

Status of Baltic grey seals: Population assessment and extinction risk

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ABSTRACT

The grey seal (*Halichoerus grypus*) population in the Baltic Sea is recovering after a century of bounty hunting and 3 decades of low fertility rates caused by environmental pollution. A conservative estimate of the population size in 2003 was 19,400 animals, and available data suggest an annual rate of increase of 7.5% since 1990. The growing population has led to increased interactions with the fishery, and demands are being raised for the re-introduction of the hunt. We provide a demographic analysis and a risk assessment of the population, and make recommendations on how to decrease the risk of overexploitation. Although hunting increases the risk of quasi-extinction, the risk can be significantly reduced by the choice of a cautious hunting regime. The least hazardous regimes allow no hunting below a ‘security level’ in population size. Obviously, to implement such a hunting regime detailed knowledge of the population size and growth rate is required. It is not possible to estimate “true” risks for quasi-extinction, but we used an approach where the relative difference for different scenarios can be compared. With a security level at 5,000 females, the population quasi-extinction risk increases 50 fold at an annual hunt of 500 females compared with a scenario with no hunting. The risk of quasi-extinction is very sensitive to declines in the mean growth rate and to increased variance in growth rate. The variance in the population estimates over the last 14 years imply that it would take 9 years to detect a decline from 1.075 to 1.027 in the rate of population increase. We also show how the age composition of killed animals influences the impact of the hunt. The overall recommendation is that hunting should be kept to a minimum, carefully documented and accompanied by close population monitoring.

Harding, K.C., Härkönen, T., Helander, B. and Karlsson, O. 2007. Status of Baltic grey seals: Population assessment and extinction risk. *NAMMCO Sci. Publ.* 6:33-56.

INTRODUCTION

We review historical and present population sizes of grey seals (*Halichoerus grypus*) (Fig. 1) in the Baltic, and present original survey data to estimate the rate of increase over the past decades. In many cases empirical data on life history parameters of Baltic grey seals are lacking, and we compile grey seal life history data from other populations, which are used both for investigating population dynamics in grey seals in general, and when applicable, to analyse the situation in the Baltic. The analyses encompass

age specific reproductive values, elasticity and sensitivity of the growth rate, maximum rate of increase in grey seals, and an ecological risk assessment. In the latter we investigate how different hunting strategies affect the long-term risk for declines to critical population sizes.

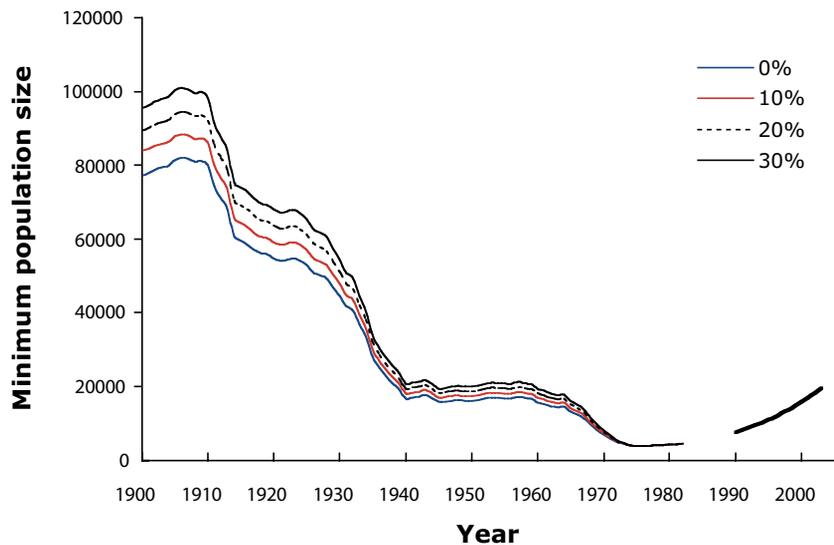
Historical numbers and trends

The Baltic grey seal population has a dramatic history. A hundred years ago the population likely exceeded 90,000 seals, but hunting pressure



Fig. 1. Grey seals often maintain breathing holes in the Baltic sea ice. (Photo: Olle Karlsson)

Fig. 2. Historical minimum population size of grey seals in the Baltic, estimated from hunting statistics (Harding and Härkönen 1999). An unknown number of killed seals were not registered (lean seals sank and wounded seals were not found) and the 4 different lines show how the population size estimate is affected by different proportions of unregistered mortality (0% to 30%). The population trend after 1990 was based on photo-id studies (Hiby *et al.* 2007), and on analyses of land based counts (*this study*).



caused a rapid decline to about 20,000 animals in the 1940s (Fig. 2). After hunting had ceased, the population did not increase as expected. Instead, a further decline to about 3,000 animals persisted up to the mid 1970s (Harding and Härkönen 1999). Environmental pollution by organochlorines was found to be a likely explanation for this decline in seal numbers (Jensen *et*

al. 1969, Jensen *et al.* 1977, Olsson *et al.* 1975, Helle 1980a, Harding and Härkönen 1999). A sample of 225 adult Baltic ringed seal females revealed alarmingly low pregnancy rates of only 30%, which dropped further to 20% during the period 1973-1979 (Helle 1980b). In female grey seals, severe reproductive disturbances were also documented (Bergman and Olsson

1986, Bergman 1999). Experimental studies on harbour seals, *Phoca vitulina* (Reijnders 1986), and mink, *Mustela vison* (Bäcklin 1996) confirmed that the high levels of PCBs in fish from the Baltic Sea cause reproductive failure. Consequently, the rapid drop from about 90,000 grey seals at the beginning of the 20th century to about 20,000 was the result of intensive hunting, whereas the population crash in the 1960s and 1970s was a consequence of ecotoxins.

Recent population size estimates

During the last 2 decades, decreasing levels of PCBs (Olsson *et al.* 2000) in the prey of seals has led to improved health conditions and reproductive capacity of the Baltic grey seal (Bergman 1999), followed by an increase in population size. The population growth rate has been monitored by annual counts since the mid 1970s in Sweden. However, systematic counts during the moult in late May-early June were first initiated in the late 1980s in Sweden, Estonia, Russia and Finland, thereby covering the entire present distribution range of grey seal in the Baltic. However since counting methods, efforts and efficiency have varied within and among nations over the study period, the survey data must be treated with great caution.

Actually counted numbers of grey seals in the entire Baltic amounted to 15,950 in 2003, which included possible double-counts of probably a few hundred seals. This because maximum counts from different localities often stem from different days during the 14-day-long survey

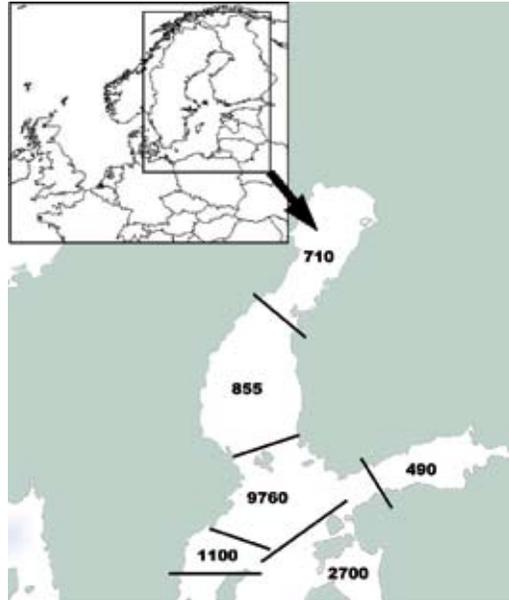


Fig. 3. The spatial distribution of 15,950 grey seals during moult in May-June in the Baltic Sea in 1996. Data are from 2003 and typical for years with a mild winter and limited ice formation. The numbers represent maximum numbers from many smaller localities accumulated over several weeks, therefore these figures are likely to represent a large proportion of the true population.

period (Halkka *et al.* 2005). Since grey seals are highly mobile (Sjöberg 1999), summing of maximum counts from all sites over a time period involves a risk that the same seals may have contributed to the maximum counts at several sites. The proportion of the population represented by counted numbers is not known, but can be close to 80% (see further in the discussion).

