



Original Article

Fitting state – space models to seal populations with scarce data

Tor Arne Øigård^{1*} and Hans J. Skaug^{1,2}

¹*Institute of Marine Research, PO Box 6404, NO-9294 Tromsø, Norway*

²*Department of Mathematics, University of Bergen, PO Box 7800, NO-5020 Bergen, Norway*

*Corresponding author: e-mail: tor.arne.oegaard@imr.no

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We estimate temporal variation in fecundity, the reproduction rate, for Barents Sea and Greenland Sea harp seals using a state – space approach. A stochastic process model for fecundity is integrated with an age-structured population dynamics model and fit to available data for these two harp seal populations. Owing to scarceness of data, it is necessary to “borrow strength” from the Northwest Atlantic harp seal population in form of prior distributions on autocorrelation and variance in fecundity. Comparison is made to a simpler deterministic population dynamics model. The state – space model is more flexible and is able to account for the variations in the data. For Barents Sea harp seals, the state – space model gives a higher estimate of current population size but also a much higher associated uncertainty. In the Greenland Sea, the differences between the stochastic and deterministic models are much smaller.

Keywords: age-structured population model, borrowing strength, fecundity, harp seals, state-space model.

Introduction

Three different harp seal populations (*Pagophilus groenlandicus*) inhabit the Arctic part of the North Atlantic Ocean (Sergeant, 1991; Nordøy *et al.*, 2008; Kovacs *et al.*, 2009). The Northwest Atlantic population whelps (gives birth) on the pack ice off Newfoundland and in the Gulf of St Lawrence, the Greenland Sea population breeds on the drift ice off the east coast of Greenland, and the Barents Sea population congregates in the White Sea to breed (Figure 1). During spring, harp seals perform a fixed sequence of activities: they whelp in March–April and then moulting of adults and subadults takes place north of each whelping location after a lapse of ~4 weeks (Kovacs *et al.*, 2009). For the Greenland Sea populations, these events occur primarily in the fringes of winter ice that lies on the seaward side of the thicker ice off the east Greenland pack and for the Barents Sea population in the White Sea and south-eastern Barents Sea. When the moult is over, the seals disperse in small herds, feeding heavily to restore their blubber reserves. Their summer distribution is mainly dependent on the distribution of the drifting pack-ice. The Greenland Sea population spreads on the drift ice along the east coast of Greenland, from the Denmark Strait or further south, towards Spitsbergen and eastwards into the Barents Sea. The Barents Sea population follows the receding

ice edge, gradually moving north into the Barents Sea. Both in summer and autumn, the Greenland Sea and the Barents Sea populations partly overlap. The southward migration towards the breeding areas begins in November–December (Kovacs *et al.*, 2009).

All populations have been subject to commercial hunt for centuries (Sergeant, 1991). Management of Barents Sea and Greenland Sea harp seals is based on assessments performed by the Joint ICES/NAFO working group on harp and hooded seals (WGHARP) and advice is provided by ICES (ICES, 2013; Øigård *et al.*, 2014). The assessments are currently based on a deterministic population dynamics model that estimates the total population size based on historical catch data from commercial hunt, estimates of pup production, and available reproductive data such as the proportion of females that are mature at age and the proportion of mature females that are pregnant. The pup production estimates are obtained from dedicated surveys during the whelping season in March (Øigård *et al.*, 2010, 2014) and all biological parameters are sampled in commercial hunt during the moulting period in April/May.

The Barents Sea population was previously assessed to be around 2 million seals (Skaug *et al.*, 2007), and as an abundant predator, they have an important role in the Barents Sea ecosystem (Bogstad

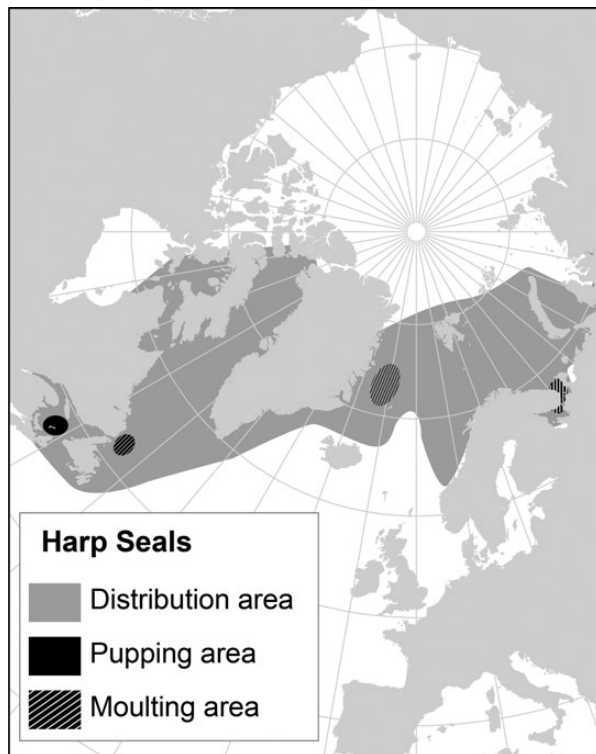


Figure 1. Distribution area, pupping area, and moulting area of harp seals in the North Atlantic Ocean.

