Historical population assessment of Barents Sea harp seals (Pagophilus groenlandicus)

Hans J. Skaug, Lennart Frimannslund, and Nils I. Øien


Harp seals are an important component of the Barents Sea ecosystem. Population size is estimated to have been around 6 million seals in 1875, when large-scale exploitation by Norwegian and Russian hunters started. The estimate is obtained by fitting a population dynamics model to all available sources of data on Barents Sea harp seals, but because of a lack of information about several key parameters in the model, the uncertainty associated with the estimate is large. A sensitivity study involving three different mechanisms for density-dependence results in a range estimate of 3–7 million seals in 1875.

Keywords: catch history, density-dependence, population estimation.

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Introduction

Barents Sea harp seals (Pagophilus groenlandicus) winter in the White Sea, then migrate into the Barents Sea to feed. They whelp in February/March, and moult about 1 month later (King, 1983). Harp seal whelping grounds are also found in the pack ice in the Greenland Sea and in the western North Atlantic. The size of the Barents Sea stock has been assessed to be around 2 million seals (ICES, 2006), but there is a lack of knowledge of several key biological parameters. With such a large population, harp seals are an important component of the Barents Sea ecosystem (Bogstad et al., 2000; Nilsen et al., 2000).

Organized human exploitation of Barents Sea harp seals started in about 1875, peaked around 1925, and has since decreased (Figure 1). Assessment of the post-World War II population trend has shown it to have increased (Ulltang and Øien, 1988; Øien and Øritsland, 1995). No estimates of the size of the population before 1945 have been published previously, but it is a generally held belief that the high catch levels in the 1920 severely depleted the population. The main goal of this analysis is to estimate the pre-exploitation population size, i.e. in 1875. If it can be assumed that the population was at equilibrium in 1875, with a constant population size $K$, then $K$ may be interpreted as a historical carrying capacity level for these seals. However, because of increased fishing activity in the Barents Sea during the 20th century, it is likely that the carrying capacity today is lower than historically, and indeed there are indications that the population growth rate has dropped (ICES, 2006).

A problem commonly faced when trying to estimate historical trends in populations of marine mammals is the lack of data. Although relatively accurate catch records may be available from several centuries back, abundance estimates are typically available only for short recent periods. An additional problem arises with harp seals, because the present census techniques only provide estimates of pup production, and knowledge of female reproductive rates is required to obtain estimates of total population size. The lack of reliable information on historical catching efforts prevents the use of catch data in a catch per unit effort (cpue) analysis for Barents Sea harp seals. However, annual catches can still be used as an exogenous variable in population dynamics equations. The unknown parameters in the population dynamics model can be fitted to all other data sources using statistical techniques.

For Barents Sea harp seals, available data sources besides information on catches include estimates of pup production, age samples taken on whelping grounds, and estimates of mean age-at-maturity for females (Frie et al., 2003). From a historical perspective, all these data sources are available only from a relatively recent period. When data are scarce, stronger assumptions about the nature of the population dynamics must necessarily be made. In such situations, it becomes particularly important to highlight the uncertainty related to model choice, as well as the statistical uncertainty arising from sampling variability in the data.

Density-dependence is required to impose an assumed equilibrium at $K$ for the population in 1875. Density-dependent changes in female reproductive parameters and other life history characteristics have been studied in detail for exploited populations of marine mammals (e.g. Fowler, 1984). Within the International Whaling Commission (IWC), the historical trends in many baleen whales stocks has been assessed under the assumption that the population was in equilibrium at $K$ before human exploitation (Butterworth et al., 2002). The assumption that the carrying capacity level $K$ has been constant over centuries is clearly unrealistic, but it provides nevertheless a first order approximation of reality, and is a stepping-stone to fitting these types of models to sparse sources of data.