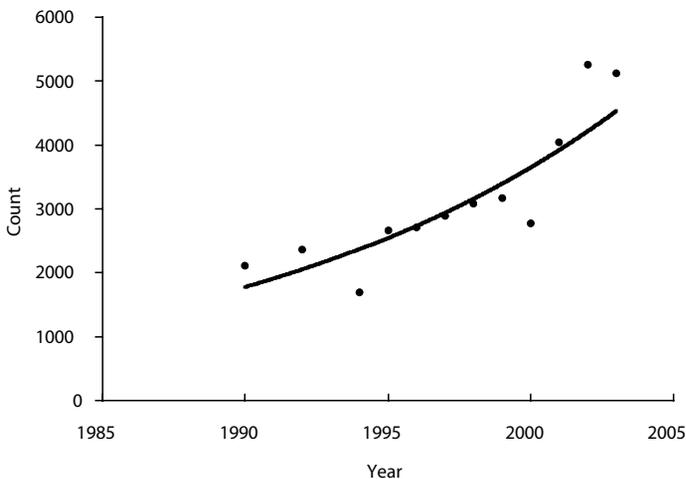


Fig. 4. A time series of maximum counts of Baltic grey seals along the Swedish coast. Exponential rate of increase, $r = 0.072$ ($\lambda = 1.0747$), 95% CL: 0.043 to 0.102, determination coefficient: 0.75, $F = 29.9$, $d.f = 11$, $P = 0.0003$.

An independent estimate of population size is based on photo identification data (Hiby *et al.* 2007). Mark-recapture statistics were applied to photo-id data producing a point estimate for the summer of 2000 at 15,631 seals, with 95% confidence limits of 9,592-19,005. Applying a mean annual per capita rate of increase (λ) of 1.075 to the mark-recapture point estimate gives an estimated total of about 19,400 Baltic grey seal in 2003.

Spatial distribution

The distribution of grey seal haul-outs and the number of counted animals in different regions of the Baltic Sea during a 2-week period in May-June, 2003, is shown in Fig. 3. The situation in 2003 is typical for ice-free spring conditions, when grey seals are predominantly found in the central parts of the Baltic. Approximately 85% of the seals are counted between latitudes 58° N-61° N.

Animals tagged with satellite transmitters show that grey seals can exhibit long-range movements encompassing a major proportion of the Baltic (Sjöberg 1999, Teilmann *et al.* 2004). Some grey seals also seem to have seasonal migrations within the Baltic, a pattern suggested by a female tagged at Rødsand in Denmark,

which moved to Estonia to give birth to her pup (Teilmann *et al.* 2004). However, a contrasting behaviour is suggested by some individual grey seals in Estonia, where females with recognisable marks were very stationary (Jüssi 1999).

Population growth rate since 1990

Available data from all Baltic haul-outs are not adequate for trend analysis, since survey efficiency and effort have varied in some regions. The population growth rate presented here is based on data from the Swedish coastline over the period 1990-2003 (Fig. 4). Here, survey methods remained constant and the counts can be treated as a 'sub-sample' permitting analyses of trends in population growth rate. Data were collected during the peak moulting season (within a 2-week period in late May to early June), and the maximum numbers of seals at each locality were summed. A regression analysis reveals that the mean annual rate of increase along the Swedish Baltic coast was 7.5% ($\lambda = 1.0747$, $r = 0.072$), with 95% confidence limits of 1.044 to 1.107 (Fig. 4).

We also obtained maximum likelihood estimates of the mean growth rate and its variance (σ^2) according to the method of Dennis *et al.*

Table 1. Basic data on maximum counts (N) of grey seals along the Swedish Baltic coast during a 13 year period. For the estimate of the minimum coefficient of variance (CV), the actual counts in the second column are scaled to zero growth rate in the fourth column by multiplication with the third column. The third column is based on the estimated mean growth rate in the population ($\lambda = 1.0747$, Fig. 2)

Year	N	Scaling	Index
1990	2,108	1.0000	2,108
1992	2,360	0.8658	2,043
1994	1,693	0.7496	1,269
1995	2,663	0.6975	1,858
1996	2,713	0.6490	1,761
1997	2,894	0.6039	1,748
1998	3,083	0.5620	1,733
1999	3,171	0.5229	1,658
2000	2,777	0.4866	1,351
2001	4,043	0.4527	1,830
2002	5,257	0.4213	2,215
2003	5,120	0.3920	2,007
Mean			1,770
SD			283.7
CV			16.03

(1991). This procedure gave estimates of the mean growth rate, $\lambda = 1,072$ (equivalent to $r = 0.069$), $\sigma^2 = 0.040$. Since sampling errors in the time series create autocorrelations, which do not represent true variation in population growth rate (McNamara and Harding 2004), the covariance (-0.007) was subtracted from the total variance, giving a resulting variance of 0.033. The maximum likelihood estimates of growth rates and variance will be used in the risk analysis.

Time to detection of a change in the trend

We used an analysis for the detection of trends according to Gerrodette (1987), and Taylor and Gerrodette (1993):

$$r^2 n^3 \geq 156 CV^2 \quad (\text{eqn. 1})$$

where r is the intrinsic rate of increase, n the number of observations (years) and CV is the coefficient of variation of annual counts. This formula is constructed for the special case where the type 1 (α) and type 2 (β) errors are equal at 0.05. The main obstacle to performing this analysis is that CVs of annual counts are lacking for Baltic grey seals. The time series (Fig. 4) is based on maximum counts, i.e. the single highest recorded counts in each area, which makes it unclear how to proceed with the analysis. However, one straight-forward approach is to estimate the CV by scaling the time series data to zero growth rate, which would give index values of annual counts (Table 1). The CV of means (16.2) of such index values would give a reasonable approximation of the variation around the mean under the condition that annual vari-

ations in the true growth rate of the population are much smaller as compared to variations of counts. We believe this to be a valid assumption.

We estimated the CV from grey seal survey data (Fig. 2, Table 1), and calculated the full span of combinations of r and n . We reduced the power analysis to the specific cases where the power of detection ($=1-\beta$) is set at more or equal to 0.95. As shown by Gerrodette (1987), the CVs of total counts are not affected by total abundance, and thus the CV is expected to be constant in this type of time series.

Using the equation 1, the numbers of observations (years) required for the detection of a 5% change in the annual rate of increase can be calculated for any rate of increase (Fig. 5). For the observed rate of increase in Baltic grey seals at 0.072 ($\lambda = 1.0747$) it is found that it will take about 9 years to detect a 5% change at $r = 0.072$ (e.g. to $r = 0.022$). At the upper confidence limit for the rate of increase $r = 0.107$ ($\lambda = 1.113$) it would take about 7 years, and at the lower confidence limit $r = 0.043$ ($\lambda = 1.044$), about 13 years to detect a change of 0.05 in the annual rate of increase.

REVIEW OF GREY SEAL LIFE HISTORY DATA

Age at first reproduction

Estimates of age at first reproduction are lacking from the Baltic population, and therefore data from other grey seal populations in the Atlantic was reviewed to study the likely variation in this parameter. Reproductive data from Norwegian grey seal females ($n = 166$) were col-

Table 2. Ages at first birth (AFB) in North West Atlantic (NWA), British (UK), and Norwegian (NO) grey seals, as based on data on actual birth rates, presence of fetuses, and Corpora Lutea (CL) or Corpora Albicantia (CA). Note that estimates based on corpora are strongly biased downwards.

	4+	5+	6+	7+	8+	9+	AFB CL1/ CA2	AFB Fetus/ pup	Reference
NWA	0.18	0.68	0.02	0.12			4.6±0.10	5.5 SD±0.12	Hammill & Gosselin (1995)
NWA	0.16	0.55	0.18	0.11					Mansfield & Beck (1977)
NWA	0.28	0.41	0.18	0.06	0.05	0.02		5.2 SE±0.06	Schwartz & Stobo (2000)
UK								5.5	Boyd (1985)
NO*		0.40	0.48	0.12			5.35	>5.7	Wiig (1991)
Mean	0.12	0.44	0.26	0.16	0.01	0.004		5.5	

Table 3. Data on grey seal fertility rates, based on data from Norwegian breeding grey seal females (Wiig 1991). All sampled females had a pup at the time of collection (second column). Reproductive performance the year before (x-1) was estimated from scars (Corpora Albicantia) of the lutenizing ovarian follicles (Corpora Lutea). The proportion of females with CAs originating from CLs formed at time x-1 is given in the third column. Mean values of fertility rates for year x, and year x-1 are shown in fourth column.

Age	Pup year x	Pup year x-1	Mean	n
6-10	1	0.80	0.9	44
11-15	1	0.93	0.965	30
16-20	1	0.74	0.87	23
21-	1	0.73	0.865	15
Mean			0.907*	112

* Mean value weighted with relative sizes of age classes.

lected from animals culled at breeding grounds (Wiig 1991). All sexually mature females in the sample also had a pup. Mean age at first birth (AFB) of females was 5.35 years (Wiig 1991), and we calculated 95% CI to ± 0.69 years according to the method of DeMaster (1981). Since this sample is from a breeding ground, it is most likely biased towards early maturing animals (Harding and Härkönen 1995).

