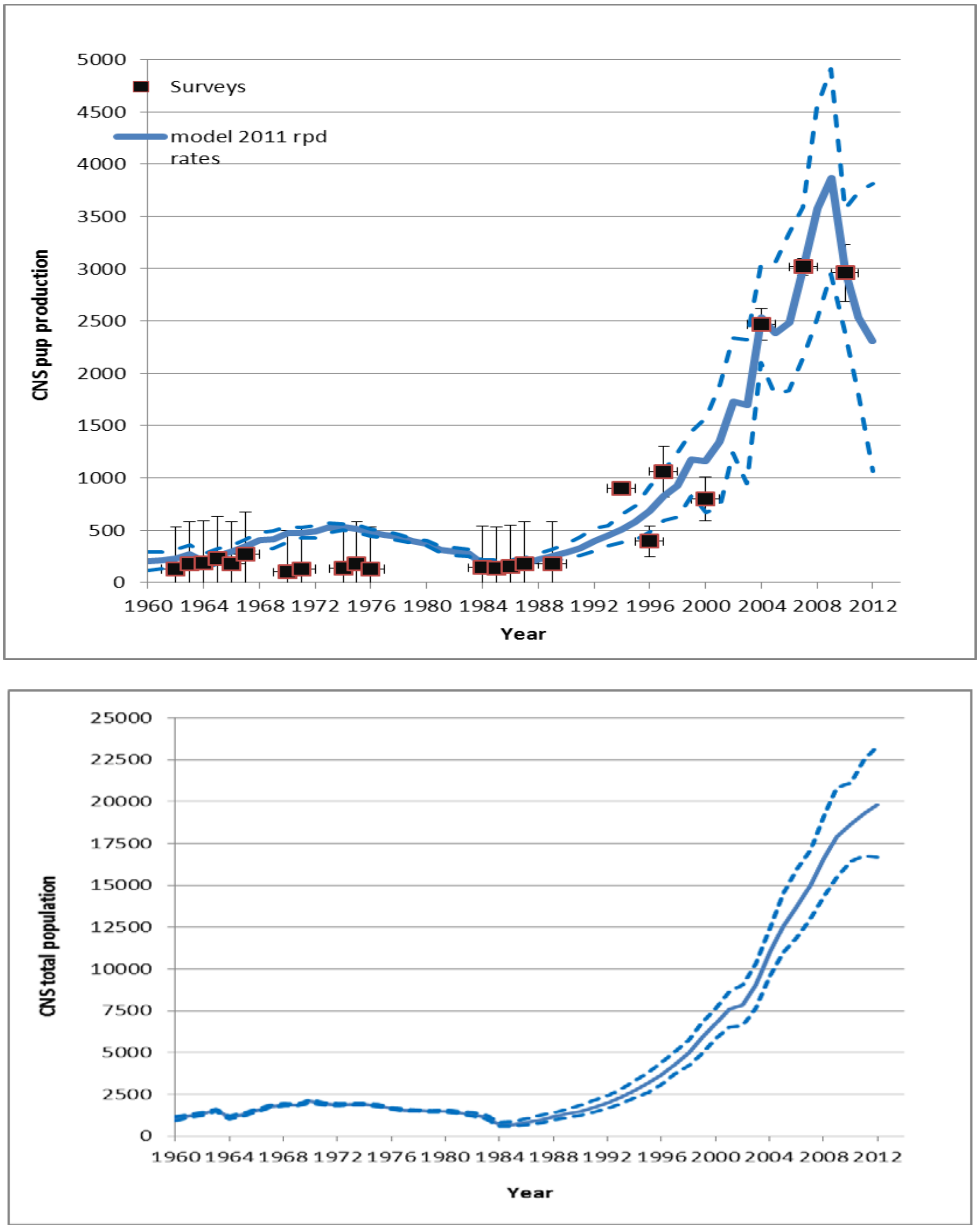


Figure 7. Coastal Nova Scotia pup production estimates (top) and total population size (bottom) through 2012 using reproductive data from 1969-2011. Dotted lines represent 95% CI.