For Barents Sea harp seals, the mean age-at-maturity has risen (Frie et al., 2003) over a period in which the population is believed also to have been increasing (Ulltang and Øien, 1988). A similar
pattern has been observed for Northwest Atlantic harp seal (Bowen et al., 1981). This makes mean age-at-maturity a natural candidate for being a density-dependent parameter. Age-dependent density is also likely to affect birth rate. For Northwest Atlantic harp seals, there is a negative correlation between pregnancy rate and population size (Siare et al., 2000). In addition to these two parameters, we also consider density-dependence through the mortality rate. Studies on large mammals have shown that adult mortality rates are relatively constant (Gaillard et al., 2000), making this parameter a less likely candidate for being density-dependent. Juvenile mortality, on the other hand, is more likely to be density-dependent. Here, we use a common parameter for juvenile and adult mortality rates.

Total fishing pressure increased steadily in the Barents and Norwegian Seas during the 20th century, up to around 1980 (Sakshaug et al., 1992). The biggest increase in fishing effort was in the period 1950–1980, when the pelagic fishery for herring (Clupea harengus) and capelin (Mallotus villosus) peaked and eventually led to the near-extinction of the Atlanto-Scandinavian stock of herring (Gjøsæter, 1995). From the 1930s, trawl fisheries developed on cod (Gadus morhua), and because cod are important prey of harp seals (Nilssen et al., 2000), it is natural to consider that the carrying capacity $K$ might have decreased since 1875.

Here, we estimate the historical trend in the Barents Sea harp seal population, by fitting an age-structured population dynamics model to all available data sources. The pre-exploitation population size of harp seals provides an important indicator of the status of the Barents Sea ecosystem before 1900. The estimated population trajectory is a crucial input to ecosystem models that take predation by harp seals into account. We study the sensitivity of the results with respect to the choice of density-regulating mechanism, age-at-menopause, and the assumption of a constant carrying capacity. Such sensitivity studies are critical in this situation, because the analysis is founded on many assumptions and relatively few data.

### Material and methods

#### Data

The sources used for compiling catch records for the period 1875–2005 are documented in the Appendix. The records distinguish between the number of pups (0-group) and the number of older animals (1+) caught per year, but no additional information about the age composition of the catches has been used in the analysis. A smoothed version of the catch records is shown in Figure 1.

Estimates of pup production (the number of pups born) are available from aerial photographic surveys for some years during the period 1968–2003 (Table 1). The series of surveys conducted before 1998 cannot be treated as absolute estimates, but is assumed to provide reliable information about the trend in pup production. The series of estimates starting from 1998, on the other hand, are treated as absolute estimates of pup production, and the estimates also have associated estimates of uncertainty.

Age readings from females sampled on whelping grounds are available for the years 1980 and 1988 (Table 2). Such data provide valuable information about several parameters in the model (mortality and age-at-maturity), provided they represent a random sample from the reproductively active part of the female population. As sampling most likely was confined to certain geographical locations, and because it is likely that different age groups are spatially segregated on whelping grounds, an assumption about random sampling is unrealistic. Although the sample may still give unbiased estimates of the age composition on average, the precision of the estimates is reduced as a consequence of the tendency to sample individuals that are similar in age. To account for this, we employ an “effective sample size” that is only 1% of the actual sampling size. The choice of the fraction 1%, which may well be too low, was made to reduce the impact of the age data in parts of the parameter space where the data contradict the rest of the model. Ages were determined from cross-sections of canine teeth by trained readers who regularly checked their abilities by looking at reference material prepared from seals of known age obtained through mark-recapture.

### Table 1. Census estimates of pup production.

<table>
<thead>
<tr>
<th>Type</th>
<th>Year</th>
<th>Estimate</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative index</td>
<td>1968</td>
<td>70 500</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>82 100</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1973</td>
<td>92 200</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>107 700</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1980</td>
<td>138 551</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>139 387</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1988</td>
<td>138 500</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>141 667</td>
<td>–</td>
</tr>
<tr>
<td>Absolute estimate</td>
<td>1998</td>
<td>286 260</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>325 643</td>
<td>0.111</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>339 710</td>
<td>0.095</td>
</tr>
<tr>
<td></td>
<td>2002</td>
<td>330 000</td>
<td>0.103</td>
</tr>
<tr>
<td></td>
<td>2003</td>
<td>327 000</td>
<td>0.125</td>
</tr>
</tbody>
</table>

The estimates for the period 1968–1976, taken from Nazarenko (1984), and estimates for 1980–1991, taken from Timoshenko (1992), are treated as relative estimates of abundance. The precision of these estimates is unknown. The point estimates and the associated CVs (coefficient of variation) for the period 1998–2003 are taken from ICES (2006).
Population dynamics model