In the Northwest Atlantic a cross-sectional study showed that mean AFB of grey seals was 5.5 ± 0.12 (n = 526), as estimated from females with foetuses (Hammill and Gosselin 1995, Table 2). This study also showed that AFB varied among years, between 5.03 ± 0.22 and 6.08 ± 0.32 within the period 1968-1992. A study based on re-observations of branded animals was carried out in the same area (Schwartz and Stobo 2000). Here, the mean AFB for 3 cohorts was 5.2 years (SE = ± 0.06 , range 4.9-5.5), but these estimates could be biased downwards since

the study had to be terminated before all maturing age classes could be taken into account.

Boyd (1985) reported that 50% of females along the British coast became pregnant for the first time during their fourth year of life, (and thus 50% of them will bear their pup at their fifth birthday). The remaining 50% of the females became pregnant during their fifth year. Consequently, the mean age at first birth is about 5.5 years also in this study. Thus, 4 independent studies estimated mean age at first birth to about 5.5 years in Atlantic grey seals.

Age specific reproductive rates

One estimate of fertility rates of sexually mature females can be calculated from the Norwegian study mentioned above (Wiig 1991). In that sample all mature females also were pregnant, and since the sample is from a breeding ground, it is likely that females skipping reproduction spent time elsewhere

Table 4. Age specific birth rates for Northwest Atlantic (NWA), British (UK), Norwegian (NO), and Baltic (BA) grey seals.

	Age							Reference
	3+	4+	5+	6+	7+	8+	>9+	
NWA	0	0.18	0.86	0.88	0.88	0.88	0.88	Hammill & Gosselin (1995)
NWA	-	-	-	0.85	0.85	0.85	0.85	Mansfield & Beck (1977)
UK	0	0	0.17	0.60	0.90	0.90	0.90	Harwood & Prime (1978)
UK*	0.05	0.15	0.56	0.92	0.93	0.71	0.92	Boyd (1985)
UK**	-	-	-	0.80	0.81	0.80	0.81	Pomeroy <i>et al.</i> (1999)
NO*	0	0	0.40	0.91	0.91	0.91	0.91	Wiig (1991), Table 3
BA	-	-	0.75	0.75	0.75	0.75	0.75	Bergman (1999, pers. comm.)

*Data from referred studies re-scaled to age at pupping from pregnancy rates earlier in the season.

**Minimum values.

Table 5. Age specific survival rates for female grey seals in northwest Atlantic (NWA), British (UK), Norwegian (NO), and Baltic (BA) grey seals.

	Age							Reference
	0-1	1-2	2-3	3-4	4-5	5-6	>7	
NWA						0.87	0.87	Mansfield & Beck (1977)
NWA	<0.831	<0.83	<0.830	<0.830	0.9	0.9	0.9	Schwartz & Stobo (2000)
NWA			0.864	0.864				Hammill & Gosselin (1995)
UK	0.493	0.493	0.493	0.493	0.935	0.935	0.935	Harwood & Prime (1978)
UK	0.620							Hall <i>et al.</i> (2001)
UK	0.832							Pomeroy <i>et al.</i> (1999)
UK	0.902							Pomeroy <i>et al.</i> (2000)
UK	0.902							Baker & Baker (1988)
UK	0.652							Summers <i>et al.</i> (1975)
NO						<0.96	<0.96	Wiig (1991)
NO								Bjorge <i>et al.</i> <i>subm.</i>
BA	0.702							Helander & Härkönen (1999)
BA	0.762							Jussi <i>et al.</i> <i>subm.</i>

¹Mean value for the juvenile segment (0-4), not including mortality from birth to tagging.

²Survival rate from birth to weaning at land breeding sites.

³Not based on empirical data.

⁴Calculated from Hammill & Gosselin (1995)

and were under represented. However, Wiig (1991) also recorded morphological signs of earlier pregnancies in his sample (Table 3).

The presence of a large Corpora Albicantia (CA) in the ovary opposite to the active ovary in the present year indicates that the female was pregnant during the previous year. The absence of a CA indicates that she skipped the previous breeding opportunity. We calculated the fertility rates as the mean value of the fertility rates of females at the year of sampling and of the previous year (Table 3). The mean fertility rate for all females of ages 6 and older was 0.91. However, females skipping reproduction for more than 1 season would further lower this estimate.

In a sample of 526 female grey seals from the northwest Atlantic, pregnancy rates were estimated from the presence/absence of a fetus (Hammill and Gosselin 1995, Table 4). Estimated age specific birth rates increased steeply from the age of 4 to the age of 6 (Hammill and Gosselin 1995). As shown in Table 4, all studies of the Atlantic population indicate that pregnancy rates are relatively stable at about 0.9 after the age of 6. Pregnancy rates in the Baltic grey seals have been drastically reduced since the 1970s as a consequence of PCB pollution

(Bergman 1999). Although increasing, pregnancy rates of mature females in some samples were still only 60% in the mid 1990s, whereas the situation has improved further in recent years (Bergman 1999, Bergman pers. comm.).

Adult survival rates

In 2 samples of British grey seals (n1 = 554, n2 = 482), adult (all age classes >4) survival rate was estimated at 0.935 (Harwood and Prime 1978), while a Norwegian study suggested 0.96 in adult (8+) females (Wiig 1991) (Table 5). The latter estimate was suggested to be biased upwards, which in part could be due to the small sample size (n = 166) (Wiig 1991). A longitudinal mark-recapture study in Canada provided estimates for 3 cohorts, where the yearly survival rates for ages 4-9 ranged between 0.88 and 0.92 (Schwartz and Stobo 2000). Adult survival rates of many seals are found to vary in the range 0.87 – 0.96 (Smith 1987, Härkönen and Heide-Jørgensen 1990, Olesiuk *et al.* 1990, Testa *et al.* 1991, Reijnders *et al.* 1993, Wickens and York 1997).

There are no survival data from the Baltic, but the oldest females become up to 40 years of age or more (Bergman 1999), which is similar to grey seals in other parts of the distribution range of the species (Harwood and Prime 1978, Wiig

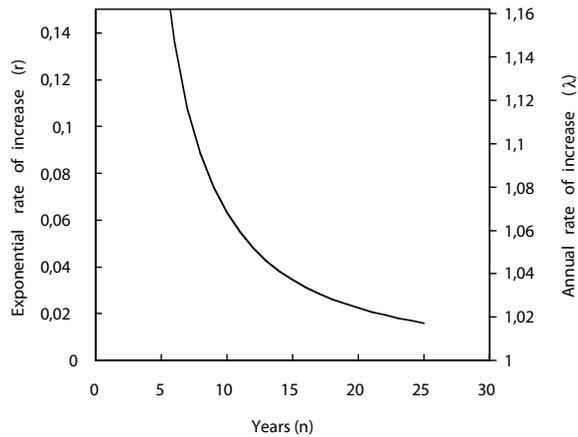


Fig. 5. The time to detect a 0.05 decline in the population growth rate depends on the mean population growth rate. It would take 25 years to detect a 5% change if the mean rate of increase was 0.02. At the observed rate of increase of the Baltic grey seals (Fig. 2) it will take about 9 years to detect a change in trends from 0.075 to 0.025.

1991, Hammill and Gosselin 1995). Thus, with the assumption of constant survival rates within the adult female segment (Charnov 1986), survival rates similar to those of Atlantic populations are suggested in the Baltic. However, reported disease complexes connected to immune system deficiencies might imply decreased adult survival in the Baltic (Bergman 1999).

Juvenile survival rates

Grey seal juvenile survival rates are variable, and estimates of survival from birth to weaning vary from 65% to 90% (Table 5). In the Baltic, pup survival rates up to weaning also vary from 70% at land breeding sites (Helander and Härkönen 1999, Jussi *et al.* *subm.*) to 98% in ice breeding areas (Jussi *et al.* *subm.*). In the UK, Hall *et al.* (2001) reported first-year survival rates at 0.62 for female pups, which is the only available estimate for grey seal females during their first year of life. In Canada, mean survival rates at 0.83 were estimated for juveniles (ages up to 4), but this estimate did not include the mortality from birth to branding of the study animals (Schwartz and Stobo 2000). In the following we will investigate the effects on model outcome of a range of juvenile survival rates.