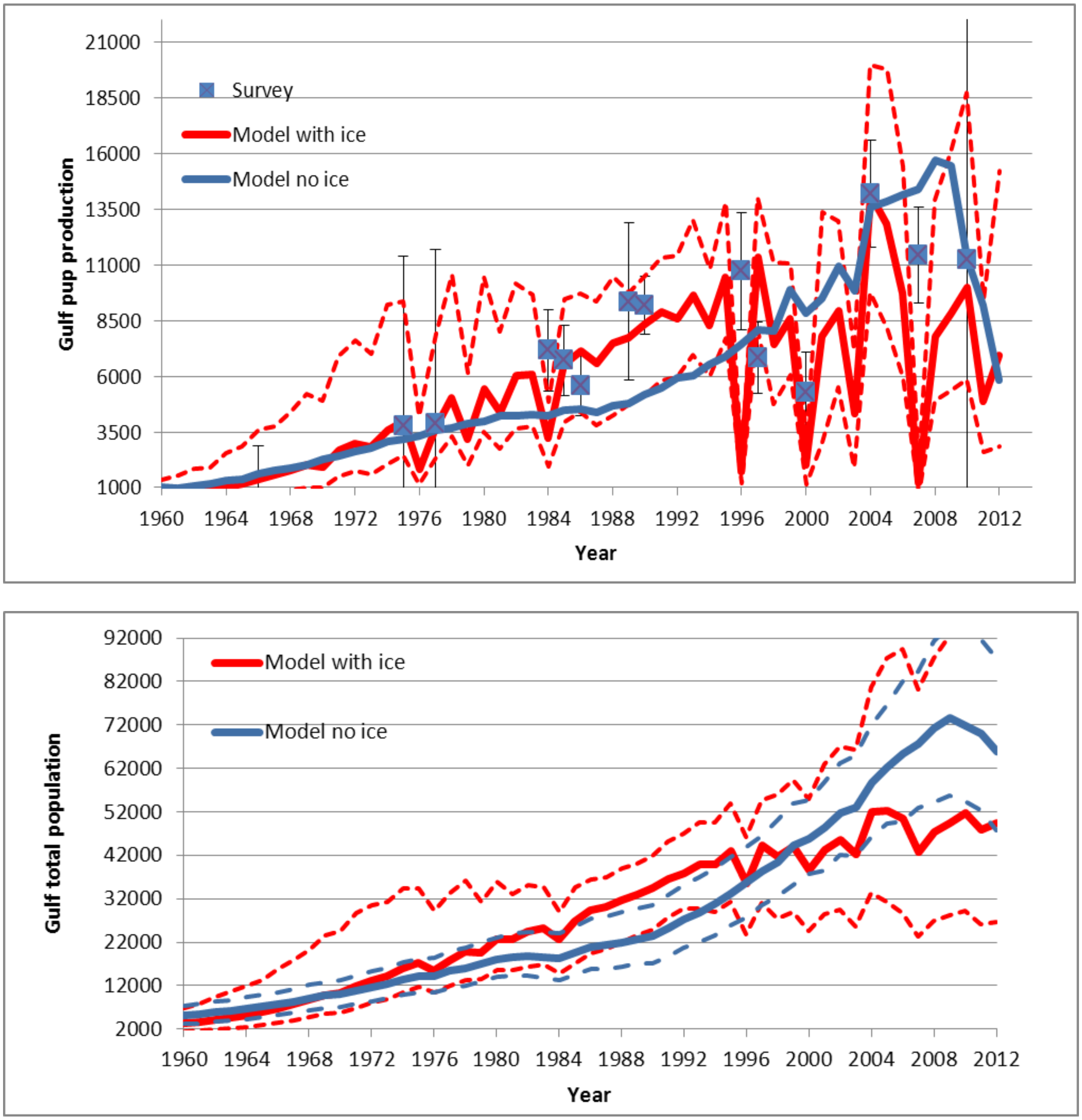
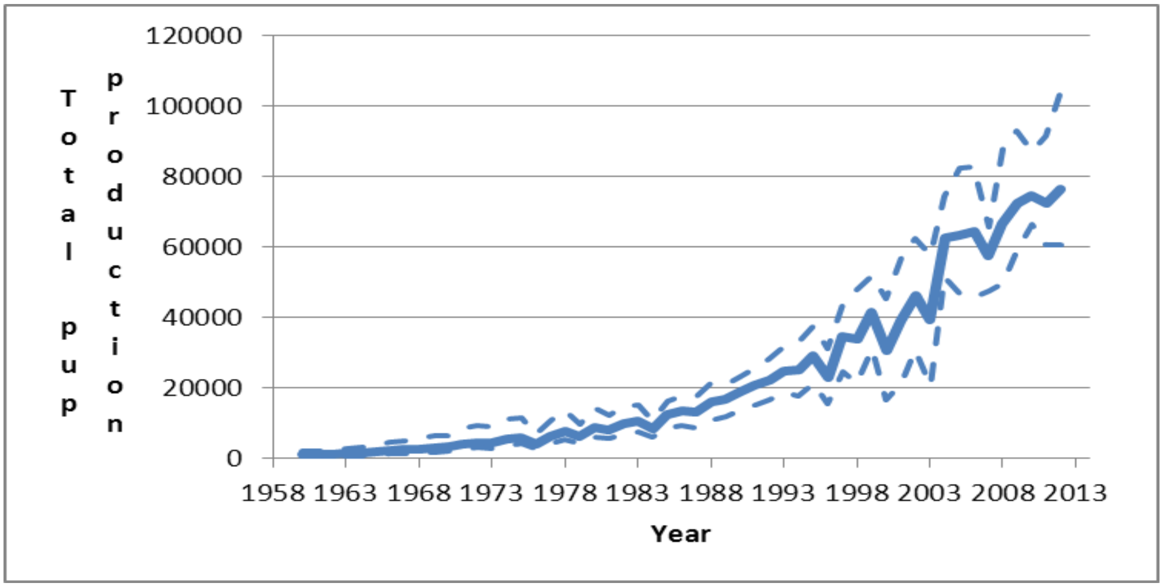