We use an age-structured population dynamics model, where the key parameters of the model are:

- \( N_{0,t} \) number of pups born in year \( t \);
- \( N_{i,t} \) number of seals of age \( i \) in year \( t \);
- \( K \), carrying capacity;
- \( M_0 \), pup mortality rate;
- \( M_{1,t} \), mortality rate for age 1+ animals;
- \( F \), birth rate among reproductively active females;
- \( a \), mean age-at-maturity;
- \( b \), mean age at the onset of menopause.

Here, “1+” denotes all ages larger than or equal to 1 year. The assumption that the mortality rate is age-independent within the 1+ group is obviously unrealistic, but the available data do not allow a more detailed age-dependence to be estimated. We have chosen to parameterize the model in terms of the continuous time mortality rates \( M_0 \) and \( M_{1,t} \). These determine the 1-year survival probabilities \( s_0 = \exp(-M_0) \) and \( s_{1,t} = \exp(-M_{1,t}) \), which are the quantities appearing in the population dynamics equations that follow. Time-varying versions of the parameters \( M_{1,t} \), \( F \), and \( a \) are considered in connection with the modelling of density-dependence. The parameter \( K \) is also treated as a dynamic quantity, to investigate the hypothesis of changes in carrying capacity.

It is assumed that before exploitation (\( t < t_0 = 1875 \)), the population was in equilibrium at its carrying capacity (i.e. \( N_{1+t_0} = K \)) and had a stable age structure, i.e.

\[
N_{i,0} = K \left( \frac{s_{1,t}}{1 - s_{1,t}} \right)^{i-1}, \quad i = 1, \ldots, A - 1,
\]

\[
N_{A,0} = K \cdot (s_{1,t})^{A-1}.
\]

Here, the maximum age group \( A \) contains all seals aged \( A \) or more. We use \( A = 50 \), which is assumed to be above the maximum age of harp seals. The catch records give information about catch in numbers of pups in year \( t \), \( C_{0,t} \), and catch in numbers of 1+ animals, \( C_{1+} \). In the absence of information about age-specific catch numbers for the 1+ group, we employ pro rata rules in the model:

\[
C_{i,t} = \frac{N_{i,t}}{N_{1+t,t}}, \quad i = 1, \ldots, A,
\]

where \( N_{1+t,t} = \sum_{i=1}^{A} N_{i,t} \). Catches are assumed to be taken before the occurrence of natural mortality, leading to the set of recursion equations:

\[
N_{1,t} = (N_{0,t-1} - C_{0,t-1}) s_0
\]

\[
N_{i,t} = (N_{i-1,t-1} - C_{1+t,t-1}) s_{1,t}, \quad i = 2, \ldots, A - 1,
\]

\[
N_{A,t} = ((N_{A-1,t-1} - C_{A-1,t-1}) + (N_{A,t-1} - C_{A,t-1})) s_{1,t}.
\]

Pup production is governed by

\[
N_{0,t} = \frac{F}{2} \sum_{i=0}^{A} p_{i,t} N_{i,t},
\]

where \( N_{i,t}/2 \) is the number of females at age \( t \), and \( p_{i,t} \) is the proportion of sexually mature females at age \( i \) (at time \( t \)). For young ages, \( p_{i,t} \) is an increasing function of \( i \) that levels off when all females have become mature, then declines to zero for greater ages (menopause). As a parametric model we assume

\[
p_{i,t} = L(i - (a_t + 1)) \cdot L(-0.5(i - b_t)),
\]

where \( L(x) = \exp(x)/[\exp(x) + 1] \) is the logistic function. Note also that, although \( a_t \) refers to the age-at-maturation, \( a_t + 1 \) is the age-at-first-giving-birth, and \( L(i - (a_t + 1)) \) is an increasing function of \( i \), whereas \( L(-0.5(i - b_t)) \) is decreasing. The maximum of \( p_{i,t} \) is approximately at \( i' = (2a_t + b_t)/3 \). When \( a_t \) and \( b_t \) are sufficiently separated (by more than 10 years), then \( p_{i,t} \approx 1 \), otherwise \( p_{i,t} < 1 \). The choice of the particular functional form \( L(i - (a_t + 1)) \) is based on Figure 4 of Frie et al. (2003). Little is known about the (negative) slope of the \( p \)-curve for advanced ages. Implicit in our assumption (3) is that the curve drops by 90% during a period of \( \sim 12 \) years, centred on age \( b_t \).

