

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

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ABSTRACT

We estimate the population size of Barents Sea harp seals to have been around 6 million individuals in the year 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. Due to 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 regulation results in the interval estimate 3-7 million individuals for the population size in 1875.

KEYWORDS: DENSITY REGULATION, CATCH HISTORY, PAGOPHILUS GROENLANDICUS.

INTRODUCTION

Barents Sea harp seals, *Pagophilus groenlandicus*, are wintering in the White Sea, and migrate into the Barents Sea to feed later in the year. They whelp in February/March, and moulting takes place about one 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 two million individuals (ICES, 2005), but a lack of knowledge about several key biological parameters is recognized. With its large population size, harp seals constitute an important component of the Barents Sea ecosystem.

Organized human exploitation of Barents Sea harp seals started around 1875, reached its peak around 1925, and has since then decreased (Figure 1). Assessment of the post-war (1946 onwards) development of the population has shown an increasing trend in population size (Ulltang and Øien, 1988; Øien and Øritsland, 1995). No attempt has so far been made to estimate the development of the population prior to 1945, although it is a general opinion that the high catch levels in the 1920ies severely depleted the population. The main goal of the present analysis is to estimate the pre-exploitation population size, i.e. the population size 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 Barents Sea harp seals. Due to increased fishing activity in the Barents Sea during the 20th century, it is likely that the carrying capacity today is lower, and there are in fact indications that the population has reduced its growth rate (ICES, 2005).

A problem commonly faced when trying to estimate the historical development of marine mammal populations is a lack of data. While relatively accurate catch records may be available from several centuries back, abundance estimates are typically available only from a short recent period. An additional problem arises with harp seals, as the currently available census techniques only provide estimates of pup production, so that knowledge about female reproductive rates is required in order to obtain estimates of the total population size. Lack of reliable information about historical catching efforts prevents the use of catch data in a catch-per-unit-effort analysis for Barents Sea harp seals. However, the yearly catch numbers can still be used as an exogenous variable in the population dynamics equations. The unknown parameters in the population dynamics model can be fit to all the other data sources using statistical techniques.

For Barents Sea harp seals available data sources besides the catch data include estimates of pup production, age samples taken on whelping grounds and estimates of mean age-at-maturity for females (Frie et al., 2003). Seen in a historical perspective, all of 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 uncertainty related to model choice, in addition to the statistical uncertainty arising from the sampling variability in data.

Density regulation is required in order to impose the assumed equilibrium at K for the population in year 1875. Density dependent changes in female reproductive parameters and other life-history characteristics have been studied in detail for

exploited population (e.g. Fowler, 1984). Within the International Whaling Commission (IWC) the historical development of many baleen whales stocks has been assessed under the assumption that the population was in equilibrium at K prior to human exploitation (Butterworth et al., 2002). The assumption that the carrying capacity level K has been constant over centuries clearly seems unrealistic, but provides nevertheless a first order approximation to reality, and is the stepping-stone to fitting these types of models to sparse sources of data.

For Barents Sea harp seals an increasing trend in mean age-at-maturity has been observed (Frie et al., 2003) over a period in which the population is believed 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. Density regulation is also likely to affect birth rate among sexually mature females. For Northwest Atlantic harp seal a negative correlation between pregnancy rate and population size has been observed (Sjare et al, 2000). In addition to these two parameters, we also consider density regulation 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 the target of density regulation. Nevertheless, mortality is a key parameter in the population dynamics model used.

The total fishing pressure increased steadily in the Barents and Norwegian Seas during the 20th century up to around 1980 (Sakshaug et al., 1992). The largest increase in the fishing effort took place in the period 1950-1980 when the pelagic fishery for herring and capelin peaked and eventually led to near extinction of the

Atlanto-Scandinavian stock of herring. From the 1930ies trawl fisheries developed on cod fishes. Since these fish species are important prey for the harp seal (Nilssen et al., 2000), it is natural to consider the hypothesis that the capacity level K has decreased since 1875.

In the present study we want to assess the historical development of the Barents Sea harp seal population, by fitting an age-structured population dynamics model to all available data sources. Estimates of the pre-exploitation population size have not previously been published. The sensitivity of the results is studied with respect to the choice of density regulating mechanism, age at menopause and the assumption of a constant carrying capacity.

MATERIAL AND METHODS

Data

The compilation of catch records for the period 1875-2005 is described 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 (number of pups born each year) are available from aerial photographic surveys for the period 1968-2003 (Table 1). The series of surveys conducted prior to 1998 cannot be treated as absolute estimates of pup production, but

is assumed to provide reliable information about trend in pup production. The series of estimates starting from 1998, on the other hand, are treated as absolute estimates of pup production, and these 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 that they represent a random sample from the reproductively active part of the female population. Since the sampling most likely was confined to certain geographical locations, and since it is likely that different age groups are spatially segregated on whelping grounds, the 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 result 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. Further, to avoid problems associated with aging of older animals (Bowen et al., 1983), we only use the age distribution for the range 1-20 years.

Estimates of mean age-at-maturity for females in the period 1962-1993 have been taken from Frie et al. (2003; Table 2, MAM_{PM} , unconstrained Richards model). Each estimate is assigned to the midpoint of the time period in which data were collected. The uncertainty estimates given in Table 2 of Frie et al. (2003) are treated as 95% confidence intervals. The birth rate, F , has been assumed to have an a priori distribution centered around $F = 0.85$ with a standard deviation of 0.075. This prior on F has been used in recent assessments of the Barents Sea harp seals (ICES, 2005).

