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Backcasting population sizes of ringed and grey seals in the Baltic and Lake Saimaa during the 20th century

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Baltic Sea populations of the ringed seal (*Phoca hispida*) and grey seal (*Halichoerus grypus*) have been dramatically declining throughout this century. They are currently recovering from a population low in the 1970s, but sizes before the decline remain unknown. The land-locked Saimaa ringed seal (*Phoca hispida saimensis*) has similarly been declining over much of the century. We use past bounty statistics to estimate sizes of these three populations at the beginning of this century, and investigate the sensitivity of our results to assumptions on population growth, density dependence, the true extent of kills, and the age of killed individuals. The possible range extends from 50 000 to 450 000 individuals for Baltic ringed seals, from 30 000 to 200 000 for grey seals, and from only 100 to 1 300 individuals for Saimaa seals. The larger estimates apply if hunting tended to remove adult individuals with high reproductive value, and if the initial population was regulated by density dependence rather than kept below its true carrying capacity by nineteenth-century hunting. The low estimate for the Saimaa seal may either indicate that it was initially less abundant than thought, or that known hunting statistics simply do not capture the true magnitude of the decline.

1. Introduction

Three seal populations live in the Finnish waters: the ringed seal (*Phoca hispida botnica*) and the grey seal (*Halichoerus grypus*) in the northern and central Baltic Sea, and a lake form of the ringed seal, the Saimaa seal (*P. h. saimensis*) in Lake Saimaa in southeastern Finland. All the three populations have decreased markedly from their former abundance. For instance, in Finland and Sweden, which were responsible for almost 80% of the total kill around the Baltic, ca. 16 000 ringed seals and 8 000 grey seals were harvested annually in the beginning of the 1910s. The total population size of these species had diminished to about only 5 000 for the ringed seal by the mid-1980s (e.g., Helle 1986, Härkönen & Lunneryd 1992) and to 1 500–2 000 for the grey seal in the early 1980s (Helle & Stenman 1990). In Lake Saimaa, the population is ca. 200 specimens today, but it has been more abundant historically (Sipilä *et al.* 1990). All these three populations have been recently steady or increasing, although the Saimaa seal population remains highly endangered (Sipilä *et al.* 1990, Ranta *et al.* 1996, Kokko *et al.* 1998).

The decline of the Baltic stocks have been caused mostly by overexploitation in several periods during the century, and lowered reproduction since the latter half of the 1960s, most probably caused by high levels of organochlorines, such as DDT and PCB compounds (Helle *et al.* 1976, 1985, Helle 1980, Bergman & Olsson 1986). The Saimaa seal has been threatened by drowning in fishing gear, artificial lowering of the water level, disturbances in the first days of nursing, and reproductive failures caused by environmental toxins (Sipilä *et al.* 1990).

All the three seal populations have been classified as threatened. In managing the populations, and not least from the conservational point of view, knowledge about the former population sizes is of importance. Little is currently known, however. The only critical backcasting estimated that the Baltic ringed seal population may have been ca. 300 000 individuals in the beginning of our century (Durant & Harwood 1986), and no estimates are available for the two other populations.

The aim of the present work is to estimate the population size of the Baltic ringed seal and grey seal as well as the Saimaa seal at to the beginning of the hunting statistics in year 1900 (1893 for the Saimaa seal). We utilize data on past harvesting statistics, by posing the question, how large should the initial population have been, to result in current population sizes after the bag of the 20th century? We assess this question using the best available information on the recent population size, population structure, reproductive capacity and mortality, and test the robustness of our conclusions by varying these assumptions around the most likely values. Furthermore, we check the likely effects of past density dependence affecting population growth.