Density-dependence

We consider three mechanisms for density-dependence:

- age-at-maturation: \( a_t = a \cdot \left( \frac{N_{1+t-1}}{K} \right)^{y_a} \),

- birth rate: \( F_t = 1 - (1 - F) \left( \frac{N_{1+t-1}}{K} \right)^{y_b} \),
natural mortality age 1 +

\[ M_{1+,t} = M_{1+,} \left( \frac{N_{1+,t-1}}{K} \right)^{\gamma_0} \]. \quad (6)

The parameters \( a, M_{1+,} \), and \( F \) now have the interpretation of being parameter values at the level of carrying capacity, i.e. when \( N_{1+,}/K = 1 \). Only one of the three mechanisms is implemented at a time in a given model. For instance, for density-dependent age-at-maturation, \( \gamma_0 = \gamma_{20} = 0 \), and \( \gamma_0 \) is a parameter that is estimated along with the other parameters of the model. Option (4) differs from (5) and (6) in that estimates of \( a_t \) are available for the period 1962–1993, whereas no direct data on \( F_t \) and \( M_{1+,t} \) are available.

The assumption that the population was at equilibrium in year \( t_0 = 1875 \), i.e. that the number of seals recruited to the population matched the number of seals dying each year, is expressed relative to \( K \) as

\[ \frac{1}{2} F \cdot s_0 \sum_{i=1}^{A} \frac{p_{i,t}N_{i,t}}{K} = 1 - s_{1+,}. \quad (7) \]

This constraint is not enforced strictly in the model, but instead the deviation from equality in Equation (7) is penalized in the log-likelihood function. The penalty may be given the following interpretation. Denote the difference between the left and right side of Equation (7) as \( \delta \), so that \( \delta \) is the proportion by which the population increases per year. The actual penalty employed corresponds to placing a Bayesian normal prior with expectation 0 and variance \( 1/100 \) 000 on \( \delta \). Hence, a 5% total change over a 10-year period is relatively unlikely under this prior, but a 2% change over 10 years is compatible with the prior.

To account for a possible reduction in the carrying capacity, it is assumed that \( K_t \) is a linear function of \( t \), with \( K_{1875} = K \) and \( K_{2005} = cK \), where \( 0 < c < 1 \). In this scenario, both \( K \) and \( c \) are parameters to be estimated.

**Parameter estimation**

Parameter estimates are obtained by maximum likelihood. The catch data enter the model through Equation (2), but do not otherwise contribute to the likelihood function. As the model involves prior distributions on some parameters, the analysis has a Bayesian flavour. The software package AD Model Builder (Fournier, 2001) is used to maximize the likelihood function. AD Model Builder uses a quasi-Newton optimization algorithm with bounds on the parameters, and calculates estimates of standard deviations of model parameters using the “delta method”. AD Model Builder also allows full Bayesian analysis via Markov chain Monte Carlo (MCMC) sampling (Gelman et al., 1995), which is used here to explore the appropriateness of the measures of uncertainty produced by the delta method.

Assuming normality for pup production estimates, their contribution to the log-likelihood function is

\[ \sum_t - \log(\tau_t n_{0,t}) - \frac{(\hat{q} \cdot n_{0,t} - \nu_t)^2}{2(\tau_t n_{0,t})^2}, \quad (8) \]

where \( n_{0,t} \) denotes the pup production estimate for year \( t \) (Table 1) and the sum extends over all years \( t \) for which there is an estimate. This summation convention is used also in what follows. For the years 1998–2003, estimates of pup production are assumed to be absolute, i.e. \( q = 1 \). For the period 1969–1991, a common coefficient of variation (CV) is estimated, \( \tau_t = \tau \), but for later years the values given in Table 1 are used.