et al., 2000; Nilssen *et al.*, 2000). For future integrated ecosystem management and, not the least, to understand the underlying process governing the dynamics of the Barents Sea ecosystem, we need multispecies or ecosystem models (e.g. Lindström *et al.*, 2009). The estimated population trajectory of harp seals is a crucial input in these models (Bogstad *et al.*, 1997). Current census techniques only provide estimates of pup production, and hence knowledge of female reproductive rates is vital for inferring total population size and predicting future changes. Population regulation through density-dependent changes in fecundity is the result of a complex interaction between intrinsic factors related to changes in population and extrinsic factors involving environmental variability (de Little *et al.*, 2007). Monitoring changes like this is difficult for most species as extensive measurements over long periods are required. Unfortunately, available data on biological parameters such as age-specific proportions of mature females and fecundity are scarce for both the Barents Sea and the Greenland Sea populations. This is a common problem when trying to estimate historical trends of marine mammal populations. In such situations, “borrowing strength” from other populations (Myers and Mertz, 1998) may provide a way forward if relevant and representative populations can be identified.

Russian aerial surveys to assess pup production of the Barents Sea stock of harp seals indicate a sudden decline in pup production after 2003 (ICES, 2013). Reduced female fertility, rather than declining population size, has been suggested as the mechanism behind the observed change in pup production. Body condition measurements of Barents Sea harp seals in 2006 and 2011 were significantly lower than similar measurements conducted before the pup production declined, and a positive correlation between pup abundance and

blubber thickness suggests that the observed decline in pup production after 2003 might be attributed to changes in the body condition of the seals (Øigård *et al.*, 2013). A plausible scenario is that insufficient availability of appropriate food for the seals led to a sequence of events such as poor condition, reduced fecundity, and in the end reduced pup production (Øigård *et al.*, 2013).

In the Northwest Atlantic, annual estimates of fecundity, defined as the proportion of mature females that were pregnant, are available for the harp seal population over a period spanning from 1950s to date (Stenson and Wells, 2011; Stenson *et al.*, 2014). The annual fecundity rates were found to be highly variable, and the proportion of pregnant females was observed to vary from 0.29 to 0.85 between years (Stenson *et al.*, 2014). Changes of this magnitude may account for the rapid decrease in pup production seen in the Barents Sea, and hence constitute an alternative explanation to a drop in total population size.

The ICES management model of the Barents Sea and Greenland Sea populations of harp seals is a deterministic age-structured population dynamics model with three unknown parameters (pup mortality, mortality of 1 year and older seals, initial population size). As opposed to being part of the data to which the model is fit by maximum likelihood, available fecundity data are treated as known quantities for the model and no uncertainty around the measurements has been accounted for (ICES, 2013; Øigård *et al.*, 2014). The low dimensional parameter space and scarceness in available data on fecundity makes the model stiff and unable to fit to variations in the observed data well and the resulting confidence intervals are too narrow. In this paper, we will improve on the deterministic population model to produce more realistic future projections. For management purposes, this is very important in order to set appropriate limits on the removals of animals, and has relevance beyond this particular study, e.g. in managing other populations subject to harvest or populations that are subject to bycatch. We propose to account for the temporal variation in fecundity using a state–space approach, and we assume the fecundity to be a stochastic process that is integrated with the age-structured population dynamics of the current ICES management model. Owing to scarceness of fecundity data for both the Barents Sea and the Greenland Sea populations, we “borrow strength” from an extensive time-series on fecundity available for the Northwest Atlantic harp seal population. Summary statistics for the Northwest Atlantic time-series, such as autocorrelation and variance in fecundity, are used as prior distributions in the state–space model for the Barents Sea and the Greenland Sea populations. A comparison of the model fits of the proposed model and the deterministic model currently used in management of the stocks is done.

Material and methods

Data

The model uses historical catch records, fecundity rates, age-specific proportions of mature females, and estimates of pup production to estimate the total population trajectory. The catch records come from commercial hunt and distinguish between the number of pups (0-group) and the numbers of older animals (1+) caught per year, but contain no additional information about the age composition of the catches. Catch data before 1946 are unreliable and they make no distinction between pups and older seals (Iversen, 1927; Rasmussen, 1957; Sergeant, 1991). For some years, only total catches for the area (number of harp and hooded seals together) were reported in the pre-1946 data. Because of this, we

start our modelling in 1946. The historical catch data for both the Barents Sea population and the Greenland Sea population are found in ICES (2013).