2. Material and methods

Let us denote the age-classified population size vector at time t with $\boldsymbol{x}_t$. According to the Leslie matrix approach, subsequent population sizes can be calculated as

$$\boldsymbol{x}_{t+1} = \mathbf{A}\boldsymbol{x}_t \tag{1a}$$

(Leslie 1945, Caswell 1989), where the matrix **A** contains the survival and fecundity values of the population. If the population is subjected to hunting, a number h_t of individuals is removed from the population annually, and the Eq. (1a) has to be modified accordingly:

$$\boldsymbol{x}_{t+1} = \mathbf{A}\boldsymbol{x}_t - h_t. \tag{1b}$$

An exact life-table for seal populations in the Baltic is not available, not to speak about the Saimaa Seal, so that the values in the matrix **A** are largely unknown. Even more so, possible changes in this data during this century have remained unnoticed until the start of detailed studies in the 1970s. Therefore, we chose to study the dynamics of a seal population under a wide range of alternatives. **A** was given an age-structured form (Caswell 1989, Manly 1990)

$$\mathbf{A} = \left\{\begin{matrix} f_1 & f_2 & f_3 & f_4 & f_5 \\ p_1 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 \\ 0 & 0 & p_3 & 0 & 0 \\ 0 & 0 & 0 & p_4 & p_5 \end{matrix}\right\}. \tag{2}$$

Here f_i denotes the fecundity of an individual in age class i, and p_i is its survival probability to the next age class. In this approach, the last stage corresponds to any adult of age 5 or more, since only relatively small differences in fecundity and survival are expected after reaching that age (Hewer 1963, Smith 1973, Mansfield & Beck 1977, Boyd 1985).

The past growth rate of seal populations is not known; translating assumptions on growth, λ, into the form of the matrix **A** requires determining the parameters f_i and p_i to yield the desired growth, defined as the dominant eigenvalue of the Lefkovich matrix **A**. In years of normal population growth (before the onset of infertility problems, *see below*), the fecundity values were chosen to match published seal life tables (Hewer 1963, Smith 1973, Mansfield & Beck 1977, Boyd 1985), i.e.

$$f_1 = f_2 = f_3 = 0, f_4 = 0.05, f_5 = 0.35 \qquad (3a)$$

This reflects the majority of seals maturing at age 5 years. With a proportion of infertile females, this is changed to

$$f_1 = f_2 = f_3 = 0, f_4 = (1 - d)0.05, f_5 = (1 - d)0.35, \qquad (3b)$$

where d stands for the proportion of infertile females due to uterine diseases. Since the annual mortality values are unknown, they were varied to give the desired λ, while the range of parameters were restricted to be similar to those obtained for seal populations in general (Hewer 1963, Smith 1973, Mansfield & Beck 1977, Boyd 1985). This was obtained by adjusting the survival coefficient s in the eigenvalue equation

$$\mathbf{A}\boldsymbol{x} = \lambda\boldsymbol{x} \qquad (4a)$$

where

$$\mathbf{A} = \left\{ \begin{array}{ccccc} 0 & 0 & 0 & (1-d)0.05 & (1-d)0.35 \\ \min\{0.87s, 1\} & 0 & 0 & 0 & 0 \\ 0 & \min\{0.91s, 1\} & 0 & 0 & 0 \\ 0 & 0 & \min\{0.91s, 1\} & 0 & 0 \\ 0 & 0 & 0 & \min\{0.91s, 1\} & \min\{0.91s, 1\} \end{array} \right\} \qquad (4b)$$

Eq. 4a was first solved with a normally reproducing population, where $d = 0$, and the value of s thus obtained was then used for populations with diseases as well. This was done to prevent an artificial compensation of reproductive failures by a decrease in mortality.

A large set of simulations were performed in order to determine the initial population size, that can lead to the observed total population after the culling period. Simulations were started from a population of size $N_{\text{init}} = n_{\text{init}}w$, where w is the stable age distribution for a population obeying Eq. 1a (Caswell 1989).

For the Baltic, a minimum estimate of the number of seals killed in the years 1900–80 is known due to bounties paid for each individual in Finland, Sweden and Russia (Fig. 1). The same holds true for the lake Saimaa in years 1893–1947 (Fig. 1). The data regarding Lake Saimaa, as well as Russia, are incomplete (Fig. 1).

We assumed even sex ratios, i.e. that females comprised half of the population as well as of the hunting bag. Simulated populations were subjected to these harvesting pressures by replacing h_t in Eq. 1b with the corresponding number of female kills. Three different age structures of h_t were analyzed: (1) with each age class being equally vulnerable to hunting, so that the age structure of h_t matches that of the current population N_t, (2) with hunting being confined to adult age classes (age structure of h_t matches that of current N_t for seals of minimum age 5, and is 0 for younger seals), (3) with hunting being confined to young seals (the reverse of case (2)). These extremes are chosen to encompass the likely true variation in the seal populations and their vulnerabilities to hunting.