Carrying capacity

The Baltic grey seal population exceeded 88,000 animals in the beginning of the 20th century (Harding and Härkönen 1999). This suggests that the present population is far from the carrying capacity and we expect density dependent effects to be negligible during the nearest decades. Consequently, the present study will focus on the phase of exponential growth. If the population size increases up to a level where density dependent effects are suspected, a new evaluation must be performed since density dependence dramatically increases the risk of quasi-extinction (Middleton *et al.* 1995).

Breeding system

Grey seals form small harems (*e.g.* Pomeroy *et al.* 2000), but genetic data have revealed that pups frequently do not have the harem master as their father, and matings are believed to also occur in the water (Worthington *et al.* 2000). This system should ensure that most receptive females are fertilized, and we assume that the population is not affected by lack of males in the span of population sizes that we investigate.

ANALYSIS OF LIFE HISTORY DATA

Life history features of grey seals

The data on fertility rates from Atlantic grey seal populations in Norway, Great Britain and along the Canadian coast are very similar. The estimated mean age at first pup is 5.5 years and the pregnancy rate of adult females is about 90%. We know that the fertility rate of Baltic grey seals is impaired, and estimates of pregnancy rates of adult females vary around 75% in adult females (Bergman 1999, *pers. comm.*). Interestingly, the British and the Baltic populations have the same observed population growth rates, at about 1.075 per year (Hiby *et al.* 1996, Fig. 4). Thus, to reach the same population growth rate, the low fertility rate of the Baltic Sea females must be counter-balanced by either higher adult survival or higher sub-adult survival.

There are limited data on survival rates of adult grey seals (Table 5). We will use the estimate by

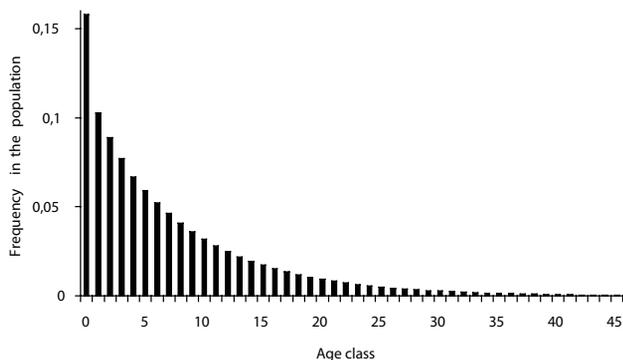


Fig. 6. The stable age distribution of Baltic grey seals at the growth rate $\lambda = 1.075$.

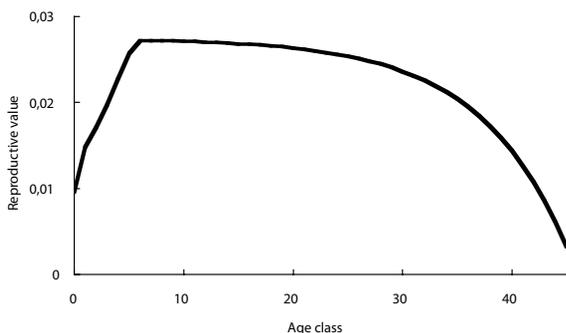


Fig. 7. Reproductive value of different age classes of Baltic grey seals at $\lambda = 1.075$

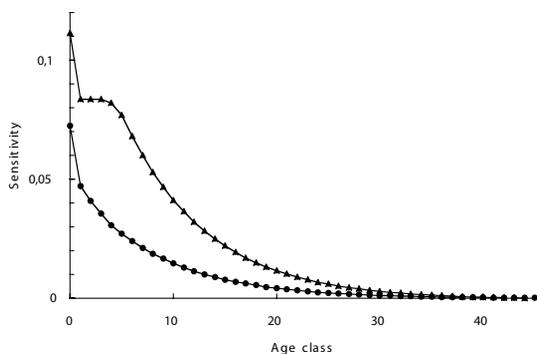


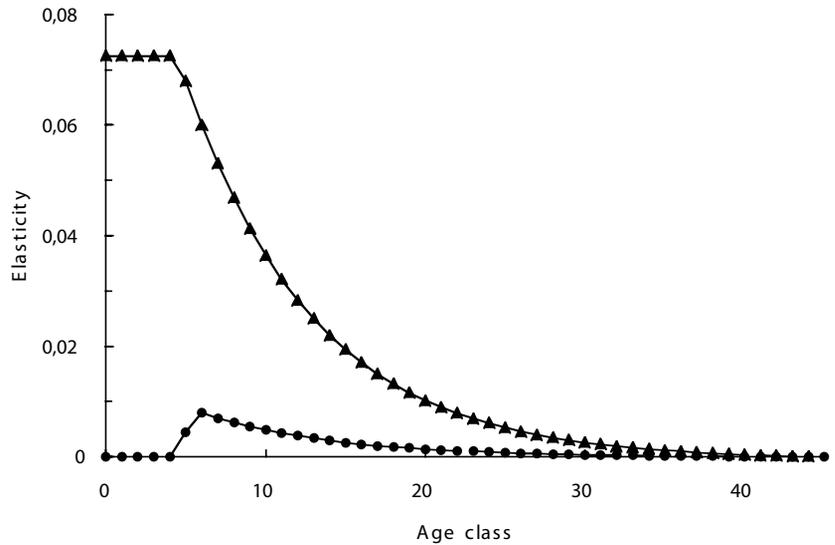
Fig. 8. Sensitivity of lambda to changes in fertility and survival of Baltic grey seals. Triangles indicate survival values, black circles fertility.

Harwood and Prime (1978) at 0.935, since it is based on a large sample size ($n = 1036$), and it is also close to the other available estimate for European grey seals (Wiig 1991). We have no indications that adult survival should be higher in the Baltic Sea. On the contrary, the disease complex associated with a disrupted immune system would suggest that adult seals could have increased mortality rates. However, new data indicate that initial juvenile survival rates can be higher in the Baltic Sea, as compared to

Atlantic populations, as during normal winters when pupping occurs on ice (Jussi *et al.* in prep).

Therefore, we find the alternative with higher juvenile survival as a more interesting hypothesis that could explain the similar growth rate in the Baltic Sea and in the Atlantic grey seal populations, despite the lowered fertility in the Baltic population.

Fig. 9. Elasticities of lambda to changes in survival and fecundity of each age class in an age structured model. It is evident that changes in survival (triangles) have the largest effect on λ , especially during the first 10 years. After age 5 or so the elasticities of lambda to changes in survival decrease monotonically. The importance of fertility values (circles) is much smaller and peaks at about 6 years whereafter it decreases gradually.



Parameterization of the life history matrix

We shall perform several analyses, using both a full age-structured model and an un-structured population model. In analysing the age-structured data we use a projection matrix constructed according to Leslie (1948):

$$A = \begin{pmatrix} F_1 & F_2 & \dots & F_{45} & F_{46} \\ P_1 & 0 & \dots & 0 & 0 \\ 0 & P_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & P_{45} & 0 \end{pmatrix} \quad (\text{eqn. 2})$$

A model for a ‘post breeding’ population was adopted (Caswell 1989). The elements in the first row of the matrix (F_i) are the fertility rates of age class i multiplied by the survival rate for age class i and the elements in the subdiagonal (P_i) are the age-specific survival rates. P_1 includes the mortality of pups of the year. Fertility rate (F_i) is defined as the number of females born in 1 time interval per female of age i . Survival rate (P_i) is defined as the probability that a female in age class x_i survived to enter age class x_{i+1} .

The young females do not reproduce and thus, F_1 to $F_5 = 0$. In the youngest maturing age class (5 years old) the fertility (F_6) is half that of the adult females. (*n.b.* matrix column 6 corresponds to age 5). Fertility of adult females is given by

the birth rate divided by 2 (counting female pups only) multiplied with female survival. The lower fertility rates in the Baltic (compared to Atlantic populations) must be counter balanced by higher survival rates in order to maintain the same population growth rate at about 7.5% annually. There are many possible combinations that can produce the observed growth rate. Based on the available information we selected this combination for the fertility values in the Baltic scenario: F_1 to $F_5 = 0$, $F_6 = 0.375/2 * P_6$, F_7 to $F_{46} = 0.75/2 * P_{7-46}$ and for survival values: $P_1 = 0.70$, P_2 to $P_4 = 0.932$, P_5 to $P_{45} = 0.95$. Sub-adult survival (P_2 to P_4) was adjusted to produce the observed population growth rate of 1.075

Sensitivity and reproductive values

A number of important population level characteristics can be described when parameterizing a projection matrix (eqn. 2) with relevant life history data (Caswell 2001). The dominant eigenvalue of a matrix is equivalent to the long-term population growth rate (λ), and the corresponding right eigenvector (w) gives the stable age distribution (Fig. 6). The reproductive values of age classes are given by the corresponding left eigenvector (v) (Fig. 7).