Pup production estimates (the number of pups born for a given year) are available from aerial photographic surveys for the period (1998–2010; ICES, 2013) in the Barents Sea (Table 1). For the Greenland Sea, pup production estimates (Table 1) are available from mark–recapture estimates (1983–1991; Øien and Øritsland, 1995; ICES, 2011) and aerial surveys conducted in 2002 (Haug *et al.*, 2006), 2007 (Øigård *et al.*, 2010), and 2012 (ICES, 2013; Øigård *et al.*, 2014). The mark–recapture estimates show high variability relative to the nominal standard deviation. Fluctuations on this scale likely reflect sampling artefacts (Øien and Øritsland, 1995). Aerial surveys are considered to be more reliable than the mark–recapture estimates, but despite this, the coefficient of variation (CV) is much smaller for the mark–recapture estimates. We believe that the uncertainties in the mark–recapture estimates are underestimated and have introduced an extra parameter (κ) in the model that scales the standard errors (s.e.) of the mark–recapture estimates.

Two types of reproductive data are used: information on the proportion of females that are mature at age (i.e. maturity ogive) and the proportion of mature females that are pregnant (i.e. fecundity rate). For the Barents Sea, population estimates of age-specific proportions of mature females are available for four historical periods: 1962–1972, 1976–1985, 1988–1993, and 2006 (ICES, 2013). These estimates are the mean estimates for each period. For the Greenland Sea population, corresponding estimates are available for the periods 1959–1990 and from 2009 (ICES, 2013). For years with no data, a linear interpolation of the age-specific proportions of mature females between two periods is assumed (ICES, 2013). As opposed to being part of the data to which the model is fit by maximum likelihood, these rates are treated as known quantities for the model.

The model also makes use of historical values of the fecundity rates that are obtained through sampling during the commercial hunt. Barents Sea population fecundity data are available as the mean estimates in the period 1990–1993 and from 2006 (Figure 2, Kjellqwist *et al.*, 1995; ICES, 2008). Greenland Sea population fecundity data are available from a Russian long-term dataset 1959–1991 (Frie *et al.*, 2003) and Norwegian data from 2008 and 2009 (Figure 3; ICES, 2013).

Table 1. Survey estimates of Barents Sea and Greenland Sea pup production.

Barents Sea population		Greenland Sea population	
Year	Estimate (CV)	Year	Estimate (CV)
1998	286 260 (0.150)	1983	58 539 (0.104)
2000	322 474 (0.098)	1984	103 250 (0.147)
2000	339 710 (0.105)	1985	111 084 (0.199)
2002	330 000 (0.103)	1987	49 970 (0.076)
2003	328 000 (0.181)	1988	58 697 (0.184)
2004	231 811 (0.190)	1989	110 614 (0.077)
2004	234 000 (0.205)	1990	55 625 (0.077)
2005	122 658 (0.162)	1991	67 271 (0.082)
2008	123 104 (0.199)	2002	98 500 (0.179)
2009	157 000 (0.108)	2007	110 530 (0.250)
2010	163 022 (0.198)	2012	89 590 (0.137)

Estimates in the period (1983–1991) from the Greenland Sea are mark–recapture estimates.

Population dynamics model

The population model is an age-structured population dynamics model. For initiation of the model, it is assumed that the population had a stable age structure in year $y_0 = 1945$, i.e.

$$N_{i,y_0} = N_{y_0} s_{1+}^{i-1} (1 - s_{1+}), \quad i = 1, \dots, A - 1, \quad (1)$$

$$N_{A,y_0} = N_{y_0} s_{1+}^{A-1}. \quad (2)$$

Here A is the maximum age group containing seals aged A and higher, and set to 20 years (ICES, 2013), and N_{y_0} is the estimated