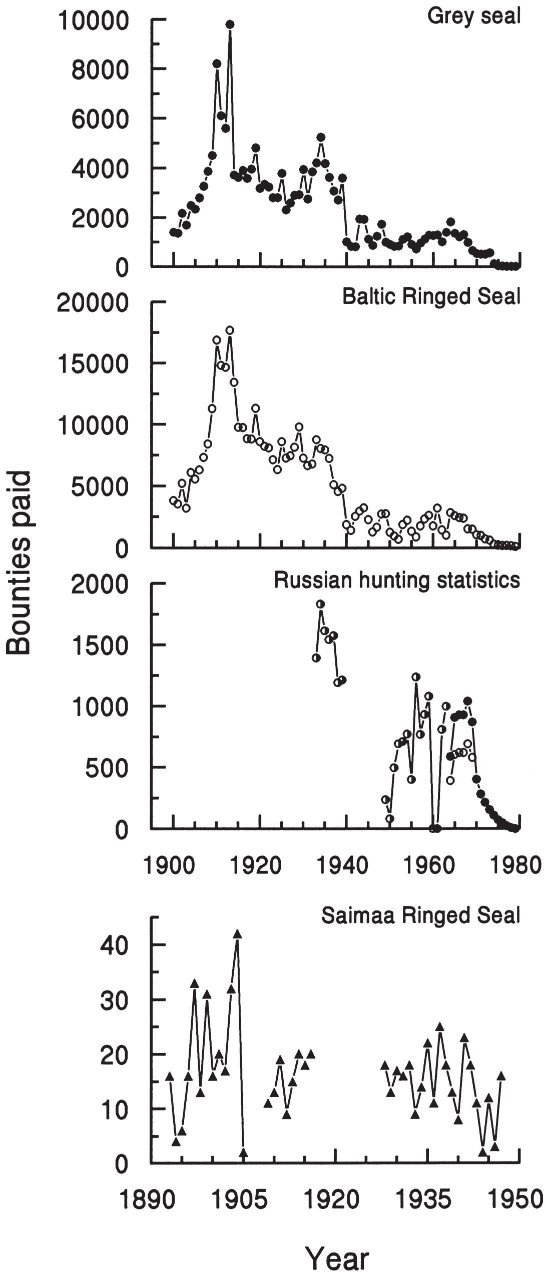

Fig. 1. Known bounty statistics for the Baltic grey seal (Sweden and Finland pooled; after Helle and Stenman 1990), the Baltic ringed seal (Sweden and Finland pooled), the Russian hunting bag (total kills before 1964; species-specific bag afterwards), and the Saimaa ringed seal bag (S. Rautiainen, pers. comm.).

Considering bag records, we investigated two different cases: (1) assuming that the official statistics are accurate, i.e. no kills ever occurred outside the official statistics, and (2) assuming that the bag records reflect only 90% of the true bag size. In the latter case we also interpolated a yearly bag of 20 individuals for Lake Saimaa for the years for which no data are available (Fig. 1), and assumed the Russian bag to equal 13%, 21% and 30% of the Finnish and Swedish bag up to 1930s and in 1950s and 1960s, respectively (based on estimates in Helle & Stenman 1990); for these years Soviet statistics are not available. For years where only the total seal bag of Soviet kills is known, the division into species was made to correspond to the proportion of grey vs. ringed seals in the Finnish and Swedish data of the same year.