The reproductive values of population segments of Baltic grey seals depend on age. In the Baltic Sea, an individual female aged 5 to 10 years is about 3 times more important for future population growth than an individual female

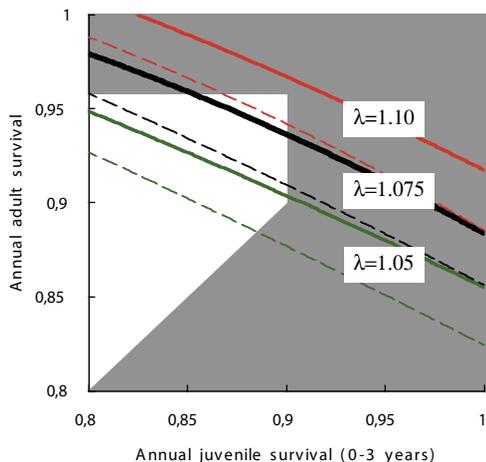


Fig. 10. Biological constraints delimit the maximum possible rate of increase in populations of grey seals. The shaded areas denote unlikely combinations of adult and juvenile survival rates. Any given point along the 6 lines shows a combination of adult survival and juvenile survival that produces a given growth rate (λ). The 2 uppermost lines are for $\lambda = 1.10$, the 2 lines in the middle for $\lambda = 1.075$ (as for the Baltic grey seals), and the lowest 2 lines show combinations that result in $\lambda = 1.05$. The stippled lines show combinations of adult and juvenile survival rates given that the mean annual pupping rate is 0.95. The bold full lines show the possible combinations given that the pupping rate is 0.75 (as suspected in the Baltic case).

pup (Fig. 7). The sensitivity of the rate of increase to changes in vital rates was estimated with a ‘sensitivity analysis’ (Caswell 1989). This gives a measure of how perturbations of parameter values of each matrix entry would influence the population growth rate (Fig. 8).

Elasticity analysis

In order to compare the importance of different vital rates it is easier to look at the *relative*, instead of the *actual*, effects on population growth rate from perturbations of different matrix en-

tries. Elasticity is a quantity that expresses the proportional contribution of a proportional perturbation of each matrix element to the long-term growth rate of a population (Caswell 2002). Elasticity is calculated as the scaled sensitivity (the scaling factor is: the parameter value of the matrix entry (a_{ij}) divided by λ).

$$e_{ij} = a_{ij}v_iw_j / \lambda \quad (\text{eqn. 3})$$

(Assuming the 2 eigenvectors v and w are scaled to sum 1.)

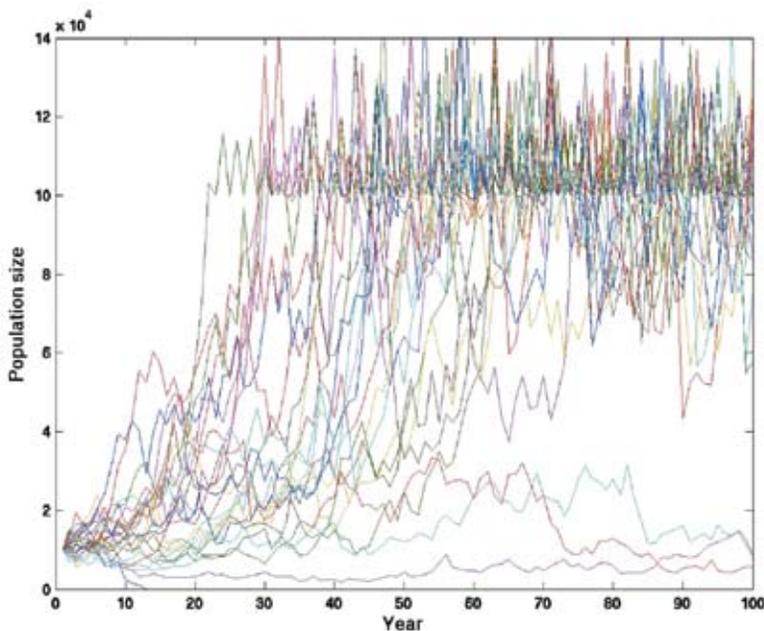


Fig. 11. Example of projection of a stochastic population model for the Baltic grey seal with 25 replications. The time frame here is 100 years, and the population is exposed to an annual hunt of 200 females. The initial female population size is 10,000, the annual rate of increase $\mu = 0.075$ and the variance (σ^2) is 0.033, the carrying capacity is 100,000 females. In the following analysis we projected the population development for 200 years with 10,000 replicates in order to estimate quasi-extinction probability (the risk for declines down to 1,000) for each given scenario.

Fig. 12a. The risk of quasi-extinction (y-axis) increases exponentially as annual hunt (x-axis) increases. The risk of quasi-extinction of the population when it is not exposed to any hunting is 0.0002. The introduction of hunt increases the risk of quasi-extinction above 10% at hunt of about 500 individuals. Here the 'security levels' (below which all hunting is stopped) 3,000. N_0 is 10,000 females. Growth rate is 1.075. Variance 0.033.

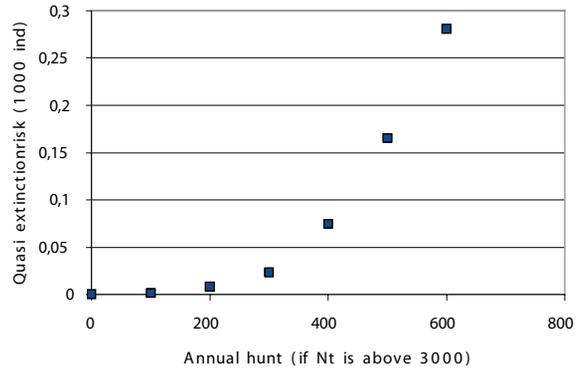


Fig. 12b. Quasi-extinction risk for different levels of annual hunt. Here the hunting is stopped if the population decreases below 5,000 animals. The quasi-extinction risk exceeds 10% at an annual hunt of 1,000 individuals. All other parameter values as in Fig. 12a.

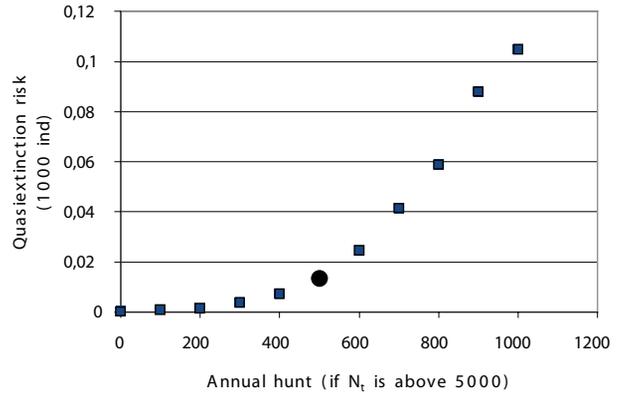


Fig. 12c. Small variations in estimated population growth rate can be very harmful. Here the security level is 5,000 females and the annual hunt fixed at 500 females. The circle indicates the growth rate 1.075 that was used in simulations in Figs 12a and b.

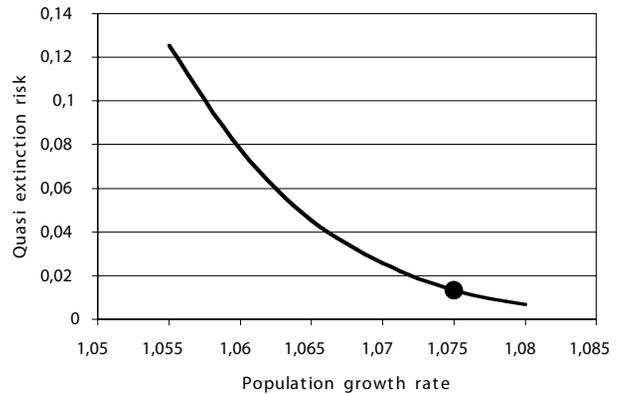
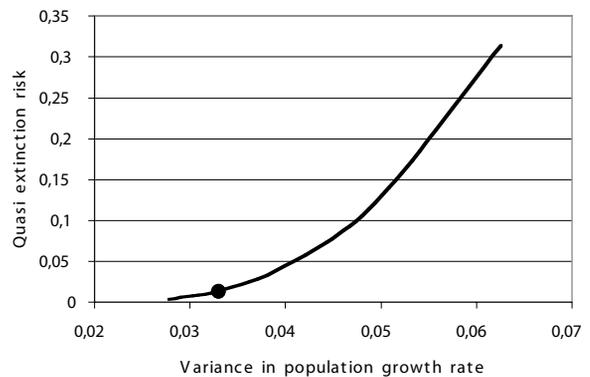


Fig. 12d. Slight changes in the variance of the mean growth rate leads to large increases in quasi-extinction risk. Here the security level is kept at 5,000 females and the annual hunt is 500. The black dot refers to the variance 0.033, as found for the Baltic grey seal and is a reference point also indicated in Figs 12b, c and e.