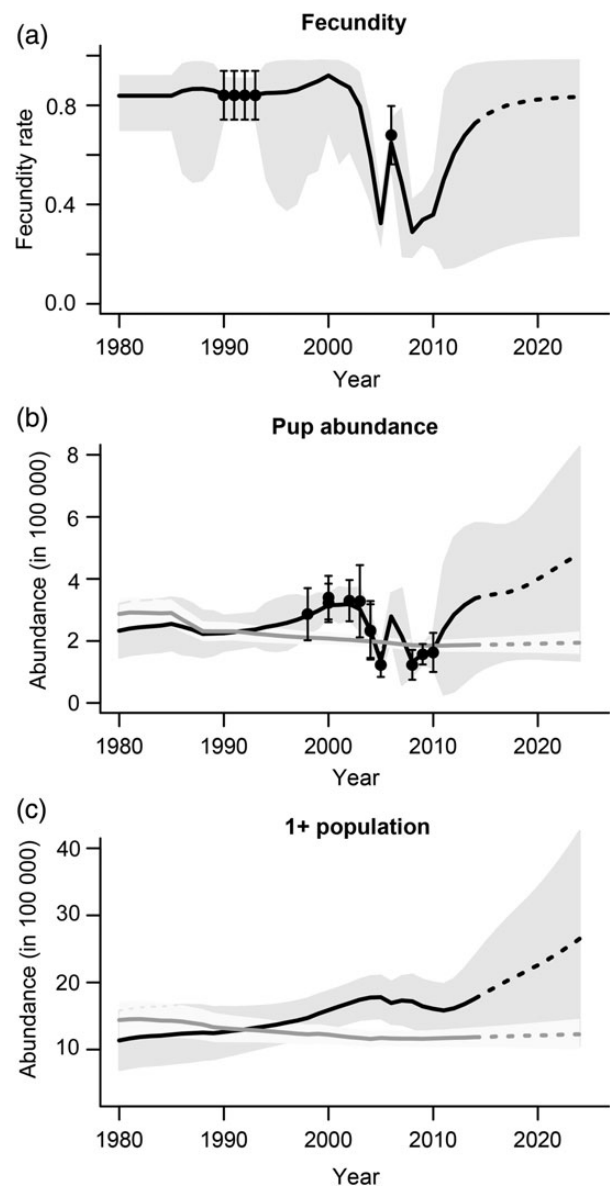


Figure 2. State–space model (black line) and ICES management model (grey line) fit to the Barents Sea harp seal population: fecundity rates (a), trajectory for the pup abundance (b), and abundance of seals of age 1 year and older. Input data (estimates of fecundity and pup production) are represented as point estimates (dots) and 95% CI (vertical bars). Dashed lines show model predictions and shaded area show 95% CI.

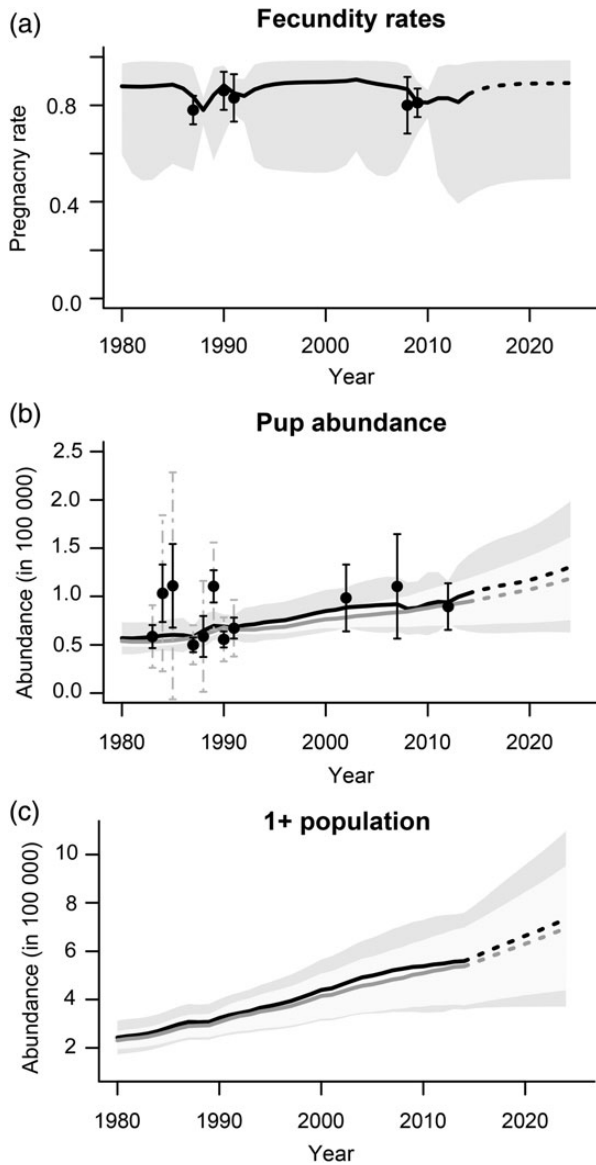


Figure 3. State–space model fit to the Greenland Sea harp seal population. See Figure 2 for explanation of symbols.

initial population size in year y_0 . The model is parameterized by the natural mortalities M_0 and M_{1+} for the pups and seals 1 year and older, respectively. These mortalities determine the survival probabilities $s_0 = \exp(-M_0)$ and $s_{1+} = \exp(-M_{1+})$.