Growth rates were varied in two different ways: we assumed either (1) that the initial population was capable of growing at its intrinsic growth rate and being kept below its carrying capacity by previous hunting, or (2) that the initial population was at its carrying capacity (hence regulated by density dependence). For both alternatives, nine possible distributions for λ_t were studied, giving three values of both the mean and variance of the yearly growth. In the first, density-independent setting, this leads to the distributions

$$\lambda_t \sim N(1.05, 0),\ \lambda_t \sim N(1.10, 0),\ \lambda_t \sim N(1.15,0),$$
$$\lambda_t \sim N(1.05, 0.01),\ \lambda_t \sim N(1.10, 0.01),\ \lambda_t \sim N(1.15,0.01),$$
$$\lambda_t \sim N(1.05, 0.05),\ \lambda_t \sim N(1.10, 0.05),\ \lambda_t \sim N(1.15,0.05).$$

The density-dependent setting is obtained by setting the intrinsic finite growth rate λ_0 obey the distributions above, but letting the yearly realized growth λ_t depend on N_t through the logistic growth equation

$$\lambda_t = \exp(r_t),\ \text{where}\ r_t = \ln(\lambda_0)(1-\Sigma N_t/\Sigma N_{\text{init}}).$$

Finally, the simulations were carried out both with and without a proportion $d = 0.5$ of uterine diseased females from the year 1970 onwards for the Baltic seal populations.

The outcome of each simulation was recorded as the final population size, $n_{\text{final}} = \Sigma(N_{\text{final}})$, after the culling period. Ideally, we seek the initial population size n_{init} which leads to a size n_{final} which lies inside the range assessed to be true for the population at the time of stopping the culling (1980 for the Baltic populations, and 1948 for the Saimaa seal). However, assuming random variations exist in the growth rate, a given n_{init} does not lead to a deterministic final population size. Instead, a single choice for n_{init} leads to a proportion p_{low} of final population sizes lying below the chosen range, and a proportion p_{high} exceeding it. For this reason, the 90% confidence interval for n_{init} was determined according to the following rules:

1. The lower end of the interval was set to the size n_{init} where $p_{\text{low}} = 0.95$, i.e., 95% of the simulations suggest that the chosen value of n_{init} is too small,
2. The high end of the interval is at the size n_{init} where $p_{\text{high}} = 0.95$, i.e., 95% of the simulations suggest that n_{init} is chosen too high.

The ranges for n_{final} used were 75 … 150 females (150 … 300 individuals) for the Saimaa ringed seal population, 500 … 1 000 females (1 000 … 2 000 individuals; Helle & Stenman 1990) for the grey seal, and 3 000 … 5 000 females (6 000 … 10 000 individuals; Helle 1986) for the Baltic ringed seal population. The resulting confidence intervals for the initial population size ($2 \times n_{\text{init}}$, as males are included in the total number), under various assumptions concerning the growth of the population and the bag data, are then reported for each species (Figs. 2–4).

Results

Our estimates of the population sizes for year 1900 range from 30 000 up to roughly 200 000 Baltic grey seal individuals (Fig. 2). The corresponding figures for the Baltic ringed seal are approximately 50 000 to 450 000 individuals (Fig. 3). For the endangered Saimaa ringed seal the values range very much lower (Fig. 4). The lowest backcast reaches as low as about 100 seals, while the highest values reach close to 1 300 individuals in the Lake Saimaa population. Note that these 95% confidence intervals cover a wide range of different scenarios regarding to population and hunting history. Consequently, the most probable population numbers are within a much narrower range.

Instead of despairing of the wide range of estimated values, it is possible to systematically investigate the effects of various model assumptions. Self-evidently, the initial size must have been greater if the actual kill has been higher, instead of the minimum kills known. It is also easy to see that assuming juvenile-biased hunting leads to lower backcasts of population sizes than the adult-biased or non-discriminating hunting strategy. This is not surprising as adult seals have higher reproductive values (Kokko *et al.* 1997).

Also, the higher the past growth, the smaller the initial size can have been, still sustaining the bag taken. Variance in the population growth rate markedly increases the width of the 95% confidence interval of the backcast, but it also tends to increase the initial size required, at least if past growth has been high; this indicates that assuming a few low-growth years can have a stronger effect on sustainability than can be compensated by the corresponding few high-growth years. By contrast, whether or not uterine occlusions from 1970 onwards were considered in Baltic seals did not markedly change the backcasted values. Although this effect has had a major effect on popu-