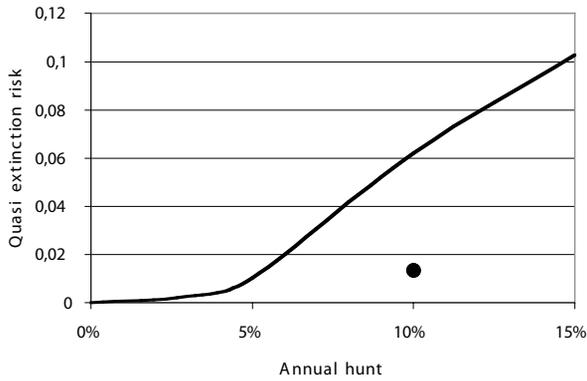


Fig. 12e. Extinction risk increases when the annual hunt increases. Here the hunt is a proportion of the population size instead of a fixed number (full line). The black dot indicates the extinction risk when 500 female seals are killed every year. The dot is a reference point that can be found in Figs 12 b-e.

$$E = S \circ I / \lambda \quad (\text{eqn. 4})$$

S is the matrix with sensitivity values. The Hadamard product (denoted ‘o’) is simply element wise multiplication.

The elasticity analysis illustrates the relative importance for long term growth rate of single fertility and survival rates for the full age structured model (Fig. 9). It is found that changes in fertility rates are relatively less important than changes in survival rates in all age classes. After sexual maturity, the population growth rate is more sensitive to a decrease in survival of younger females than in older females (Fig. 9).

Long term maximum growth rates

The maximum rate of population growth is limited by several factors in grey seals. Females have at most 1 pup a year, and first parturition occurs at about 5.5 years of age (Table 2). It is also evident that not all adult females bear a pup each year (Table 4), especially not young females (Pomeroy *et al.* 1999). An additional limitation for the population growth rate is given by the survival of adults. In most seal species the highest measures of adult survival are about 0.95-0.96, and for grey seals the best estimate available is 0.935 (Harwood and Prime 1978). An additional constraint is the observation that pup and subadult survival is always found to be lower and more variable compared to adult survival in all studied species of seals (Table 5, Boulva and McLaren 1979, Boyd *et al.* 1995, Härkönen *et al.* 2002.). These biological constraints impose an upper ceiling of possible rates of long-term population growth for any seal spe-

cies, which can be found by manipulations of the life history matrix (eqn. 2). In Fig. 10 we illustrate how fertility and mortality rates known for grey seals can combine to produce different long-term population growth rates. It is found that growth rates exceeding 10% ($\lambda = 1.10$) per year are unlikely in healthy grey seal populations (top full line in Fig. 10). In the specific case of the Baltic grey seals, the documented lower fertility rate makes long term population growth rates above 10% even less likely (dotted red line in Fig. 10). Reported values above 10% should be treated sceptically since they imply unrealistic fecundity and longevity rates. Such high growth rates can only occur temporarily, and can be caused by *e.g.* transient age structure effects (Härkönen *et al.* 1999, Caswell 2000), but are also to be expected in populations influenced by considerable immigration.

RISK ANALYSIS

Risk assessment is a tool used to investigate the vulnerability of populations to different future scenarios (Dennis *et al.* 1991, Burgman *et al.* 1993). The probability that the population declines to a lower threshold is estimated by projecting the population size forward in time, taking the stochastic nature of population growth into account.

$$N_{t+1} = (N_t * (\lambda \pm \alpha)) \quad (\text{eqn. 5})$$

where N_{t+1} is the projected female population size at year $t+1$, and λ is the long term population growth rate, α is a random number from a normal distribution with mean zero. H_t is the number of seals killed by hunting. The risk of reaching low population sizes under different harvesting regimes and levels of environmental

noise was investigated. We used 1,000 as the quasi-extinction level, the level beyond which the population size is getting alarmingly low. This level could be varied, however 1,000 females in the entire Baltic Sea should be regarded as a serious situation. If population size decreases to about 1,000 females, other processes such as lack of males to fertilize all females, or demographic stochasticity in segments of the spatially subdivided population could begin to act.

Cautious hunting regime

Presuming the hunt will not be undertaken independently of the population size, we assumed a certain number of individuals are killed each year under the condition that the population size is above a given minimum population size (N_{\min}).

$$H_{(t)} = \begin{cases} H & \text{if } N_{(t)} > N_{\min} \\ 0 & \text{if } N \leq N_{\min} \end{cases} \quad (\text{eqn. 6})$$

The threshold values (N_{\min}) investigated were 3,000 and 5,000 females in the different scenarios. A risk analysis was performed by counting the number of population trajectories that hit the 1,000 limit (Fig 11). By varying the size of the annual hunt, the mean population growth rate and the variance in growth rate, the effects from different hunting regimes and levels of environmental stochasticity on the risk of quasi-extinction could be explored.

Risk for quasi-extinction under different scenarios

In our baseline simulations, initial population size was set at 20,000 seals, i.e. about 10,000 females, and λ was 1.075 as estimated for the Baltic grey seal (this study, Helander 2000). The simulations were repeated 10,000 times and gave consistent results.

Some different hunting regimes with ‘security levels’ were compared. With a security level at 3,000 females (6,000 individuals in the population), the risk of quasi-extinction increases 100 fold (from 0.0002 at no hunt, to 0.02 for the scenario) at an annual hunt of 300 females, and up to 375 fold (0.075 for the scenario) at an annual hunt of 400. If more than 400 females are hunted, the risk for quasi-extinction increases rapidly, see Fig. 12a.

If a higher security level is implemented, such that all hunt is banned if the population size declines to 5,000 females (10,000 seals), then the population can sustain a somewhat higher annual hunt (Fig. 12b). An annual hunt of 400 females increases the risk of quasi-extinction 3.5 fold (from 0.0002 to 0.007). The 1% level is reached at an annual hunt of 500 females in this scenario (0.0135). A 10% risk of quasi-extinction is reached at an annual hunt of 1,000 females with the security level at 5,000 (Fig. 12b).

Thus, with a strongly positive growth rate (1.075), and a modest variance ($\sigma^2 = 0.033$), a security level at 5,000 seems to be an efficient protection against excess hunting as long as the hunt is below 500 females. However, this result also presumes that an array of assumptions are met. For example, the mean growth rate and the variance are supposed to be measured accurately, there is no density dependence, and no catastrophes are allowed to occur. However, assuming a scenario where the annual growth rate is slightly over- or under-estimated we can explore effects of growth rates for the risk for quasi-extinction. We run the same model as above, with a security level at 5,000, $\sigma^2 = 0.033$, and an annual hunt of 500 females (this point is indicated by a black circle in Fig. 12b). Here the mean growth rate is varied between 1.055 up to 1.075. The risk in the baseline case was 0.0135 with a λ at 1.075 as indicated by the black circle also in Fig. 12c. The quasi-extinction risk increases sharply at lower mean growth rates, and is almost 10 times greater already at $\lambda = 1.055$. Thus the population quasi-extinction risk is very sensitive to variations in the mean population growth rate (Fig. 12 c).

The estimate of the variance, $\sigma^2 = 0.033$, is not exact and can change with time. Therefore we made numerical projections for a range of variance values, but kept the λ at 1.075 and all other parameter values as before. Slightly higher estimates of variance ($\sigma^2 = 0.04$) increased extinction risk 3.7 times compared with the baseline case at 0.0135 (at $\sigma^2 = 0.033$) (Fig. 12d). The risk of quasi-extinction increases exponentially as the level of unpredictability of the environment increases.

Finally we illustrate the importance of hunting regime by comparing the hunt of a fixed number of 500 with a hunt that takes a given propor-

tion of the population each year (Fig. 12e). This ‘proportional hunt’ is also assumed to stop if the total population size declines to 5,000 females. An annual harvest of more than 5% quickly leads to high quasi-extinction risks (Fig. 12e).

Calculating the cost of the age composition of the hunt

The age composition of harvested animals is likely to deviate from the stable age structure. Since female seals of different ages have different reproductive values, and thus contribute to different extent to the population growth rate, the age structure of the hunt must be taken into account.