In models runs with F being a dynamic parameter, the prior is applied to the year 1950 in which the population was at a relatively low level.

Population dynamics model

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

$$\begin{aligned}
 N_{0,t} &= \text{number of pups born in year } t, \\
 N_{i,t} &= \text{number of individuals at age } i \text{ in year } t, \\
 K &= \text{carrying capacity,} \\
 M_0 &= \text{pup mortality,} \\
 M_{1+} &= \text{mortality among 1+ animals,} \\
 F &= \text{birth rate among reproductively active females,} \\
 a &= \text{mean age-at-maturity,} \\
 b &= \text{mean age of menopause.}
 \end{aligned}$$

Here, ‘1+’ denotes all ages larger or equal to one year. Time varying versions of the parameters M_{1+} , F and a are considered below in connection with modelling of density regulation. The parameter K will also be treated as a dynamic quantity, in order to investigate the hypothesis of changes in carrying capacity.

It is assumed that prior to 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.

$$(1) \quad \begin{aligned}
 N_{i,t_0} &= K \cdot e^{-(i-1)M_{1+}} (1 - e^{-M_{1+}}), & i = 1, \dots, A-1 \\
 N_{A,t_0} &= K \cdot e^{-(A-1)M_{1+}}.
 \end{aligned}$$

Here, the maximal age group A contains all individuals aged A or more. In the present analysis we use $A = 50$, which is assumed to be above the maximal age of harp seals.

The catch records give information about the following quantities:

$$\begin{aligned} C_{0,t} &= \text{catch in numbers of pups in year } t, \\ C_{1+,t} &= \text{catch in numbers of 1+ animals in year } t. \end{aligned}$$

In absence of information about age specific catch numbers for adults we employ the following pro-rata rules in the model:

$$C_{i,t} = C_{1+,t} \frac{N_{i,t}}{N_{1+,t}}, \quad i = 1, \dots, A,$$

where $N_{1+,t} = \sum_1^A N_{i,t}$. Catches are assumed to be taken prior to the occurrence of natural mortality, leading to the following set of recursion equations:

$$(2) \quad \begin{aligned} N_{1,t} &= (N_{0,t-1} - C_{0,t-1})e^{-M_0} \\ N_{i,t} &= (N_{i-1,t-1} - C_{i-1,t-1})e^{-M_{1+}}, \quad i = 2, \dots, A-1, \\ N_{A,t} &= ((N_{A-1,t-1} - C_{A-1,t-1}) + (N_{A,t-1} - C_{A,t-1}))e^{-M_{1+}}. \end{aligned}$$

The pup production is governed by the equation

$$N_{0,t} = \frac{F}{2} \sum_{i=1}^A p_{i,t} N_{i,t},$$

where $N_{i,t}/2$ is the number of females at age i , and $p_{i,t}$ is the proportion of sexually mature females at age i (at time t). For low ages $p_{i,t}$ is an increasing function of i , reflecting that individuals get mature at different ages. The p -curve levels off at unity when all females have become mature, and then declines to zero for large ages (menopause). As a parametric model we assume

$$(3) \quad p_{i,t} = L(i - (a_t + 1)) \cdot L(-0.5(i - b)),$$

where $L(x) = \exp(x)/[\exp(x) + 1]$ is the logistic function. Note that $L(i - (a_t + 1))$ is an increasing function of i , while $L(-0.5(i - b))$ is a decreasing function. Note also

that while a_t refers to the age at maturation, $a_t + 1$ is the age at first birth. The choice of the particular functional form $L(i - (a_t + 1))$ is based on Figure 4 in Frie et al. (2003). Little is known about the (negative) slope of the p -curve for large ages. Implicit in our assumption (3) is that the curve drops by 90% during a period of approximately 12 years centered at age b .

Density regulation

We consider three different density regulation mechanisms:

$$(4) \quad a_t = a \cdot \left(\frac{N_{1+,t-1}}{K} \right)^{\gamma_a},$$

$$(5) \quad F_t = 1 - (1 - F) \left(\frac{N_{1+,t-1}}{K} \right)^{\gamma_F},$$

$$(6) \quad M_{1+,t} = M_{1+} \cdot \left(\frac{N_{1+,t-1}}{K} \right)^{\gamma_M}.$$

The parameters a , M_{1+} , and F are still quantities to be estimated, but they now have the interpretation of being parameter values at the carrying capacity level, i.e. when $N_{1+} / K = 1$. Only one of the three mechanisms is allowed to be active at a time, so (4), (5) and (6) give rise to three different models, with all other aspects of the population dynamics being identical. For instance, we obtain Model (4) by requiring that $\gamma_F = \gamma_M = 0$, while γ_a is a parameter that is estimated along with the other parameters of the model. Model (4) differs from models (5) and (6) in that estimates of a_t are available for the period 1962-1993, while 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 individuals recruited to the population matched the number of individuals dying each year, is expressed mathematically as

$$(7) \quad \frac{1}{2} F \cdot \exp(-M_0) \cdot \sum_{i=1}^A \frac{P_{i,t_0} N_{i,t_0}}{K} = 1 - \exp(-M_{1+}).$$

This constraint is not enforced strictly in the model, but instead the deviation from equality in (7) is penalized in the log-likelihood function. The penalty may be given the following interpretation. Denote by δ the difference between the left and right hand side of (7), so that δ is the proportion by which the population increases per year. The penalty employed in the present analysis corresponds to placing a Bayesian normal prior with expectation 0 and standard deviation 1/1000 on δ . Hence a 5% total change over a 10-year period is very unlikely under this prior, while a 2% change over 10 years is compatible with the prior.