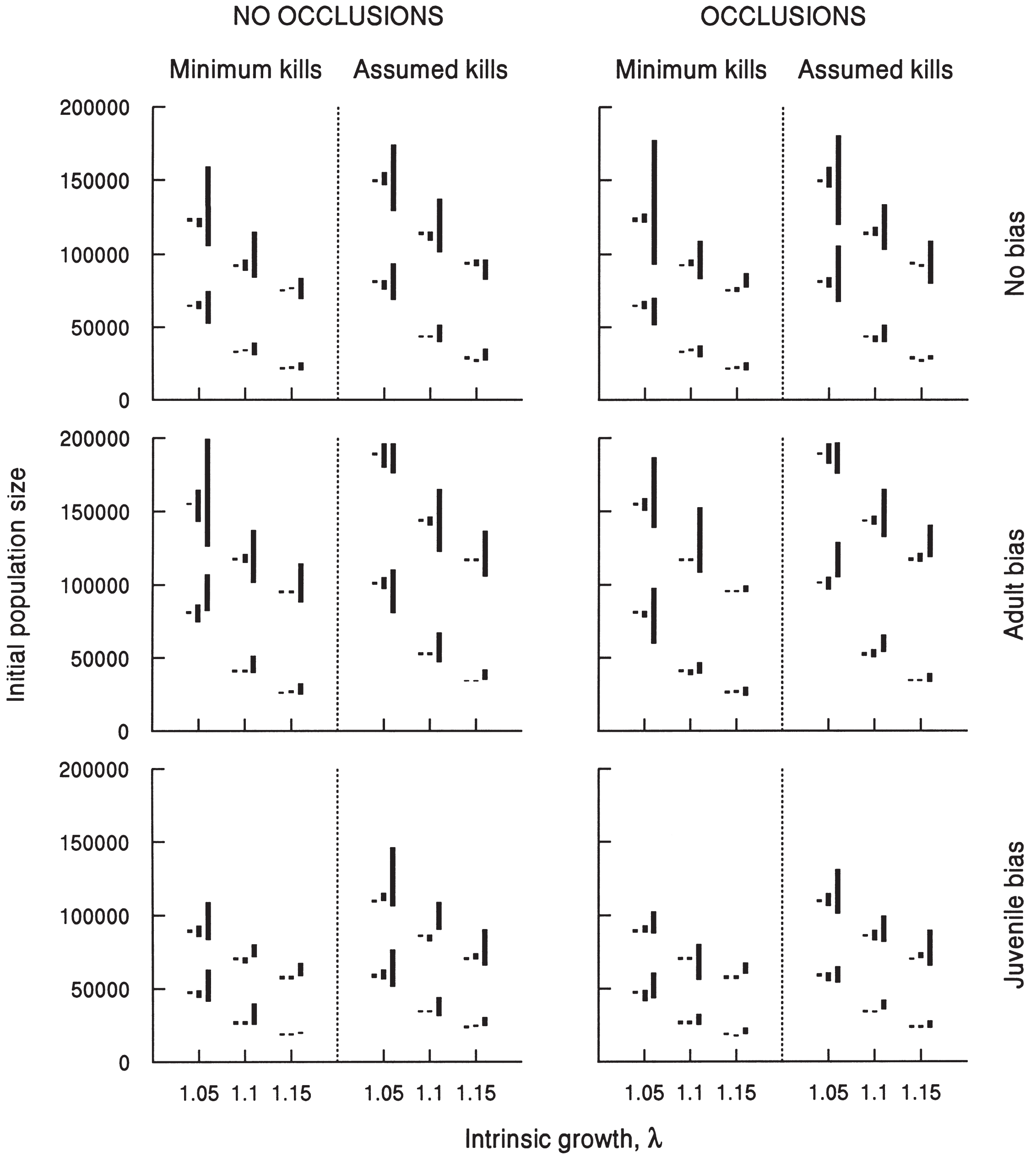

Fig. 2. Backcasted population size in 1900 for the grey seal in the Baltic Sea. The bars indicate approximate 90% confidence intervals for population backcasts (see text). For each growth rate three different standard deviations were used in the simulations (0%, 1% and 5%, from left to right), together with assuming either density dependence (upper bar) or density independence (lower bar) at the beginning of the century. Population sizes were backcasted with two different levels of annual kills, known (Fig. 1) and 10% higher kills than reported, the latter case including assumed values for Russian kills for years lacking data. The effect of uterine occlusions on birth rates was either excluded or taken into consideration, as indicated. Finally, hunting was either unbiased regarding the age of seals, biased towards adults, or biased towards juveniles.

lation viability in recent decades (Helle *et al.* 1976, Helle 1980), its effect in absolute numbers is negligible compared to the extreme hunting pressure of the beginning of the century.