Assuming normality, the log-likelihood contribution from the series of mean age-at-maturity estimates \( \hat{a}_t \) from Frie et al. (2003) is

\[ -\frac{1}{2} \sum_t (\hat{a}_t - a_t)^2 / \text{SD}(\hat{a})^2. \quad (9) \]

where the standard deviations \( \text{SD}(\hat{a}) \) are obtained from the confidence intervals in Table 2 of Frie et al. (2003).

The log-likelihood contribution for the number \( m_{1,t} \) of females at age \( i \) sampled on the whelping grounds in year \( t \) (Table 2), assuming a multinomial distribution, is

\[ \frac{1}{100} \sum_t \sum_{i=1}^{10} m_{1,t} \log \left( \frac{p_{i,t}N_{i,t}}{\sum_{i=1}^{10} p_{i,t}N_{i,t}} \right)^{-1}. \quad (10) \]

To account for non-random sampling, an effective sample size of 1% is used.

**Results**

In all, 12 models defined by combinations of the following three factors were fitted to data: density-dependence mechanism [options given by Equations (4), (5) or (6)], mean age-at-menopause \( (b = 30 \text{ or } b = 50) \), and time-varying carrying capacity \( K_t \) (Yes or No). Figure 2 shows the estimated population trajectories for 11 of the models. The model omitted has density-dependent birth rate [Equation (5)] in combination with late

![Figure 2. Estimated population trajectories under different model assumptions [Equations (4)–(6)]. Different density-dependence mechanisms are shown in different colours. Dashed lines indicate fits in which a reduction in carrying capacity \( K \) has been allowed. There are two versions of each curve (except the one case mentioned in the main text) corresponding to \( b = 30 \) and \( b = 50 \), but the labelling does not distinguish between the two. The two dots represent the estimates of \( N_{1+,} \), population size from Yakovenko (1961) used for model validation.](https://academic.oup.com/icesjms/article-lookup/doi/10.1093/icesjms/fst049)
mean age-at-menopause ($b = 50$) and a time constant $K_a$, which did not fit the estimates of pup production satisfactorily. It is clear from Figure 2 that density-dependent maturation age [models based on option (4)] yielded the largest estimate of population size in year 1875, regardless of other assumptions.

Table 3 lists likelihood values for all 12 models, and Table 4 gives the parameter estimates for a subset of the models, and for some additional model fits. Table 4 also introduces a nomenclature [the “variants” (4)i, (4)ii, etc.] that is used for easy reference to models.

In terms of the log-likelihood value, option (4) in combination with $b = 30$ and constant $K_0$ [variant (4)ii in Table 4] had the best fit of all models tested (Table 3). This conclusion also holds if the Akaike Information Criterion (AIC) is used, taking into account the fact that the number of active parameters differs across models. Confidence intervals for parameters under the best-fitting model are given in Table 5. The estimated pre-exploitation population size ($N_{1+, 1875}$) under the best-fitting model was 6.3 million of 1+ seals, with a 95% confidence interval ranging from 5.7 to 6.9 million, not taking model uncertainty into account.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$b = 30$</th>
<th>$b = 50$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_{1875}$</td>
<td>$-161.4$</td>
<td>$-160.9$</td>
</tr>
<tr>
<td>Density-dependent birth rate (Equation 5)</td>
<td>$-273.1$</td>
<td>$-273.0$</td>
</tr>
<tr>
<td>Density-dependent 1+ natural mortality (Equation 6)</td>
<td>$-270.2$</td>
<td>$-283.1$</td>
</tr>
</tbody>
</table>

$^a$Did not fit pup production data well.

Models with density-dependent mechanisms (4) or (5) and early mean age-at-menopause ($b = 30$) had better fits than those with $b = 50$. Hence, goodness-of-fit was assessed in detail only for models with $b = 30$. Figures 3–5 show the population trajectories for the period 1875–2005. The best fitting model [variant (4)ii in Table 4] fitted both the estimates of pup production and the age distribution data well (Figure 4). Values of mean age-at-maturity ranged from $a = 19$ (which is an upper bound in the optimization routine) in 1875 to $a = 5$ around 1960. The model also fitted the data from Frie et al. (2003) well.