The model has the following set of recursion equations:

$$\begin{aligned} N_{1,y} &= (N_{0,y-1} - C_{0,y-1})s_0, \\ N_{a,y} &= (N_{a-1,y-1} - C_{a-1,y-1})s_{1+}, \quad a = 2, \dots, A-1, \\ N_{A,y} &= [(N_{A-1,y-1} - C_{A-1,y-1}) + (N_{A,y-1} - C_{A,y-1})]s_{1+}. \end{aligned} \quad (3)$$

Since available data do not allow for more detailed age-dependence in survival to be estimated, it is assumed that the mortality rates are age-independent within the 1+ group. The $C_{a,y}$ are the age-specific catch numbers. Catch records are aggregated over age, and only provide information about the annual number of pups and

number of 1+ seals caught. To obtain $C_{a,y}$ in (3), we assume that the age-distribution in the catch follows the modelled age distribution and employ the *pro rata* rule (Skaug *et al.*, 2007):

$$C_{a,y} = C_{1+,y} \frac{N_{a,y}}{N_{1+,y}}, \quad a = 1, \dots, A, \quad (4)$$

where $N_{1+,y} = \sum_{a=1}^A N_{a,y}$, with $N_{a,y}$ being the number of individuals at age a in year y .

The modelled pup abundance is given by

$$N_{0,y} = \frac{F_y}{2} \sum_{a=1}^A p_{a,y} N_{a,y}, \quad (5)$$

where $N_{a,y}/2$ is the number of females at age a in year y , F_y the time-varying fecundity rates, and $p_{a,y}$ are the time-varying age-specific proportions of mature females.

State–space model

Because available data on fecundity rates are scarce, we define a stochastic process model for fecundity and estimate the temporal variation in fecundity using a state–space approach. For an initial period $y \in [y_0, y_s]$ with no estimates of fecundity, it is assumed that $F_y = f_{\text{init}}$ is constant. Starting in year y_s a first-order autoregressive (AR) process $x_y = ax_{y-1} + u_y$, is used as a perturbation around f_{init} (see below), with $x_{y_s} = 0$. Here, a is the AR parameter and u_y the zero mean normally distributed “innovation term” with standard deviation σ . This component of the model introduced two extra parameters, a and σ , to be estimated by maximum likelihood, while the AR process x_y itself will be handled by a Kalman filter approach.

Because we require $0 \leq F_y \leq 1$, we cannot simply add x_y to f_{init} . We therefore employ the logistic transformation

$$F_y = \frac{\exp(\zeta + x_y)}{1 + \exp(\zeta + x_y)}, \quad (7)$$

where $\zeta = \log\{f_{\text{init}}/(1-f_{\text{init}})\}$. In the state–space terminology, F_y (or x_y) is the “state variable”. The Kalman filter approach provides estimates of F_y within the time range for which data exist, and predictions of future values of F_y . For the latter, the lack of data results in increased uncertainty. While the existing fecundity estimates provide direct information about F_y , the Kalman filter approach takes all data sources into account when estimating F_y .

Parameter estimation

The model is fitted to the survey pup production estimates and the fecundity rates by maximum likelihood. Assuming normality for the pup production estimates, their contribution to the log-likelihood function is

$$\sum_y -\log(\sigma_{0,y}) - \frac{1}{2} \frac{(n_{0,y} - N_{0,y})^2}{(\sigma_{0,y})^2}, \quad (9)$$

where $n_{0,y}$ and $\sigma_{0,y}$ denote the survey pup production count and corresponding s.e. for year y . The extra parameter κ for scaling the s.e. of the mark–recapture pup production estimates in the Greenland Sea enters the model in Equation (9) by replacing $\sigma_{0,y}$ with $\kappa\sigma_{0,y}$ for the

years with mark–recapture estimates only. A truncated normal distribution has traditionally been assumed for the fecundity data to ensure $F_y \in (0,1)$ (Skaug *et al.*, 2007; ICES, 2013; Øigård *et al.*, 2014). This was also assumed in the proposed model, and the contribution to the log-likelihood function is

$$\sum_y -\log(\sigma_{f,y}) - \frac{1}{2} \frac{(f_y - F_y)^2}{(\sigma_{f,y})^2}, \quad (10)$$

where f_y , and $\sigma_{f,y}$ is the observed fecundity rate and corresponding s.e. in year y .

Prior distributions

The model has a Bayesian flavour as priors are imposed on some of the parameters. In a situation with scarce data, special care must be given to the choice of priors as it may potentially affect the outcome of the analysis.

A vague normal prior is assumed for the initial population size N_{y_0} . For the Barents Sea population, a truncated normal prior with mean 0.27 and standard deviation 0.20 was used for the mortality M_0 and a truncated normal prior with mean 0.09 and standard deviation 0.10 was used for the mortality M_{1+} . For the Greenland Sea population, a truncated normal prior with mean 0.24 and standard deviation 0.20 was used for the mortality M_0 and a truncated normal prior with mean 0.08 and standard deviation 0.10 was used for the mortality M_{1+} . The mean of the priors for the mortalities M_0 and M_{1+} is the same as used in management of the respective populations (ICES, 2013), but the prior distributions are slightly wider. The early period fecundity rate f_{init} for the Barents Sea population was assumed to have truncated normal prior centred around $f_{\text{init}} = 0.84$, with a standard deviation of 0.17 (ICES, 2005). The fecundity rate f_{init} for the Greenland Sea population was assumed to have a truncated normal prior distribution centred around $f_{\text{init}} = 0.81$, with a standard deviation of 0.2 (ICES, 2009).