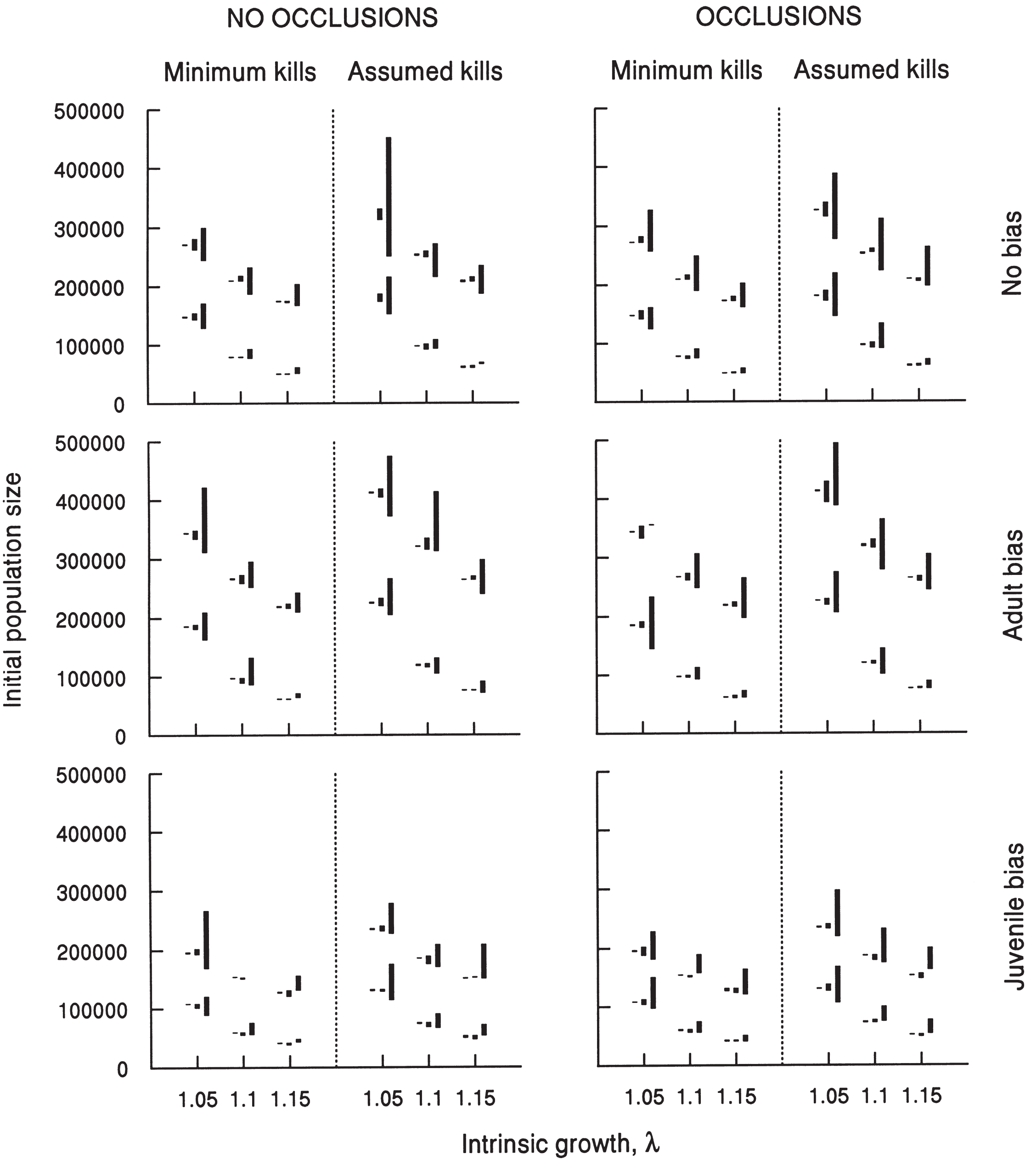

Fig. 3. Backcasted population size in 1900 for the ringed seal in the Baltic Sea (details as in Fig. 2., known kills from Fig. 1).