To account for a possible reduction in the carrying capacity level 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. Information about c partly comes from an assumption that the population has reached a new carrying capacity cK in year 2005.

Parameter estimation

Parameter estimates are obtained by maximizing a likelihood function, which contains contribution from the different data sources. The catch data enters the model through equation (2), but does not otherwise contribute to the likelihood function. Since 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”, but also allows a full Bayesian analysis via Markov chain Monte Carlo (MCMC) sampling (Gelman et al., 1995). The MCMC facility of AD Model Builder is used to obtain alternatives to the uncertainty bounds based on the delta-method.

Pup production estimates

Denote by $n_{0,t}$ the pup production estimate for year t as given in Table 1. For the series of pup production indices (1968-1991) it is assumed that $n_{0,t}$ is normally distributed with expectation $q \cdot N_{0,t}$ and a common coefficient of variation τ . Both q and τ are unknown parameters that are estimated along with the other parameters of the model. For the series of absolute abundance estimates (1998-2003) it is assumed that $n_{0,t}$ is normally distributed with expectation $N_{0,t}$ and with coefficient of variation τ_t as given in Table 1. Hence, the contribution to the log-likelihood function coming from the series of pup production estimates is

$$(8) \quad \sum_t -\log(\tau_t n_{0,t}) - \frac{(q \cdot N_{0,t} - n_{0,t})^2}{2(\tau_t n_{0,t})^2},$$

where the sum extends over all years t for which there is an estimate. This summation convention is used also in the following. It should be understood that $q=1$ for the years 1998-2003, and that $\tau_t = \tau$ for the years 1968-1991. The

parameters of the population dynamics model enter the likelihood function through $N_{0,t}$.

Mean age-at-maturity

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

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

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

Age distribution on whelping grounds

Denote by $m_{i,t}$ the number of females at age i sampled on the whelping grounds in year t (Table 2). Under the assumption of random sampling, $m_{i,t}$ would be multinomially distributed. To account for non-random sampling an effective sample size of 1% is used, and the log-likelihood contribution becomes

$$(10) \quad \frac{1}{100} \sum_t \sum_{i=1}^{20} m_{i,t} \log \left(p_{i,t} N_{i,t} \left(\sum_{i=1}^{20} p_{i,t} N_{i,t} \right)^{-1} \right).$$

RESULTS

The model was fitted to data for all combinations of the following three factors: density regulation mechanism (models (4), (5) and (6)), mean age-of-menopause ($b = 30$ and $b = 50$) and time varying K_t (Yes, No). Figure 2 shows the estimated population trajectories for 11 of these combinations. The omitted model is (5) in

combination with $b = 50$ and a constant K_t , which did not fit the pup production estimates satisfactorily (Table 3). It is clear from Figure 2 that Model (4) gives the highest estimate of population size in year 1875, regardless of other assumptions. The estimate for the best fitting model (Table 4) is 6.3 millions 1+ animals for the year 1875 with a 95% confidence interval ranging from 5.7 to 6.9 millions.

For models (4) and (5) scenarios with $b = 30$ has a better fit than $b = 50$, so goodness-of-fit is assessed in detail only for models with $b = 30$. Table 4 summarizes parameter estimates, while Figures 3-5 show the population trajectories for the period 1875-2005. Model (4) fits both the pup production estimates and age distribution data well (Figure 3). Values of mean age-at-maturity range from $a = 19$ (which is an upper bound in the optimization routine) in 1875 to $a = 5$ around 1960, and the model fits the data from Frie et al. (2003) well.

Panel c in Figure 3-5 contains a plot of the time development of

$$(11) \quad P_t = \frac{F_t \cdot \sum_{i=1}^A p_{i,t} \cdot N_{i,t}}{\sum_{i=1}^A N_{i,t}},$$

which is the proportion of females giving birth in year t . As expected, the largest temporal variation in P_t is seen for models (4) and (5), as these density regulation mechanisms acts 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 Model (4) and highest for Model (5). Corresponding measures of uncertainty

obtained with the MCMC facilities of AD Model Builder were very close to those shown in Figure 3-5.

DISCUSSION

All models considered in this study yields a similar shape of the 1+ trajectory. Heavy hunting pressure depleted the population severely in the first half of the 20th century. The increase in population size during 1940-45 results from the temporal halt in the hunt during the second world war, and the increasing trend since 1960 is consistent with the results from Ulltang and Øien (1988).

Model (4) gives the highest estimates of population size in year 1875, regardless of what other assumptions are made (Figure 2). Estimates of current population size N_{2005} range from 1.4 to 2.6 million (Table 4). The lowest estimates of N_{2005} are obtained under Model (6) where density regulation acts through mortality alone. As noted earlier, this model is the biologically least plausible among the density regulation mechanisms considered in the present study. Finally, it should be noted that the assumption of a new carrying capacity level currently being reached, lower than the one for 1875, tends to decrease the estimate of current population size, which is to be expected.