The models with $b = 30$ yield unrealistically low estimates of $M_{1+.}$ To investigate the sensitivity of the fit with respect to $M_{1+.}$ model variant (4)iii in Table 4 was re-fitted with $M_{1+.} = 0.06$ fixed [Table 4, model (4)iv]. The parameter of main interest here, $K_{1875+}$, only changes by 8%, whereas, for instance, $M_0$ decreases by 50%.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Point estimate</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_{1875}^a$</td>
<td>6.270</td>
<td>5.650</td>
</tr>
<tr>
<td>$M_{1+.}$</td>
<td>0.011</td>
<td>0.000</td>
</tr>
<tr>
<td>$M_0$</td>
<td>0.940</td>
<td>0.807</td>
</tr>
<tr>
<td>$F$</td>
<td>0.821</td>
<td>0.678</td>
</tr>
<tr>
<td>$q$</td>
<td>0.581</td>
<td>0.472</td>
</tr>
<tr>
<td>$\tau$</td>
<td>0.078</td>
<td>0.039</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>0.612</td>
<td>0.542</td>
</tr>
<tr>
<td>$N_{1+, 2005}^a$</td>
<td>2.638</td>
<td>1.972</td>
</tr>
</tbody>
</table>

Confidence intervals are based on standard deviations calculated by AD Model Builder. The mean age-at-maturity $a$ is omitted because it was hitting the upper bound $a = 19$ for parameter space.

$^a$In millions.

Table 4. Estimated parameters for a selected set of models fits.

<table>
<thead>
<tr>
<th>Density-dependence mechanism</th>
<th>Maturation age</th>
<th>Birth rate</th>
<th>Natural mortality age 1+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variant</td>
<td>(4)i</td>
<td>(4)ii</td>
<td>(4)iii</td>
</tr>
<tr>
<td>Time-varying carrying capacity</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>$K_{1875}$</td>
<td>6.270</td>
<td>5.777</td>
<td>6.335</td>
</tr>
<tr>
<td>$M_{1+.}$</td>
<td>0.0111</td>
<td>0.0879</td>
<td>0.0236</td>
</tr>
<tr>
<td>$M_0$</td>
<td>0.9396</td>
<td>0.2$^d$</td>
<td>0.8626</td>
</tr>
<tr>
<td>$F$</td>
<td>0.8207</td>
<td>0.9009</td>
<td>0.8511</td>
</tr>
<tr>
<td>$a$</td>
<td>19.00$^a$</td>
<td>16.03</td>
<td>19.00$^a$</td>
</tr>
<tr>
<td>$q$</td>
<td>0.5808</td>
<td>0.5$^d$</td>
<td>0.538</td>
</tr>
<tr>
<td>$\tau$</td>
<td>0.07816</td>
<td>0.1176</td>
<td>0.0853</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>0.6116</td>
<td>0.5484</td>
<td>0.5797</td>
</tr>
<tr>
<td>$c$</td>
<td>1.000$^d$</td>
<td>1.000$^d$</td>
<td>1.000$^d$</td>
</tr>
<tr>
<td>$N_{1+, 2005}$</td>
<td>2.638</td>
<td>2.284</td>
<td>2.349</td>
</tr>
<tr>
<td>Loglik</td>
<td>$-160.9$</td>
<td>$-165.4$</td>
<td>$-161.4$</td>
</tr>
</tbody>
</table>

$^a$The row “Variant” is included for ease of reference within the options (4), (5) and (6).

$^a$M = 0.06 fixed.

$^d$Parameter held fixed during estimation.

$^c$Parameter hitting lower (l) or upper (u) bound in estimation procedure.
Panel c in Figures 3–5 contains a plot of the trajectory of

\[ P_t = \frac{F_t \cdot \sum_{i=1}^{A} p_{it} \cdot n_{it}}{\sum_{i=1}^{A} n_{it}}, \quad (11) \]

which is the proportion of females giving birth in year \( t \). As expected, the greatest temporal variation in \( P_t \) is for models based on Equations (4) and (5), because these density-dependence mechanisms act directly on the female reproduction rate.