We instead find a major effect of density dependence. If the initial population was regulated by density dependence, its initial size must have been invariably much greater than if it was still capable of growing from its initial level. This result is also intuitive: a population initially suffering from density dependence has experienced lower growth rates in the past than a density-independent population, hence more individuals must have been be initially present to make the density-dependent population survive despite its lower growth.

4. Discussion

Past bag statistics can be used to inform us on past population sizes and densities (Durant & Harwood 1986, Gjertz *et al.* 1998, Milner-Gulland & Lhagvasuren 1998), with a clear logic: the initial population size must have been large enough to have survived the past hunting. Uncertainties regarding population growth and structure, however, can have major effects on the sustainability of a hunting bag (e.g., Ludwig *et al.* 1993, Walters & Punt 1994, Kokko *et al.* 1997), and this problem also transfers to backcasting population sizes in cases where hunting has been unsustainable.

Our results provide an interval which includes the previous estimate of 300 000 Baltic ringed seals (Durant & Harwood 1986). This previous estimate was based on relatively low adult survival (0.88 per year) leading to low growth rate; we find, however, that about 300 000 seals may be a realistic estimate even at up to 10% annual growth, if assumptions on unrecorded kills are included, and if populations were initially regulated by density dependence. Even higher initial sizes must be suspected if hunting has tended to remove mainly adult seals from the population. It is known, however, that hunting used to be rather juvenile-biased rather than adult-biased (Helle, unpublished). We also show that ringed seal population size at 1900 could have been much lower, in the likely range of 100 000 ... 200 000 individuals, if hunting in the nineteenth century had been strong enough to bring the population down from its carrying capacity, hence enhancing past growth rates. It is commonly accepted that the decline was just because of overexploitation during those early times.

The grey seal, which is the nowadays the faster growing species in the Baltic, has had smaller population sizes at the beginning of this century, but still in the range of tens of thousands, or even exceeding 100 000 if density dependence was important in the past. Its estimates follow the same kind of logic as those of the ringed seal, with the highest estimates being found if hunting in the nineteenth century was not bringing the population down from its carrying capacity, and if hunting tended to kill adult seals rather than juveniles or pups. It is commonly considered that overexploitation was the very reason which has caused the marked decline of the Baltic grey seal population, and here, hunting has been potentially even more juvenile-biased than in the ringed seal: breeding time used to be an important hunting season and pups had a high value as catch. The age structure of the whole kill depends on the balance between this juvenile-bias on one hand and the tendency to also kill the pup's mature mother on the other.