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 is not 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 1953-1959 (Yakovenko 1961). The estimate for 1928 is higher than those obtained in the present study, while the estimate from the period 1953-1959 lies in the band of fitted curves (Figure 2).

Model (4) yields in general higher likelihood values than the two other models (Table 3), reflecting the fact that Model (4) has the flexibility to adjust to the trend in the age-at-maturity data, while the other models assume a fixed value for a . Parameter estimates and associated 95% confidence intervals for the best fitting model are given in Table 5. Several aspects of this model fit are biologically unrealistic. For instance the estimate of an age-at-maturity at $a = 19$ year should not be interpreted as an estimate of age-at-maturity in the year 1875. Rather, it is the value of a required in order 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. By comparison with the model with the higher mean age-of-menopause $b = 50$ (Model (4)-ii in Table 4), it is seen that the low estimate M_{1+} is caused by the assumption that females stop reproducing around $b = 30$, although the dramatic difference in M_0 values between the two models should be noted. All of this indicate that the model fit as a whole is unstable. However, certain aspects of the model fit, such as the estimated 1875 population size, are not very sensitive to the assumptions made.

The estimated uncertainty in the fitted 1+ population trajectory (Figures 3-5, panel a) is unrealistically low. Firstly, it only reflects the sampling uncertainty in the data, not the uncertainty related to the choice of model. Figure 2 shows that the latter is dominating. A second reason might be that due to 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 Figure 3-5 and in 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 to 7 million. This interval covers all different assumptions/scenarios considered in the present study.

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APPENDIX

CATCH HISTORY OF BARENTS SEA HARP SEALS

The White Sea and Barents Sea stock of harp seals have been hunted by Norwegian and Russian sealers over a long time period; the documentation of these catches is however scarce. The catching grounds comprise the breeding and moulting grounds in the White Sea and feeding grounds in the Barents Sea and has been referred to as the “East Ice” in contrast to the “West Ice” which comprised harp seal catching grounds in the Greenland Sea and around Jan Mayen. Catching of harp seals in the White Sea

area has been going on at least since the 12th century (Nazarenko 1984). This fishery was shore based, taking place along the coasts of the White Sea and around the Kanin Peninsula (Sergeant 1991). Offshore hunting started when vessels from Troms and Finnmark, northern Norway, caught harp seals off the White Sea in 1867 (Iversen 1927); they were joined by vessels from southern Norway from 1919 onwards and by Soviet vessels during the 1920ies. Norwegian catches over the period 1821-1926 have been given by (Iversen 1927) who comments that there are long periods without traces of catch data, and for many years only the number of vessels participating has been available. Prior to 1875 there are many years without information, but the harp seal catches at that time were probably quite low, supposedly in the order of hundreds annually, although many vessels participated in the Arctic hunting operations. However, the target species of these hunting expeditions were walrus, beluga, polar bears, reindeers and birds' eggs and down in addition to seals of several species. Up to and including 1919, Norwegian catches were attributed to home port of the vessel rather than to sealing area and therefore catch numbers prior to 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 catches given for 1919 and earlier. Norwegian catches 1927-1939 are from (Sivertsen 1941), and 1946 to present from ICES (2005). There is no quantitative information on Russian catches prior to 1875, but Russian/Soviet catches 1875-1945 are from Table 2 in (Nazarenko 1984), which is supported by (Yakovenko 1963) although there are some minor differences between these two sources. Soviet catches 1946-1989 are from ICES (2005).

No quantitative information has been found on the age structure of the early harp seal catches prior to 1926, but it was apparently some proportion of young of the year in the catches according to (Iversen 1927). (Sivertsen 1941) gives numbers for the proportion of pups in the annual catches for 1926 and a mean number for 1928-1939 which has been used in the statistics compiled here for 1927 and 1937-1939, as 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 WW II 1940-1945, and postwar catches have been recorded in official statistics as pups or one year old and older animals, with the exception of the years 1946-1952 and 1955. For these years all catches have been assumed as of one year old or older.

Although (Nazarenko 1984) gives information on total Russian/Soviet catches, no information is given on age distributions. For the years 1927-1932 and 1936 proportion pups in the catches have 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. Proportion pups in the catches 1937-1945 has been taken from Table 8 (Soviet catches 1937-1958) in the Russian report on sealing in the Northeast Atlantic to the “Norwegian-Soviet Sealing Commission” 1978. Postwar distributions are from ICES (2005).

Incidental catches 1979-2000 is taken from Table 6 in ICES (2005). These catches have been assumed to be of one year or older animals 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).

Tables

	Year	Estimate	CV
Relative indices	1968	70,500	-
	1970	82,100	-
	1973	92,200	-
	1976	107,700	-
	1980	138,551	-
	1985	139,387	-
	1988	138,500	-
	1991	141,667	-
Absolute estimates	1998	286,260	0.073
	2000	325,643	0.111
	2000	339,710	0.095
	2002	330,000	0.103
	2003	327,000	0.125

Table 1 Census estimates of pup production. 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 are not known. The estimates for the period 1998-2005 are taken from ICES (2005).