In order to evaluate the effect of a given age composition in the hunt compared to a harvest of animals according to the stable age structure, the value of the harvested animals in terms of the effect on the population growth rate (λ), can be compared to the reproductive value (v) (Fig. 7) of the same number of killed animals according to the stable age distribution (w) (Fig. 6).

$$y = \sum_{i=0}^{i=38} \mathbf{w}_{(i)} \cdot \mathbf{v}_{(i)} \quad (\text{eqn. 7})$$

Thus, y is a sum of the products obtained by multiplying the age structure vector w with the vector of reproductive values v , for each single age class i . This sum (y) can be compared to the synonymous value of the actual hunt. The age structure vector of the harvested animals (a) is subtracted from the stable age structure (w) for each age class multiplied with their reproductive values, and then summed:

$$y_h = \sum_{i=0}^{i=38} [(\mathbf{a}_{(i)} - \mathbf{w}_{(i)}) \cdot \mathbf{v}_{(i)}] \quad (\text{eqn. 8})$$

The ratio of y_h/y gives the proportional difference for the cost of the hunt (Fig. 13). By multiplying this factor with the number of killed seals, the hunt can be evaluated in terms of numbers of killed seal equivalents to the number of seals in a stable age structure.

DISCUSSION

Population survey data

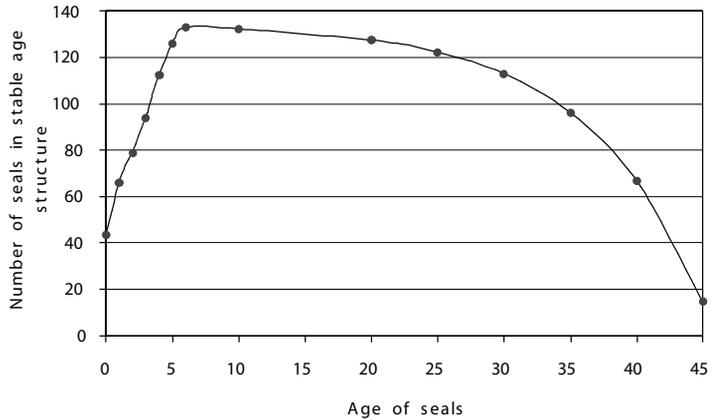
Based on information from international surveys (Fig. 3), supported by an independent mark-recapture study (Hiby *et al.* 2007), the total population size was estimated at 19,400 seals in 2003. Census data from the Swedish Baltic coast allowed estimation of the mean rate of increase which was found to have been about 1.075 over the last 14 years. The rate of increase in the population has been reported to be higher than 1.075 in Finland and lower in Estonia (Unpublished data). As long as these data are unpublished we cannot judge how this information will influence the overall trend. Grey seals are highly migratory (Sjöberg 1999), and it can be difficult to sort out if a local increase in abundance results from true population increase, or is an effect of migration. The wide confidence limits of the slope of the trend line are probably partly caused by migrations between Swedish, Finnish and Estonian localities. Thus, the effects of migrating seals are incorporated in the estimates of variation. It will be important to increase the accuracy of population trend estimates in the coming years.

On the use of data from other populations The Baltic grey seal is genetically unique (Boskovic *et al.* 1996), and also differs morphologically from other grey seal populations. Breeding time and body size are plastic features, and in the Baltic grey seal are adjusted to the conditions in the Baltic Sea. Thus, vital rates cannot be transferred from other populations uncritically. On the other hand, the Baltic grey seal has most likely been isolated from other North-East Atlantic grey seal populations for less than 9,000 years (Härkönen *et al.* 2007) and they share many basic biological features with other grey seal populations. Our approach has been to utilize data from other grey seal as a ‘best guess’ and adjust values when information from the Baltic was available. Although the exact values of the age related fertility and survival rates might deviate from those we have used, the main dynamics of the population would not be much affected.

Maximum rate of increase

The upper limit of individual reproductive rate is reflected at the population level, and gives an upper theoretical limit for the population

Fig. 13. The value of an individual female seal for future population growth depends on age. A hunt of 100 females of a given age (x-axis) corresponds to a number of 'mean females' (according to the stable age distribution) (y-axis). A hunt of 100 Baltic grey seal pups corresponds to a hunt of 40 females with a stable age distribution.



rate of increase (Fig. 10). The mean values of fecundity and mortality will always be lower than the theoretical maximum rate of increase, also for populations which live under favourable conditions. Chance events such as failed fertilisation or early abortions reduce annual pregnancy rates, and in samples of reasonable sizes, mean pregnancy rates rarely reach 0.96 (Boulva and McLaren 1979, Bigg 1969, Härkönen and Heide-Jørgensen 1990). Another factor that will decrease mean pregnancy rates is senescence (Härkönen and Heide-Jørgensen 1990). Further, environmental factors will reduce fecundity and survival rates. The impact from extrinsic factors may occur with different frequency and amplitude. Environmental pollution and high burdens of parasites can decrease population-specific long-term averages of fecundity and survival (Bergman 1999), while epizootic outbreaks and excessive hunting have the capacity to drastically reduce population numbers on a more short-term basis (Fig. 2, Dietz *et al.* 1989, Harding and Härkönen 1999).

The type of variation in fecundity and survival rates will determine the structure of a population. In a population with a constant rate of increase (thus no temporal variability), the age- and sex-structure quickly reaches a stable distribution, where the frequencies of individuals at each age class are constant (Fig. 6). Populations with low juvenile survival typically have steeper age distributions compared to populations with higher juvenile survival rates (Lotka 1956, Caswell 1989). We have shown the full span of theoretically possible combinations of vital rates at different population growth rates (Fig. 10). It turns out that population growth rate

of grey seals can only reach 10% if fertility rates are high (0.95). Since the Baltic grey seal still have high levels of PCB that can cause reproductive failure, the maximum possible growth rate should be lower than 10% at present (Fig. 11).

The risk for quasi-extinction

The risk for declining to 10% of present population size is a common estimate in population risk assessment. The estimate should be regarded as a relative measure that can be used in comparing different scenarios. We studied how extinction risk changed with different hunting regimes and different mean values of the long term growth rate and its variance in. In the baseline case with no hunting, the projected grey seal populations parameterized with data from the Baltic had a quasi-extinction risk at 0.0002. This low risk is primarily a result of the strongly positive growth rate that quickly takes the population away from the lower boundary (Fig. 12a). Adding a gradually higher hunt to the population leads to sharply increased extinction risk, also if a lower security level is implemented (Fig. 12a). The risk for quasi-extinction can be reduced substantially by setting a high security level (Fig. 12b). (The higher the security level is set, the lower the risk for quasi-extinction). With a security level of 5,000 females and an annual hunt of 500 females the extinction risk increases 67.5 fold (to 0.0135 for the scenario, point indicated in Fig. 12b, and also in Figs 12c-e, as a point of reference). A decline in the mean growth rate has a very strong influence on extinction risk (Fig. 12c). Therefore, it is worrying that the time for detection of a decline in growth rate is about a decade in Baltic grey seals (Fig. 5).

The risk of dangerously low population sizes increases exponentially at certain threshold values of environmental variability (Burgman *et al.* 1993). In the Baltic grey seal model, extinction risk increases to 5% at a variance of 0.04 (Fig. 12d). Also, harvesting a constant proportion of the population each year will significantly increase the quasi-extinction risk (Fig. 12e), which can be illustrated by that an annual hunt of 10% of the population (when larger than 5,000 females) is 3 times more harmful than harvesting 500 females each year (Fig. 12e).

The harmful effect of hunting stems from the over-all reduction in population growth rate, which increases the risk, especially at small population sizes. The risk for quasi-extinction is decreased with harvesting regimes where all hunting is stopped when the population drops to a given threshold value. The reason why this strategy is much more favourable is that it allows the population to resume to its maximum growth rate at low population sizes, and thereby rapidly leave the dangerous zone close to the quasi-extinction border. The higher the rate of population growth, the lower the security level can be set, maintaining the same vulnerability to environmental variation. Thus, it is evident that a careful harvesting regime markedly decreases the risk for population extinctions due to unexpected events as compared to a more careless harvesting regime.

In analysing results from the extinction risk model it is important to acknowledge the “precautionary principle” – to be on the safe side, we should consider the range of parameters which leads to the highest risk, when data are ambiguous or lacking. Too optimistic estimates of population size and growth can lead to drastically increased extinction risks.