Priors for the AR parameters a and σ were obtained from the time-series of fecundity of female harp seals in the Northwest Atlantic (Stenson and Wells, 2011; Stenson *et al.*, 2014). From this time-series of annual fecundities, the AR parameters a and σ were estimated to be $a = 0.7$ with s.e. = 0.1 and $\sigma = 0.85$ (s.e. = 0.1). A logistic transformation was applied to the Canadian fecundity data before estimating the AR parameters. The “borrowing strength” aspect of our method is that we assume that a and σ are invariant among harp seal populations in the North Atlantic, and that the above estimates can be used as (normal) priors for a and σ in the state–space model.

No prior was imposed on κ or total population size. The combined likelihood-contributions for all priors are

$$-\frac{1}{2}(\mathbf{b} - \mathbf{m})^T \Sigma^{-1}(\mathbf{b} - \mathbf{m}) - \frac{1}{2} \log|\Sigma| - \frac{6}{2} \log(2\pi), \quad (11)$$

where $\mathbf{b} = (N_{y_0}, M_0, M_{1+}, a, \sigma, f_{\text{init}})^T$ is a vector containing the parameters estimated by the model, \mathbf{m} a vector containing the respective mean values of the normal priors for the parameters in \mathbf{b} , and Σ a diagonal matrix with the variance of the respective prior distributions on the diagonal. The values used for \mathbf{m} and Σ are summarized in Table 2 for the Barents Sea population and the Greenland Sea population.

All parameter estimates are found by maximizing the likelihood function using the statistical software AD Model Builder (Fournier *et al.*, 2012). AD Model Builder uses a quasi-Newton optimization algorithm with bounds on the parameters, and calculates estimates of standard errors of model parameters using the δ -method (Casella and Berger, 1990). The (non-linear) Kalman filter referred to above is handled via the Laplace approximation (Skaug and Fournier, 2006) in AD Model Builder. Handling of data and visualizations were done in R (R Core Team, 2012).

Results

Estimates of the parameters used in the model for the Barents Sea population and the Greenland Sea population are presented in Table 2, and modelled fecundity and abundance are visualized in Figures 2 and 3, respectively. Shaded areas denote 95% credible intervals (CI). The model back-calculates the population to 1946 (to impose the constraint of historical catches), but for space considerations, we only visualize results from 1980 as most events of interest happen later.

The stochastic process for modelling the fecundity is activated in $y_0 = 1985$ for the Barents Sea population. The fecundity in the period 1946–1985 was estimated to be $f_{\text{init}} = 0.84$ (s.e. = 0.06). The modelled fecundity rate (Figure 2a) reaches a peak at 0.92 in 2000 and drops rapidly to 0.33 in 2005. A sudden increase in the fecundity rate up to 0.65 is estimated in 2006 before it drops rapidly reaching a minimum of 0.29 in 2008, where it remains low until 2010 and then increases and stabilizes around 0.84 for the model predictions. The state–space model fits tightly to the survey pup production estimates (Figure 2b, black) as it captures the sudden drop in the survey estimates in 2004 and 2005, whereas the ICES management model (grey) is very stiff and fits a straight line through the mean of the survey estimates. The state–space model estimates a sudden increase in the pup abundance in 2006 and then drops back down to a low level matching the survey estimates

Table 2. Estimated parameter used in the model for the Barents Sea and the Greenland Sea harp seal populations.

	Barents Sea population		Greenland Sea population	
	Mean	s.e.	Mean	s.e.
N_{y_0}	1 153 700 (900 000)	171 720 (900 000)	294 910 (900 000)	41 904 (900 000)
M_0	0.275 (0.270)	0.100 (0.200)	0.254 (0.240)	0.196 (0.200)
M_{1+}	0.100 (0.090)	0.016 (0.100)	0.118 (0.080)	0.020 (0.100)
a	0.739 (0.700)	0.088 (0.100)	0.632 (0.700)	0.092 (0.100)
σ	0.851 (0.850)	0.091 (0.100)	0.764 (0.850)	0.103 (0.100)
f_{init}	0.838 (0.840)	0.057 (0.168)	0.892 (0.810)	0.044 (0.200)
κ			2.713	0.732

Priors used are shown in parentheses.