Confidence bounds for the 1+ trajectory were calculated using AD Model Builder (Figures 3–5: panel a). The uncertainty in the estimated 1875 population size is lowest for the model based on Equation (4) and highest for that based on Equation (5).
Corresponding measures of uncertainty obtained with the MCMC facilities of AD Model Builder were very close to those shown in Figures 3–5.

**Figure 4.** Estimated population trajectories under the assumption of density-dependence of mean age-at-maturity, based on Equation (4). Corresponding parameter estimates are given in Table 4 variant (4). Comments to panels: (a) scaled catches are shown on the bottom of the figure (see Figure 1 for the absolute scale); (b) 95% confidence intervals are shown as vertical dashed lines for absolute estimates, and pup production indices (crosses) are scaled by $q$; (c) proportion $P_i$ of females giving birth each year as given by Equation (11); (d) time-varying mean age-at-maturity (solid lines) with 95% confidence intervals taken from Frie et al. (2003) represented by vertical dashed lines; (e) and (f) observed proportion of females in different age classes among seals sampled on whelping grounds in the years 1980 and 1988 (solid lines), together with the corresponding modelled proportions of mature females.

**Discussion**

All models considered in this study yielded a similar shape of the 1+ temporal trajectory. Heavy hunting pressure depleted the
population severely in the first half of the 20th century. The increase in population size during the period 1940–1945 results from the temporary halt in hunting during World War II, and the increasing trend since 1960 is consistent with the results from Ulltang and Øien (1988).

Models assuming density-dependent age-at-maturation [equation (4)] gave the highest estimates of population size in year 1875 (Figure 2). Estimates of current population size $N_{2005}$ ranged from 1.4 to 2.6 million. The lowest estimates of $N_{2005}$ were obtained under Equation (6), where density-dependence acted through mortality alone. Recall in this connection that $M_{1+}$ encompasses both juvenile (excluding 0-group) and adult mortality.

The assumption of a decreasing carrying capacity tended to yield a lower estimate of current population size. This assumption goes together with the assumption that the carrying capacity

Figure 5. Estimated population trajectories under the assumption of density-dependence of mortality rate $M_{1+}$, based on Equation (6). Corresponding parameter estimates are given in Table 4, variant (6). Notes on panels are similar to those of Figure 4, except for panel (d), which here shows the trajectory for mortality rate $M_{1+}$. 

(a) Population size (1+)
(b) Number of pups
(c) Proportion of females giving birth
(d) $M_{1+}$ evolving in time
(e) Age distribution in 1980
(f) Age distribution in 1988
actually was reached in 2005. For variants (4)\(\text{iii}\) and (5)\(\text{ii}\) in Table 4, the population was still increasing in 2005. The reason is that the penalty used to enforce the 2005 equilibrium in these two cases was not strong enough, and a better objective function value could be obtained by violating the equilibrium assumption.

From 1928 to 1959, three aerial photographic surveys were carried out in moulting patches to determine population sizes (Yakovenko, 1961). These data have not been used to fit the model, because it was not \textit{a priori} clear whether the resulting estimates should be treated as absolute or relative indices of abundance. In 1928, the 1+ population was estimated to be 3–3.5 million harp seals. This estimate was reduced to 1.2–1.5 million animals in the period 1953–1959 (Yakovenko, 1961). The estimate for 1928 is higher than those obtained in the present study, whereas the estimate for the period 1953–1959 lies in the band of fitted curves (Figure 2).

Density-dependence mechanism (4) yielded generally higher likelihood values than the two other options, reflecting the fact that this model has the flexibility to adjust to the trend in the age-at-maturity data, whereas the other models assume a fixed value for \(a\). However, several aspects of this model fit were biologically unrealistic. For instance, the estimate of an age-at-maturity at \(a = 19\) years should not be interpreted as an estimate of age-at-maturity in 1875. Rather, it is the value of \(a\) required to bring the population into equilibrium in a situation where density-dependence is acting only through the parameter \(a\). Further, the mortality estimate \(M_{1+} = 0.011\) cannot be interpreted literally. This is true to an even larger extent for the extremely low mortalities under density-dependence model (6) for the period following 1940 (Figure 5d). By comparison with the model with mortalities under density-dependence model (6) for the period 1953–1959 lies in the band of fitted curves (Figure 2).