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1980	0	0	0	0	1	6	14	27	28	39	39	38	28	9	25	27	26	25	21	20
1988	0	0	0	0	0	0	7	14	32	57	46	38	40	35	31	23	25	18	16	19

Table 2 Number of females by age (truncated at age 20) sampled on whelping grounds in 1980 and in 1988 (Potelov and Svetochev 1997).

K_t time varying	$b = 30$		$b = 50$	
	Yes	No	Yes	No
Model (4)	-211.31	-210.88	-232.17	-215.31
Model (5)	-323.07	-322.94	-338.14	-343.35 ^A
Model (6)	-320.13	-333.10	-319.70	-321.25

^ADoes not fit pup production data

Table 3 Likelihood values for all combinations of density regulation mechanism, mean age-of-menopause (b) and time varying K_t .

	Model (4)				Model (5)		Model (6)	
Variant	i	ii	iii	iv	i	ii	i	ii
K_t time varying	No	No	Yes	Yes ^A	No	Yes	No	Yes
b	30	50	30	30	30	30	30	30
^B K_{1875}	6.270	5.777	6.335	5.838	4.476	4.383	4.660	4.240
M	0.0111	0.0879	0.0236	0.060 ^F	0.0380	0.0613	0.010 ^L	0.0919
M_0	0.9396	0.2 ^L	0.8626	0.4432	0.6179	0.3422	1.588	0.8869
F	0.8207	0.9009	0.8511	0.7686	0.3068	0.3324	0.8306	0.8765
a	19.00 ^U	16.03	19.00 ^U	13.55	6.105	6.105	6.105	6.103
q	0.5808	0.5 ^L	0.538	0.5 ^L	0.6667	0.6414	0.5 ^L	0.5 ^L
τ	0.07816	0.1176	0.0853	0.1817	0.06862	0.06869	0.1538	0.03765
γ	0.6116	0.5484	0.5797	0.6067	1.135	1.121	3.0 ^U	2.426
c	1.000 ^F	1.000 ^F	1.000 ^U	0.6729	1.000 ^F	1.000 ^U	1.000 ^F	0.3214
$N_{1+,2005}$	2.638	2.284	2.349	2.39	2.154	2.33	2.377	1.373
Loglik	-210.9	-215.3	-211.3	-226.3	-322.9	-323.1	-333.1	-320.1

^A $M = 0.06$ fixed, ^B In millions, ^F Parameter held fixed during estimation, ^{L,U} Parameter hitting lower (L) or upper (U) bound in estimation procedure.

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

	Point estimate	95% interval	confidence
		Lower	Upper
${}^A K_{1875}$	6.27	5.65	6.89
M	0.011	0.000	0.024
M_0	0.94	0.807	1.072
F	0.821	0.678	0.963
q	0.581	0.472	0.69
τ	0.078	0.039	0.117
γ	0.612	0.542	0.682
${}^A N_{1+,2005}$	2.638	1.972	3.305

^A In millions

Table 5 Parameter estimates under the best fitting model (4) with $b = 30$ and constant carrying capacity. Confidence intervals are based on standard deviations calculated by AD Model Builder. The mean age-at-maturity a is omitted from the table as this parameter were hitting the upper bound $a = 19$ for the parameter space.

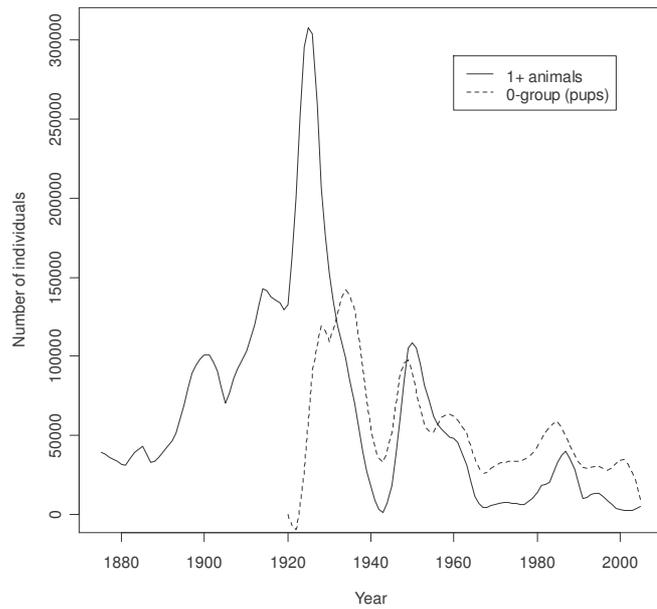


Figure 1 Number of harp seals caught per year by Norwegian and Russian sealers in the White Sea. The numbers have been smoothed using the function `loess` of the statistical software package R. During the period 1940-1945 the catches of pups and 1+ animals were reduced, due to the second world war.