in 2005–2010. The ICES management model predicts that the pup abundance stays at a low level, whereas the state–space model predicts that the pup abundance will increase substantially from 2010. A comparison of the modelled population trajectory of the 1+ age group using the state–space model (black) and the ICES management model (grey) is shown in Figure 2c. Both models estimate a decreasing 1+ population from 1946 to 1965 followed by an increasing number of seals. The ICES management model estimates a peak around 1980 before it declines and appears to stabilize, whereas the state–space model estimates a peak in 2005 followed by a short period of declining number of seals before it starts increasing again. The state–space model estimates a 1+ population of 1 759 000 (s.e. = 328 760) animals in 2014 and predicts a 50% increase of the population over the next 10 years. The ICES management model estimates a 1+ population of 1 184 000 (s.e. = 74 772) animals in 2014 and predicts a 4% (s.e. = 0.05) increase of the 1+ population over the next 10 years. No hunt is assumed in the model predictions. Estimated pup mortality was $M_0 = 0.28$ (0.28), and 1+ mortality $M_{1+} = 0.10$ (0.11) for the state–space model (ICES management model). The estimates of a and σ are not affected much by data, i.e. the estimates are mostly driven by the priors (Table 2).

The estimated/predicted fecundity is increasing after the last year with pup production data ($y = 2010$). It is a property of the AR process that it will return to its equilibrium point $x_y = 0$ in the absence of any “forces” (data) pulling it away. Consequently, according to Equation (7), the predicted F_y will approach f_{init} .

The stochastic process for modelling the fecundity is activated in 1960 for the Greenland Sea population (Figure 3). The fecundity in the period 1946–1960 was estimated to be $f_{\text{init}} = 0.89$ (s.e. = 0.04). The model indicates a stable fecundity rate with average around 0.87 for the whole period (Figure 3a). Both models estimated trajectories of the pup abundance appear within most CI of the survey pup production estimates (Figure 3b) and the trajectories are almost identical. The estimate of the scaling factor κ for scaling the standard errors of the mark–recapture pup production estimates was 2.71 (s.e. = 0.73). The dashed CI shown in Figure 3b are the 95% CIs using the scaled standard errors. A comparison of the modelled population trajectory of the 1+ age group using the state–space model (black) and the ICES management model (grey) is shown in Figure 3c. The estimated trajectories for the 1+ group are almost identical for the state–space model and the ICES management model. The state–space model estimates a 1+ population of 560 200 (s.e. = 103 070) animals in 2014 and predicts a 31% (s.e. = 0.14) increase of the 1+ population over the next 10 years. The ICES management model estimates a 1+ population of 536 800 (s.e. = 81 973) animals in 2014 and predicts a 30% (s.e. = 0.07) increase of the 1+ population over the next 10 years. The model predictions in both cases assume no hunt. Estimated pup mortality was $M_0 = 0.27$ (0.28), and 1+ mortality $M_{1+} = 0.12$ (0.11) for the state–space (ICES management) model.

Discussion

The current model used by the ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP) is a deterministic age-structured population dynamics model with only three free parameters, and the time-varying fecundity is treated as a known quantity. Owing to scarcity of historical data on fecundity, the current management model provided a poor fit to the pup production data for the Barents Sea population. In this paper, we have demonstrated how the state–space approach provided a more

flexible model that gave a better fit to the different data sources, and better reflected the modelling uncertainty. We increased the parameter space with only 3 and 4 degrees of freedom for the Barents Sea population and the Greenland Sea population, respectively, and constructed a highly flexible age-structured population dynamics model that treated fecundity as a time-varying state variable.

The ICES management model was unable to capture the dynamics of the survey pup production estimates of the Barents Sea population with the sudden drop in pup production in 2004 and 2005, whereas the proposed state–space model fit the pup production data well. According to the state–space model, the fecundity peaked in 2000 before dropping rapidly, and the pup abundance peaked in 2002 before also dropping rapidly as a consequence of the decreased fecundity rate. The model suggested that the fecundity was low in the period 2004–2010, but due to the observed fecundity in 2006, the modelled fecundity displayed a sharp increase that year to match this observation. This was explored by relaxing the precision of the estimated fecundity by adding an extra parameter in the model to scale the standard error of the observed fecundity rate in 2006—similar to what was done by scaling the s.e. of the mark–recapture pup production estimates for the Greenland Sea population. The model was allowed more flexibility around this period, and a scaling factor of 5.3 for the s.e. of the observed 2006 fecundity was estimated. The modelled fecundity in 2006 was then estimated to be 0.42 and the modelled pup abundance remained low around 2006. This illustrates a problem with not having temporally overlapping fecundity data and pup production data. As a result, the model seemed to be overly flexible and pulled in the direction of available data.