Figure 8. Gulf of St. Lawrence pup production estimates (top) and total population size (bottom) through 2012 using reproductive data from 1969-2011 and accounting for increased pup mortality due to poor ice conditions (red), or not (blue). Dotted lines represent 95% CI.



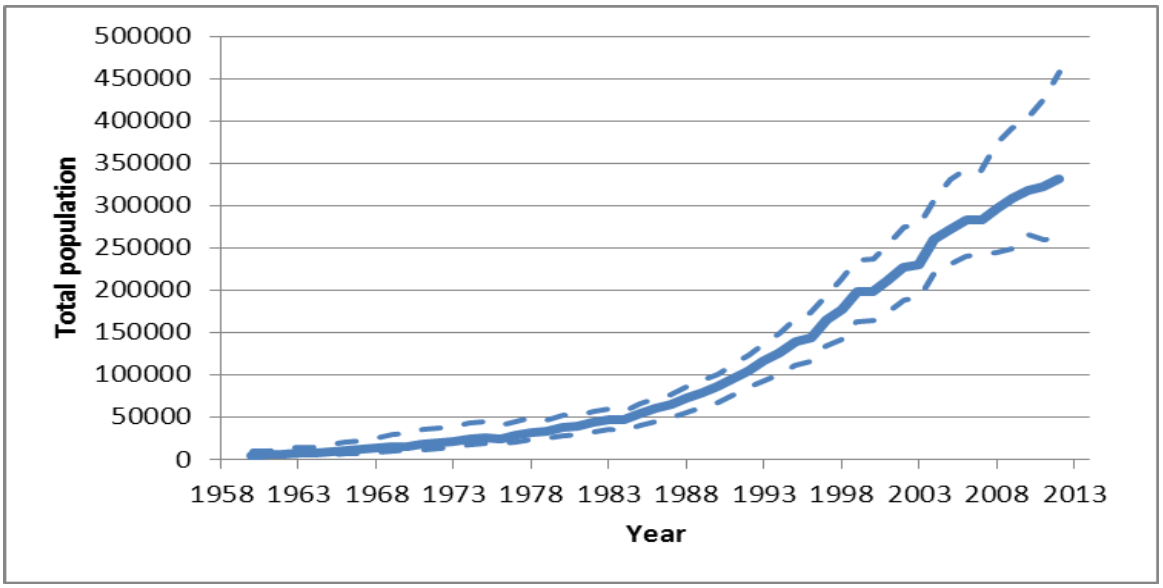


Figure 9. Total NW Atlantic grey seal pup production estimates (top) and total population size (bottom) through 2012. Dotted lines represent 95% CI.

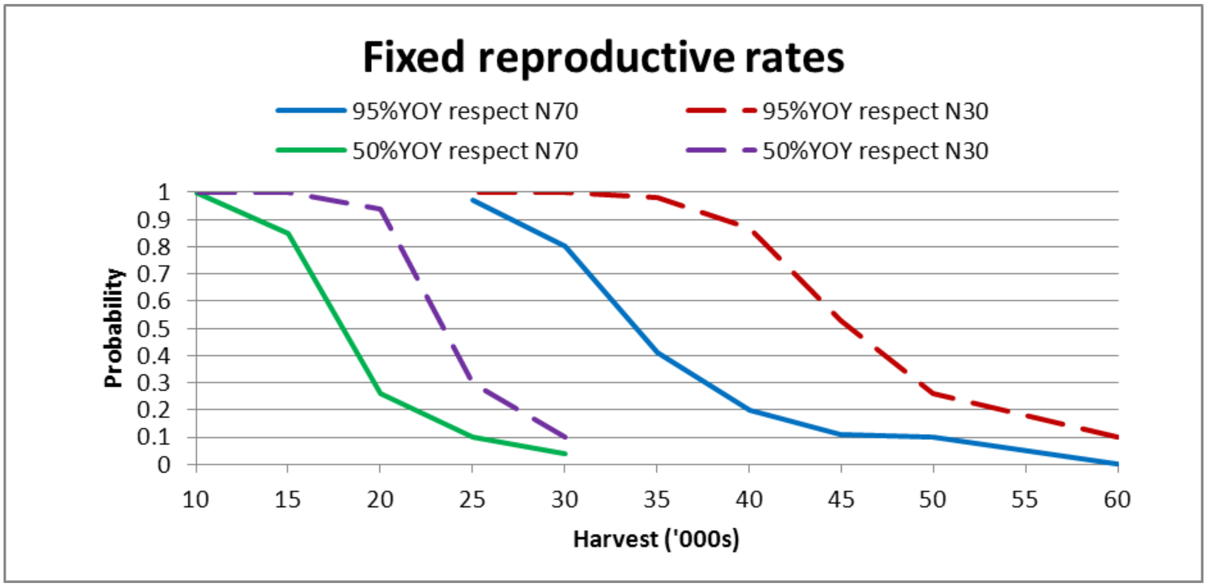
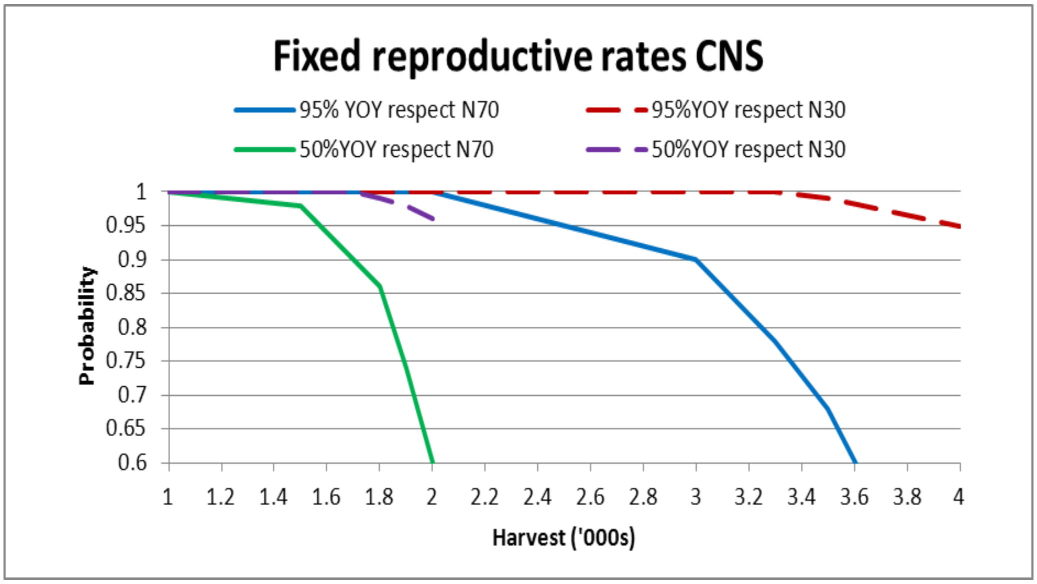