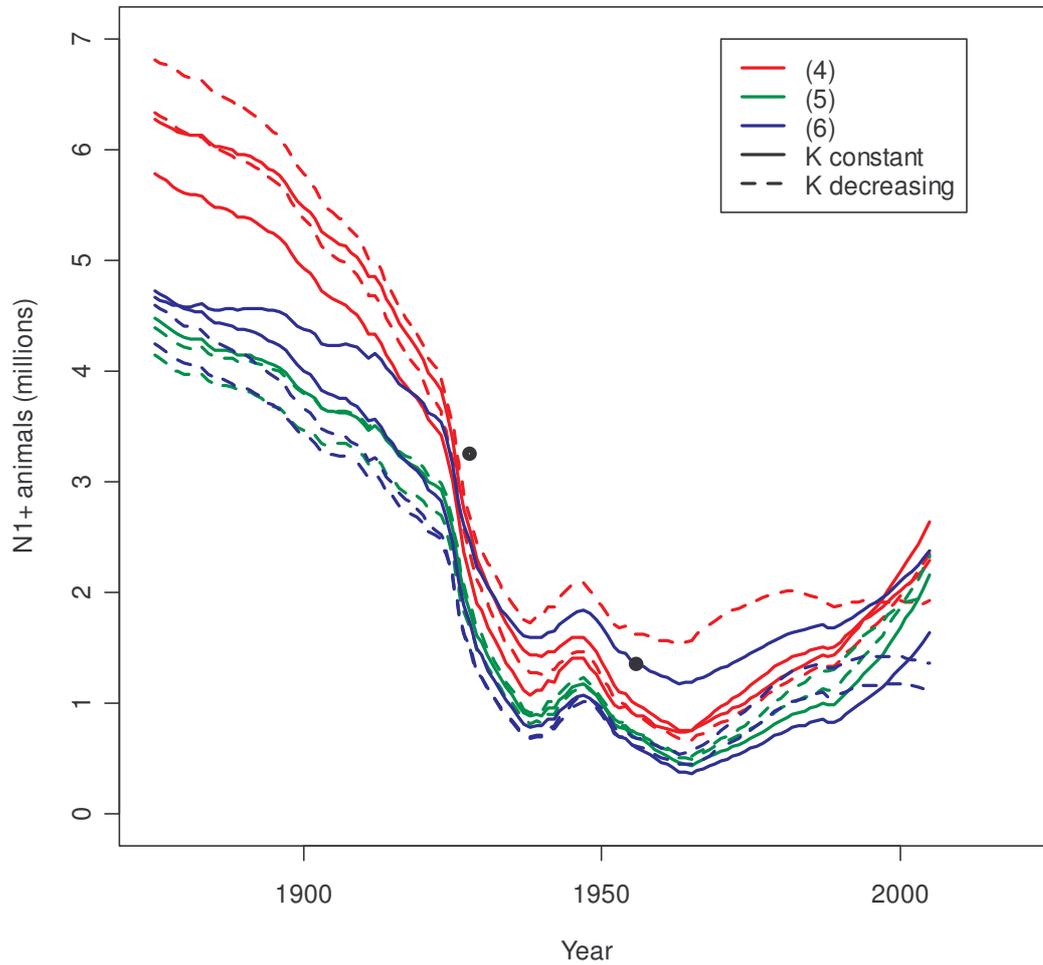


Figure 2 Estimated population trajectories under different model assumptions (equation (4)-(6)). Different density regulation mechanisms are shown in different colours. Dashed lines indicate fits in which a reduction in carrying capacity K has been allowed. There are two versions of each curve (except 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 filled dots

represent estimates of N_{1+} population size from Yakovenko (1961), that are used for model validation.