Composition of the hunt

The risk analysis is based on an unstructured model where each individual has the same mean reproductive value. In nature, seal populations are separated into different ages and contribute thereby to varying extent to the population growth. The cost of any given age composition of the hunt is readily calculated by taking the reproductive value and the age structure of the hunt into account. A harvest of 100 pups will for

example have the same impact on the population as a hunt of 42 ‘mean’ females (Fig. 13). A hunt that kills 100 mature females on the other hand will be equivalent to the death of 130 ‘mean’ females (Fig. 13, eqn. 7 and 8). This exercise makes it possible to estimate the actual impact of the annual hunt, and to evaluate the effect of the hunt on the quasi-extinction risk.

Population size considerations

Ecological risk assessment attempts to estimate the probability that a population declines to a specified fraction of the present population size. The biological relevance of this chosen level, the critical population size, can be: If the population falls below a level where demographic stochasticity begins to act, the variation in population growth rate is expected to increase substantially. Some basic mechanisms could be that, due to chance events, the proportion of reproducing individuals could vary, or that some fertile females do not always get fertilised. Consequently, both the amplitudes and frequencies of “bad” years will increase with decreasing size of the population. This can eventually lead to a situation where the capacity for increase is critically hampered (Burgman *et al.* 1993).

The critical population size, for all animals including seals, is also affected by the age- and sex-structure of the population on the one hand, and on how it is distributed geographically on the other. Typically, the reproducing fraction of the population is smaller in long-lived animals as compared with species with short life spans. In spatially structured populations the demographic effective population size can be substantially smaller than in a panmictic population (Kokko and Ebenhard 1996, Kokko *et al.* 1998). Consequently, the critical size in a structured population is considerably greater as compared with a panmictic population.

Another important criterion is given by stochastic loss of genetic variation in small populations, which eventually leads to inbreeding depression. An increasing amount of evidence also suggests that genetic variation plays an important role in the susceptibility to infectious diseases (e.g. Acvedo-Whitehouse *et al.* 2003) and parasites (e.g. Paterson *et al.* 1998). Therefore, genetically impoverished populations are expected to

be more vulnerable to both lowered reproduction and increased mortality. Hence, the critical population size should be considerably greater in populations with limited genetic variation.

Health status is an additional factor that will affect the critical population size in the Baltic area, where a wide spread disease syndrome (Bergman and Olsson 1986) linked to OC pollution (Jensen *et al.* 1969, 1977) caused population crashes in ringed seals (*Phoca hispida*) and grey seals (*Halichoerus grypus*) (Harding and Härkönen 1999). Weakened health status can result in impaired reproduction and increased mortality (Reijnders 1986, Bergman 1999).

Assuming no catastrophes

Most models investigating risks for quasi-extinctions assume exponentially increasing populations. However, all populations will eventually experience dramatic declines caused by variations in food supply (Kjellqwist *et al.* 1995), fatal poisoning (Geraci *et al.* 1989, O'Shea *et al.* 1991, Scholin *et al.* 2000), or epidemic diseases (Dietz *et al.* 1989, Heide-Jørgensen *et al.* 1992a,b). Such sudden declines dramatically increase the vulnerability of populations to quasi-extinction (Harding *et al.* 2002, 2003). Since this array of factors will influence the critical population size, there is no obvious way to incorporate all parameters into a single framework, where a fixed critical population size can be given for specific populations. Therefore the extinction risk cannot be taken as absolute values, only as a tool for comparing one scenario to another.

Sources of environmental variation

Long-term climate change can also affect the Baltic grey seal. Baltic grey seals alternate between breeding on ice and on land, depending on the extent of ice coverage (Jüssi *et al.* *subm.*). The weaning weights of pups born on ice are significantly greater both in males and females (Jüssi *et al.* *subm.*). Mean weaning mass of male pups born on ice was 50 kg, but only 38 kg for male pups born on land. For female pups the weaning mass on ice was 47 kg, compared with only 37 kg. on land. This difference in weaning weight is probably related to stress in the large and dense colonies on land (Jüssi *et al.* *subm.*). Since pup survival is related to weaning weight (Bonner 1972, Hall *et al.* 2001) it can be expect-

ed that ice born pups have higher survival probabilities. Furthermore, pre-weaning morbidity and mortality rates are significantly greater at land breeding sites (Jüssi *et al.* *subm.*). Thus, the availability of suitable drift ice for breeding is directly linked to the reproductive success in Baltic grey seals. The extent of sea ice in the Baltic has varied from less than 5% to 100% among years and decades over the past 250 years (Seinä and Palosuo 1996). The frequency of winters with low ice coverage has increased and is predicted to increase even more in the coming decades, as a consequence of global warming.

By-catches

The sporadic and incomprehensive data on by-catches of Baltic grey seals in the fishery, suggest that numbers of seals caught in fishing gear could amount up to 1,000 animals during some years (Ivar Jüssi *pers. comm.*, Lunneryd and Westerberg 1997). The magnitude of this accidental killing vary with the type of fishery, since some types of gear such as bag nets, fish traps and drift nets, have proved to be especially dangerous for seals (Ivar Jüssi *pers. comm.*, Lunneryd and Westerberg 1997). The suggested high level of undocumented by-catches adds a substantial uncertainty to any type of risk analysis. Before a management regime is implemented, the mortality caused by the fishery must be quantified systematically (as also has been requested by ICES). It is also important to assess age and sex compositions of by-caught seals.

Hunting and historical extinctions

Deliberate killing by humans has been a major factor causing dramatic declines in most seal populations along the European (Reijnders 1994, Reijnders *et al.* 1993, Harding and Härkönen 1999) and American (Bigg 1969) coast lines. Although only 1 species, the Caribbean monk seal (*Monachus tropicalis*), has gone globally extinct (LeBoeuf *et al.* 1986), several others, such as the Mediterranean monk seal (*M. monachus*), the Hawaiian monk seal (*M. schauinslandi*), and the Saimaa ringed seal (*Phoca hispida saimensis*) all are at alarmingly low global levels (Reijnders *et al.* 1993, Kokko *et al.* 1998). The Northern elephant seal (*Mirounga angustirostris*) was close to extinction at the end of the 19th century (Cooper and Stewart 1983).

Hunting caused regional extinctions of grey seals in France, the Wadden Sea, the Kattegat- Skagerak, the Limfjord, the southern Baltic (Härkönen *et al.* 2007), and the US Atlantic coast (Barlow *et al.* 1995). After protective measures were undertaken in the mid 20th century, some of these regions have been re-colonised since the 1970s. However, reproducing grey seal populations are still absent from several regions where they were abundant only 2 centuries ago (Härkönen *et al.* 2007). Thus, experience tells us that grey seals are vulnerable to hunting pressure and great care should be taken if hunting is introduced.

Checklist

The demographic analysis and population assessment rely on estimates of biological parameters such as population growth rate, population size, fecundity, and survival. Access to such data allows the possibility of making population projections, to evaluate the risk of population extinction and the effects of different management strategies or hunting regimes, following the procedure in the present study. However, several factors can confound the analysis, and before results of extinction risk analyses are implemented it is important to address some specific questions. Below is a checklist that will reveal the validity of inherent assumptions in risk assessment models for given seal populations:

- Is the population spatially subdivided?
 - Do the different subpopulations have different vital rates?
 - Are there significant migrations to and/or from the study population?
 - Is the genetic variation low in the population?
 - Can the availability of males influence the population dynamics?
 - Are any of the subpopulations close to carrying capacity?
- a) Are there signs of density dependence in any of the vital rates (survival, fecundity, migration rates) in any of the subpopulations?

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b) Are there other clues, such as lack of breeding grounds or other limiting resources, suggesting that exponential growth cannot be expected?

- Is the age structure distorted?
- Have there been any recent dramatic events with high mortality?
- Has the population growth rate during the past 10-15 years been irregular or declining?
- Are there indications of impaired physiological functions?

If the answer is yes to any of the above questions, special considerations are to be taken for population modelling and before management plans including hunting are implemented. In case the population is spatially structured, the risk of local extinctions can increase as a result of demographic stochasticity (Kokko and Ebenhard 1996). Spatially structured populations might be better modelled with spatially explicit models (Lande 1993, Kokko *et al.* 1999), when such data are available. More complex models are also needed to include the effects of males and density dependence (Caswell 1989). Further, age- and sex-related migration behaviours can create complex networks of inter-connected subpopulations (Härkönen and Harding 2001). The population model can be constructed for subunits of populations when data are available to parameterize migration rates. And finally, do not forget to only use the results as index values of risk, where different scenarios can be compared. The true long term extinction risk is unfortunately always very very high.

ACKNOWLEDGEMENTS

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