Figure 10. Probability of an annual harvest of the Sable herd with an age composition of 95% Young of the year (YOY) or 50% YOY remaining above N70 or N30. The current management plan calls for an 80% probability that the management plan will remain above N70. The expectation is that the harvest will maintain a 95% probability of remaining above N30. Reproductive rates were assumed to vary with values observed during the last 5 years.



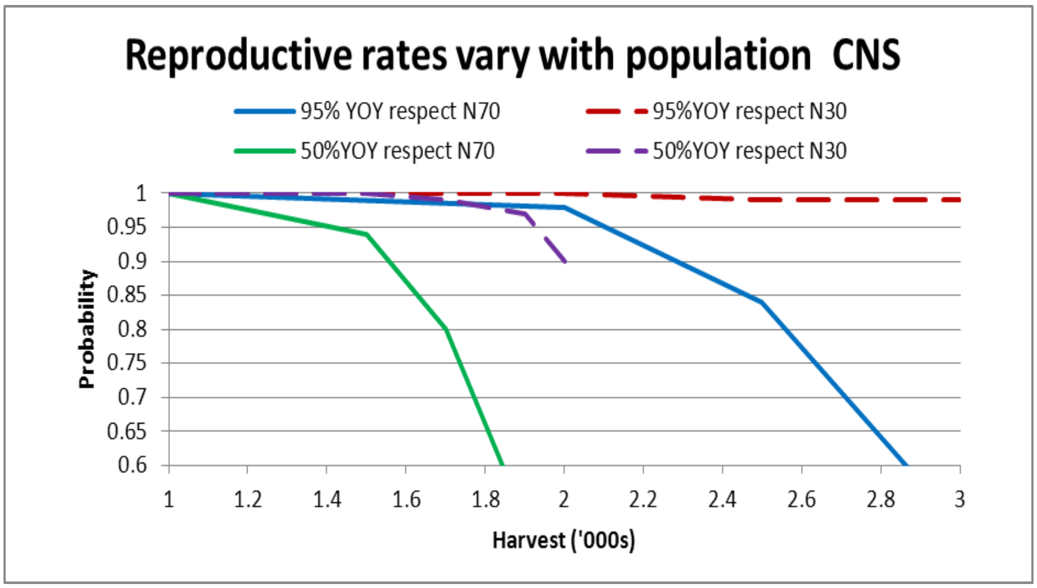


Figure 11. Probability of an annual harvest of the Coastal Nova Scotia herd with an age composition of 95% Young of the year (YOY) or 50% YOY remaining above N70 or N30. The current management plan calls for an 80% probability that the management plan will remain above N70. The expectation is that the harvest will maintain a 95% probability of remaining above N30. Reproductive rates were assumed to vary with values observed during the last 5 years (top), or in a density dependent matter with reproductive rates varying with population size (bottom).