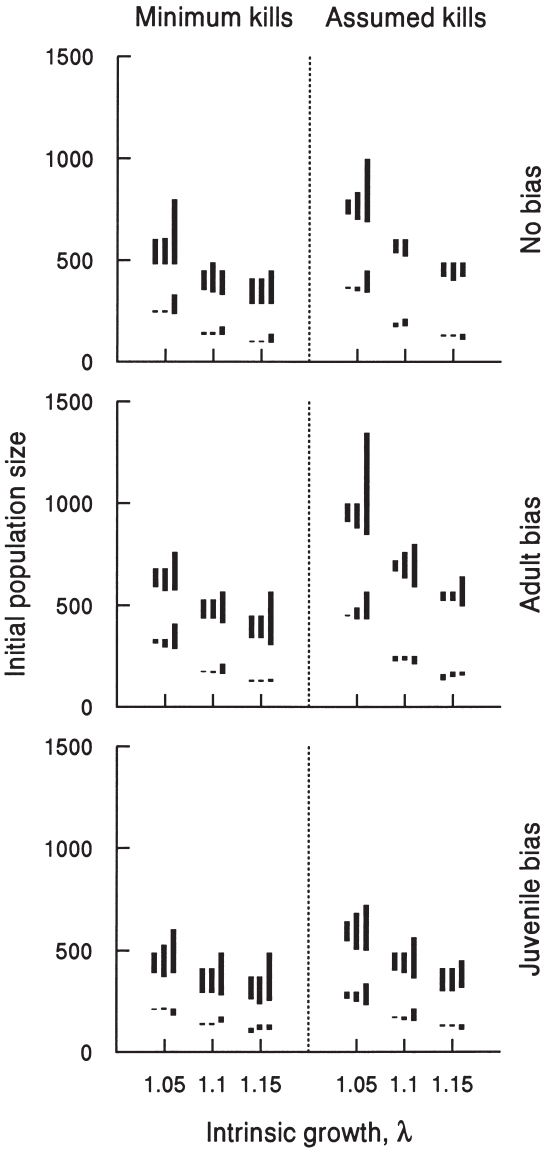

Fig. 4. Backcasted population size in 1893 for the Saimaa Ringed Seal in the Lake Saimaa (details as in Fig. 2, but omitting the possibility of uterine occlusions).

The Saimaa seal data shows, in many cases, very small initial population sizes. The "natural" carrying capacity of Lake Saimaa has been estimated to be at least 2 000–2 500 seals (Hyvärinen & Sipilä 1992); this estimate is based on current densities of seals in the remaining pristine habitats, and extrapolating this to the whole area of the lake. Our estimates for the population size in 1893 remain below 1 000 seals even if we assume a regulatory role for density dependence. This result can be interpreted in two ways. It may be that the Saimaa seal population 100 years ago really was smaller than previously thought; this might be reassuring as it suggests that such a small population has been capable of persistence for a long time (the seals became isolated in Saimaa about 8 000 years ago, Müller-Wille 1969), and would hence not need to grow very much larger than its present size, to ensure its persistence. But it is also possible that our results simply indicate that the recorded bounty statistics do not carry the whole truth of the population decline. The statistics themselves are incomplete (Fig. 1) and do not contain data before 1893. Also, several other factors than direct killing have been identified to reduce population growth, such as increased pup mortality in collapsing birth lairs caused by water level fluctuations (Lake Saimaa is regulated for electric power production, although conservation measures in recent years aim at holding a roughly constant water level during wintertime).

Our method, despite an attempt to evaluate a very wide range of possibilities for past population growth, obviously cannot encompass every possible form of uncertainty; for example, details of the initial age structure of the population are simply unknown. However, in another study (Kokko *et al.* 1997) we found that the overall growth rate λ can be used to summarize the response of seals to hunting, irrespective of the details of the life table over the range that describe seal population growth. Also, in the current context, we can state the simple rule that every additional factor (including unrecorded hunting) that has reduced past population growth will increase the initial size estimate, especially if it weakens the performance of adults, and especially if it was affecting population growth at the time when the population still was large.

As an example, one factor we have not evaluated concerns the sex ratio of the initial seal population. If killing tended to remove females from the population more than males (as it might in forms of hunting where the mother and her pup are killed together, as in the past grey seal hunt), the true hunting bag of females must have been larger than the half of the records. Hence the initial size of the female population $n$init must have been larger to result in an extant population today. Since this would have additionally led to a male-biased adult sex ratio, the total number of individuals would have exceeded $2 \times n$init. Likewise, if males were more vulnerable to hunting, this would reduce our estimate of the total population size in year 1900. As another example, the initial seal populations must have exceeded even our estimates that take density dependence into account, if the carrying capacity itself has been declining together with the seal population, as this would counteract the increase in growth rates when hunting reduces population densities. However, we consider this alternative unlikely, given that the estimated biomass of fish in the Baltic has increased rather than decreased during the first half of this century (Thurow 1997).

Regardless of the details of the estimates, our results confirm that seal populations in the Baltic must have been substantially larger in the beginning of this century than at present: even the minimalistic assumptions that ignore all unrecorded hunting and assume 15% annual growth throughout the century produce sizes that are at least ten times the recent population estimates, and changing these assumptions may lead to a difference of several tenfolds. Also, regardless of the exact assumptions, the Saimaa seal differs drastically from this result, as it has either been only about five times as numerous as at present, or alternatively, the recorded hunting does not account for the whole of the population decline.

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