In reality, the three density-dependence mechanisms (4), (5), and (6) act simultaneously, not one at a time as assumed in the present analysis. A joint model would, however, require more data than available for parameters to be identifiable. Another phenomenon that has been ignored is the fact that pup mortality is much influenced by ice conditions, and hence will vary between years. Historical records on ice condition do not exist for the whole period, but a model with randomly varying annual pup mortality could have been employed. Again, we do not have the data to estimate the variance of the random component.

The estimated uncertainty in the fitted 1+ population trajectory (Figures 3–5, panel a) is unrealistically low. First, it only reflects the sampling uncertainty in the data, not the uncertainty related to the choice of model. Figure 2 shows that the latter dominates. A second reason might be that because of the strong non-linearities in the model, the delta method employed by AD Model Builder may be inaccurate. The fact that MCMC-based measures of uncertainty were similar, does not guarantee that the sampling uncertainty is properly reflected in Figures 3–5 and Table 5.

In conclusion, it seems reasonable to believe that the 1+ population size in 1875 was around 6 million harp seals, bracketed by the interval 3–7 million. This interval covers all different assumptions/scenarios considered here.

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References

Vessels participating was available. Before 1875, there are many traces of catch data, and that for many years only the number of Norwegian catches in the period 1821–1926 are listed by Iversen in 1867 (Iversen, 1927); they were joined by vessels from southern Finnmark, northern Norway, caught harp seals in the White Sea. Offshore hunting started when vessels from Troms and Finnmark, northern Norway, caught harp seals in the White Sea and around the Kanin Peninsula (Sergeant, 1991).

The White Sea and Barents Sea stock of harp seals was hunted by Norwegian and Russian sealers for a long time. Unfortunately, documentation of the catches is scarce. The hunting operations. However, the target species of such hunts were walrus, beluga, polar bears, reindeers, and birds’ eggs and down, in addition to several species of seal. Up to and including 1919, Norwegian catches were attributed to home port of the vessel rather than to sealing area, so catch numbers before 1920 may include West Ice (the Greenland Sea populations of harp and hooded seals) catches, although they were probably small. Iversen (1927) indicates that catches of hooded seals may have been 3–4% of the catches listed for 1919 and earlier. Norwegian catches for the period 1927–1939 are from Sivertsen (1941), and from 1946 to current from ICES (2006). There is no quantitative information on Russian catches before 1875, but Russian/Soviet catches 1875–1945 are from Table 2 of Nazarenko (1984), which is supported by Yakovenko (1963), although there are some minor differences between the two sources. Soviet catches for the period 1946–1989 are from ICES (2006).

No quantitative information has been found on the age structure of early (before 1926) harp seal catches, but it was apparently some proportion of the young-of-the-year, according to Iversen (1927). Sivertsen (1941) gives numbers for the proportion of pups in annual catches for 1926 and a mean number for the years 1928–1939, which has been used in the statistics compiled here for 1927 and 1937–1939, because absolute numbers for the age distributions were available in a handwritten note attributed to Wollebæk for the period 1928–1936. There were no Norwegian catches in the East Ice during World War II 1940–1945, and post-war catches have been recorded in official statistics as pups or seals 1 year of age and older, with the exception of the years 1946–1952 and 1955. For those years, all catches have been assumed as being of seals 1 year of age or older.

Although Nazarenko (1984) gives information on total Russian/Soviet catches, he gives no information on age distributions. For the years 1927–1932 and 1936, the proportion of pups in the catches has been calculated from information in handwritten notes left by Iversen. For the years 1933–1935, a mean of the proportions for 1932 and 1936 has been used in this compilation. The proportion of pups in the catches for 1937–1945 has been taken from Table 8 (Soviet catches 1937–1958) of the Russian report on sealing in the Northeast Atlantic to the “Norwegian-Soviet Sealing Commission” of 1978. Post-war distributions are from ICES (2006).

Incidental catches for the period 1979–2000 are taken from Table 6 of ICES (2006). These catches have been assumed to be of seals 1 year of age or older, based on age compositions published from samples taken during the main seal invasion years on the Norwegian coast, 1986–1988 (Haug et al., 1991; Ugland et al., 1993).