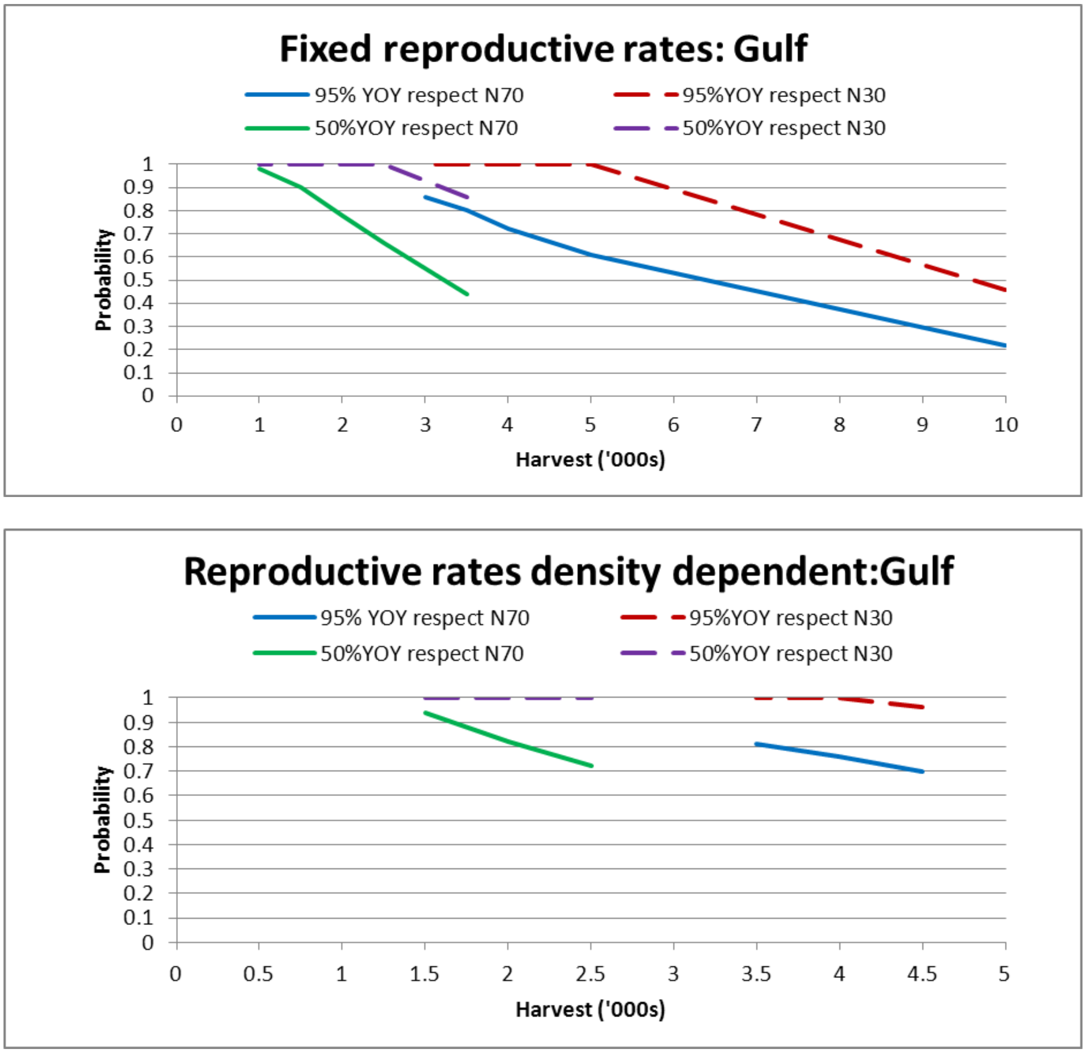


Figure 12. Probability of an annual harvest of the Coastal Nova Scotia herd with an age composition of 95% Young of the year (YOY) or 50% YOY remaining above N70 or N30. The current management plan calls for an 80% probability that the management plan will remain above N70. The expectation is that the harvest will maintain a 95% probability of remaining above N30. Reproductive rates were assumed to vary with values observed during the last 5 years (top), or in a density dependent matter with reproductive rates varying with population size (bottom).