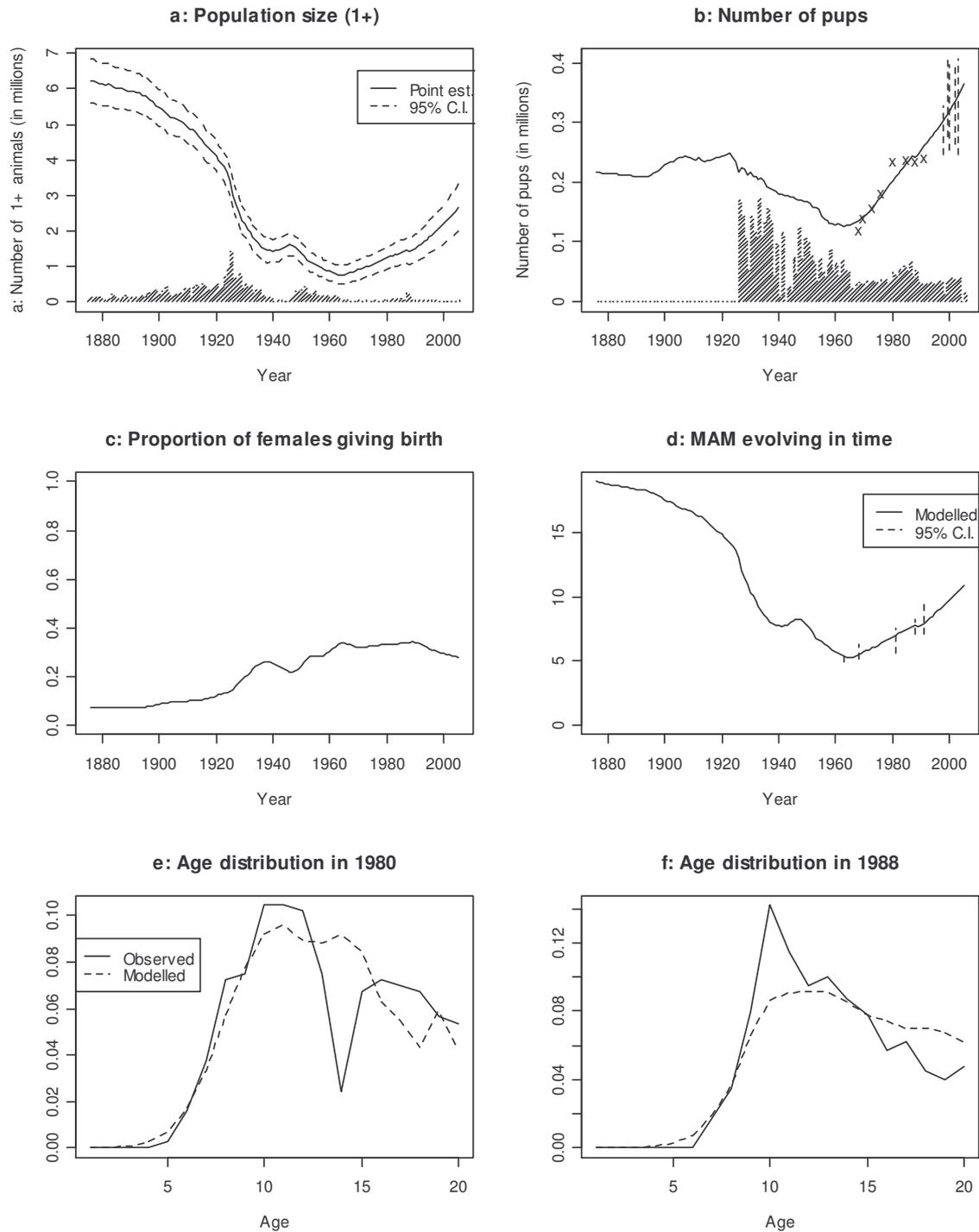


Figure 3 Estimated population trajectories under the assumption of density regulation mechanism (4), i.e. density regulation in mean age-at-maturity. Corresponding parameter estimates are given in Table 4, (4)-i. Notes on panels: a) scaled catches are shown on the bottom of the panel; b) 95% confidence intervals are shown as vertical dashed lines for absolute estimates, and pup production indices (crosses) are scaled by

q ; c) proportion P_t 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) proportion of females in different age classes among individuals sampled on whelping grounds in the years 1980 and 1988 (solid lines) together with the corresponding modelled proportions.