The state–space model estimated a minimum fecundity rate of 0.29 for the Barents Sea population, which is considered to be low and far below the available fecundity data for this population. A long time-series of late-term pregnancy rates, fecundity, and abortion of Northwest Atlantic harp collected off the coast of Newfoundland and Labrador from 1950s up to present show highly variable reproductive rates between years resulting in significant impact of the population modelling (Sjare and Stenson, 2010; Stenson and Wells, 2011; Stenson *et al.*, 2014). In the same dataset, the proportion of females that were pregnant has been observed to vary from <0.3 to more than 0.85 between years. Owing to the timing of sampling the reproductive data of Northwest Atlantic harp seals, it has been possible to estimate late-term abortion rates for this population. Abortions were found to occur every year with high variability between years, and maximum abortion rate of 0.24 was observed. In general, the abortion rates appeared to be higher in years with lower overall fecundity (Stenson and Wells, 2011). For the Barents Sea and the Greenland Sea populations, reproduction data were sampled during the moulting season (Frie *et al.*, 2003). Because of this, it was not possible to estimate abortion rates for these populations and the observed fecundity rates are most likely overestimated. The low fecundity rates estimated by the state–space model could therefore be plausible.

We have chosen to let the fecundity F_y be time varying, but let the mortalities M_{1+} and M_0 be time invariant. The state–space approach can conceptually be extended to allow time variation also in mortality, but in practice that would require more data than is currently available. As M_0 and F_y are closely related parameters, variation in M_0 will to some extent be compensated for by changing F_y .

There is considerable heterogeneity in the mark–recapture pup production estimates of the Greenland Sea population, and weighting this source of data differently could change the prediction of the trajectory of the population (ICES, 2013). As the mark–recapture estimates appear fluctuating between two levels, two very different scenarios of the changes in the pup abundance are indicated. The lowest level indicates increasing pup abundance up to present with a possible stabilization at the moment, whereas the highest mark–recapture estimates indicate that the pup abundance might have been stable over the last two decades.

Although the s.e. of the mark–recapture pup production estimates were scaled in the state–space model to relax the importance of those estimates, the four lowest mark–recapture estimates were weighted more by the model than the higher mark–recapture estimates, and the difference in the estimated population trajectory of the Greenland Sea population was insignificant between the two models. It has been proposed to reanalyse the mark–recapture estimates so they are updated with new information obtained since the original analyses were completed (ICES, 2013).

The state–space model trajectories had wider CIs than the ICES management model. This is a result of allowing the fecundity to fluctuate stochastically and that the CIs of the ICES management model are likely underestimated because it uses the available data on fecundity as known quantities with no uncertainties. Thus, any uncertainties associated with these measurements are not taken into account. Also, as the available data are scarce, and it has been seen that the fecundity data have large interannual variability, it is reasonable to expect the CIs from the ICES management model are underestimated. The ICES management model assumes a fixed fecundity rate in the model predictions, whereas the state–space model takes into the account random changes of the fecundity in the model predictions. For management purposes, it is important that uncertainties around future predictions are realistic.

State–space models (via the Laplace approximation) are computationally more expensive than classical population dynamics models fitted by non-linear least squares. However, in the models in our study, the time-series are relatively short, and it took only 18 s (Barents Sea) and 35 s (Greenland Sea) to fit the models in AD Model Builder.

The age-structured model for estimating the total population size requires information on age-structure in the hunt. For the Greenland Sea population, field data on the age structure in the catch data are not available, and for the Barents Sea population, a small sample from the period 1963–2006 is available. Because of the lack of data on age structure in the catch, the age-structured model assumes that the age structure in the catch data represents the age structure of the population. In reality, the age structure of the catch data are biased for several reasons (see also Kjellqvist *et al.*, 1995): the preferences among hunters have changed over the decades (in some cases, adult males were preferred), younger seals may be easier targets than older seals, and there is a sex- and age-based segregation of harp seals on the moulting grounds where the hunt for adult seals occurs. For sensitivity analysis, an age-determined sample from commercial hunt in the period 1963–2006 in the Barents Sea was used as input for the age-structured catch in the modelling of the Barents Sea population. The model was not much affected by these changes, but it is natural to expect that severe changes in the catch distribution over a long period will increase the bias of the model.

Previously, a version of the ICES management model with density-dependent fecundity F_y was fitted (Skaug *et al.*, 2007) with a logistic relationship between F_y and population size. That

study used catch data back to 1875, and the fitted F trajectory does not correspond well with that of the current study in the overlapping period. This is perhaps not surprising since in our (non-parametric) state–space model, F_y was allowed to vary independently of total population size, while Skaug *et al.* (2007) modelled F_y as a function of population size.

We have demonstrated that the state–space approach is very flexible, and that in situations with scarce data, it is possible to borrow strength from observations on other populations. This latter is a non-trivial task, both with respect to determining which populations are relevant and which parameters can be expected to be invariant across populations. By treating F_y as a stochastic process, we get a close fit to data (maybe too close) and an increased uncertainty about predictions. To obtain more precise and realistic predictions, one might have to move beyond the stochastic-only approach used here and use it in further studies to find out what the real underlying mechanisms driving fecundity and other population parameters are. This could involve density-dependence, environmental covariates, and competition (Øigård *et al.*, 2013). This could be done by, e.g. having the ζ parameter in Equation (7) trended, making it density-dependent or a function of environmental covariates such as ice conditions or abundance of key prey species.

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