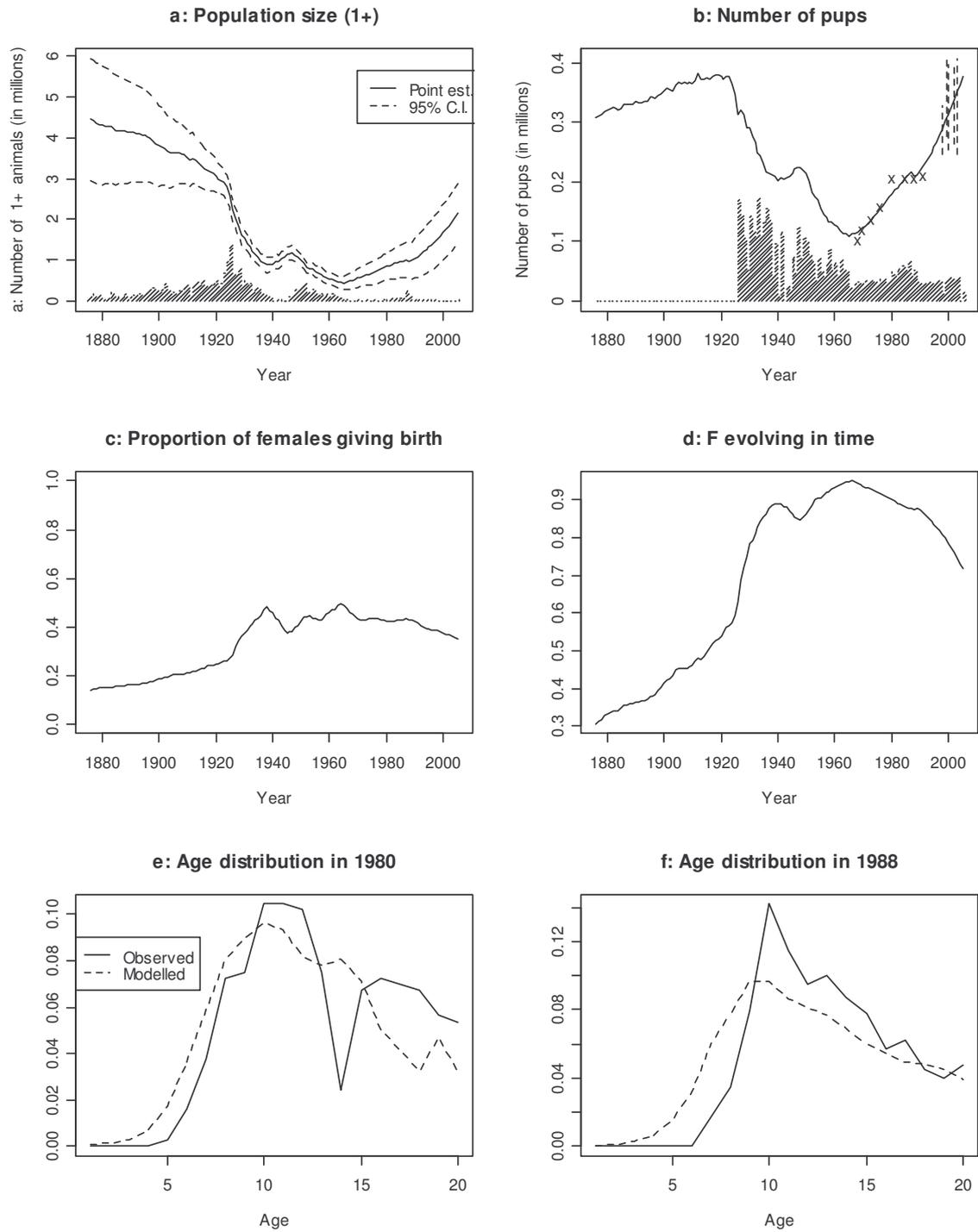


Figure 4 Estimated population trajectories under the assumption of density regulation mechanism (5), i.e. density regulation in birth rate F . Corresponding parameter estimates are given in Table 4, (5)-i. Notes on panels are similar to those of Figure 3, except for Panel d) which here shows the trajectory of the birth rate F_t .

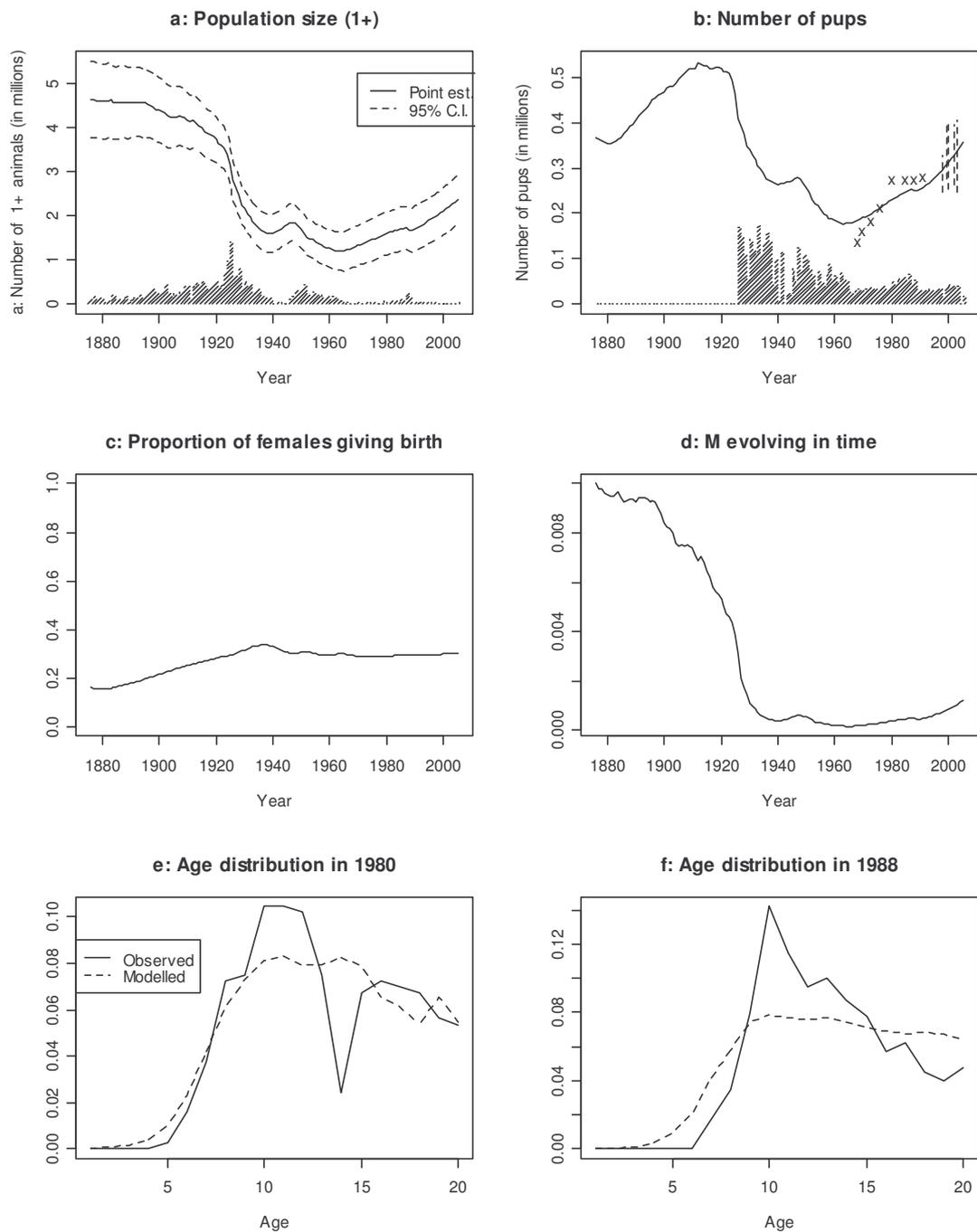


Figure 5 Estimated population trajectories under the assumption of density regulation mechanism (6), i.e. density regulation in mortality rate M_{1+} . Corresponding parameter

estimates are given in Table 4, (6)-*i*. Notes on panels are similar to those of Figure 3, except for Panel d) which here shows the trajectory for mortality rate M_{1+} .