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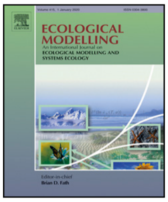

Bayesian integrated population model of Baltic grey seals (*Halichoerus grypus grypus*) informs on population carrying capacity and the impact of Baltic herring (*Clupea harengus membras*) on reproduction

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ABSTRACT

Baltic grey seal (*Halichoerus grypus grypus*) is a top predator of the Baltic Sea ecosystem that has just recently recovered from near-extinction induced by historical bounty hunting and pesticides. However, increasing seal population has initiated a conflict between seal conservation and fisheries. We also lack understanding of the ecological constraints of grey seal population in the rapidly chancing Baltic Sea. To address these challenges, we developed a Bayesian integrated population model for the Baltic grey seals. We used our model to estimate their historical population development, demography, and life history parameters, and to assess their future prospects under alternative hunting and prey scenarios. Our results show that the grey seal population has recovered to approximately 57,000 seals in 2025, with an average yearly growth rate of 4.9% in the last two decades. The current carrying capacity of Baltic grey seals was estimated at 120,000 individuals, which is 30% larger than previous estimates from historical hunting statistics. The weight-at-age of Baltic herring (*Clupea harengus membras*) was found to have a strongly positive effect on grey seal reproduction. Scenario predictions suggest that the Baltic grey seal population can remain viable under the current hunting quota of 3050 individuals. However, with yearly hunting of 3600 individuals, probability of extinction was considerable, and depended on both prey quality and the demographic composition of the hunted seals. With yearly harvest of 4800 seals, the population was predicted to go extinct by 2070 at the latest.

1. Introduction

Baltic grey seals (*Halichoerus grypus grypus*) are a genetically isolated subspecies of the grey seal (*Halichoerus grypus*) (Fietz et al., 2016; Ahlgren et al., 2022), residing in the whole Baltic Sea. Throughout the past century, the population decreased due to overexploitation by hunting and a sharp decline in fertility rates due to the introduction of organic pollutants into the Baltic Sea in the 1960s (Helle et al., 1976; Blomkvist et al., 1992; Bergman, 1999; Britt-Marie et al., 2021). The population size at the beginning of the twentieth century has been estimated to approximately 90,000, after which it dropped to around 3000 by the 1970s (Carroll et al., 2024). This dramatic decline prompted the ban on seal hunting in the 1980s in all countries surrounding the Baltic Sea. Together with stricter regulation of organochlorines (PCB and DDT), this resulted in a gradual recovery of the population (Varjopuro, 2011; Kauhala et al., 2012; HELCOM, 2023b; Suuronen et al., 2023; Carroll et al., 2024). However, as the population size grew, seal-induced losses and damages to coastal fisheries also became increasingly common. As a result grey seal hunting was reintroduced in Finland and Sweden in 1998 and 2001, respectively. The increasing seal population and the increase in hunting quotas have lead to an ongoing debate about the appropriate level of yearly hunting (Kauhala et al., 2012; Eschbaum et al., 2021; Carroll et al., 2024; Räsänen, 2025). Moreover, the Baltic sea ecosystem has changed considerably during the past century (Reusch et al., 2018) but we lack a proper

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understanding of the current ecological constraints that determine the maximum attainable population size (i.e., carrying capacity) and demographic rates of Baltic grey seals, as well as the drivers of variation in them. For example, current population assessments are based on annual aerial census counts that provide an index for monitoring long-term population trends but not actual population size estimates. Estimates of the carrying capacity of Baltic grey seals, on the other hand, are based on historical hunting statistics dating back a hundred years (e.g., Kokko et al., 1999; Harding and Härkönen, 1999; Carroll et al., 2024).

To help mitigate the debate between fishers and conservation, and to update our understanding of demographic and life history processes of the Baltic grey seal population to current time, we built a Bayesian integrated population model (IPM) for them. We fitted the model to data from annual censuses, hunting statistics, and necropsy samples of bycaught and hunted grey seals from 2003–2024. We then used the calibrated IPM to analyse the current state of the Baltic grey seal population and predict their future prospects under alternative scenarios for hunting and prey, namely herring (*Clupea harengus membras*) weight-at-age. By combining multiple complementary data sets into a single analysis, our IPM allows information integration which consequently makes the population parameters better identifiable compared to what would be possible with any of the data sets alone or with more traditional sequential model fitting approaches (Ersalman et al., 2024). Moreover, as we followed the Bayesian approach, our results are complemented with rigorous uncertainty estimates. Bayesian methods are increasingly being used in ecological modelling, as the development of statistical software has made them more easily accessible to practitioners. For example, the basis for our model was the Bayesian IPM for the Baltic ringed seal (*Pusa hispida botnica*; Ersalman et al., 2025), which we adapted and modified to fit the Baltic grey seal population. Another important reference and inspiration for our model was the Bayesian state–space model for British grey seal populations (Newman et al., 2009; Thomas et al., 2019). Bayesian population dynamics models have also been applied to other pinniped populations such as ringed seals in Svalbard (Nater et al., 2024), harbour seals (*Phoca vitulina*; Matthiopoulos et al., 2014; Caillat et al., 2019), harp seals (*Pagophilus groenlandicus*; Tinker et al., 2026), South American sea lions (*Otaria flavescens*; Romero et al., 2017; Punt et al., 2021) and South American fur seals (*Arctocephalus australis*; Punt et al., 2021).

Just recently, Carroll et al. (2024) presented an age-structured matrix population model for Baltic grey seals, which they used to estimate the effects of hunting on the future development of the population. Similar matrix population analyses have earlier been conducted by Kokko et al. (1999), Harding and Härkönen (1999), and Harding et al. (2007) for the purposes of understanding the dynamics of Baltic grey seal population and backcasting the population sizes. However, unlike our Bayesian IPM, these earlier population dynamics models have been parameterised in a sequential (frequentist) manner using one data set at time and, thus, they have not provided rigorous uncertainty estimates for the model parameters. The earlier works have neither estimated the current carrying capacity of Baltic grey seals since none of the monitoring data alone are informative on it. Moreover, in the earlier works the total grey seal population size estimates have relied on scaling the aerial census counts by an estimate of the proportion of seals hauling out during the surveys, provided by Hiby et al. (2007). Before our work, the accuracy of this scaling has not been assessed though. We also move beyond the existing models and methods to analyse Baltic grey seals by deriving a mechanistic description for the mortality and reproduction processes of the grey seals starting from the first principles. We first describe the population level effects of hunting and other mortality through a system of ordinary differential equations, which we then transform to stochastic transitions in time. The population level reproduction model in our IPM is, likewise, derived from individual level biological processes from embryo implantation to birth, while simultaneously quantifying the effect of mean weight-at-age of over five-year-old herring (WAA hereafter) to intrinsic birth rate of grey seals.

Baltic herring (*Clupea harengus membras*) is one of the main food sources for Baltic grey seals (Scharff-Olsen et al., 2019), and the quality of herring stocks can affect seal body condition and reproductive success (Kauhala et al., 2019). While other food sources of grey seals, such as sprat (*Sprattus sprattus*), can also be expected to affect the viability of the seal population, studies have suggested a predictive link between herring weight-at-age and the pregnancy rate of the Baltic grey seal population (Lundström et al., 2007; Gårdmark et al., 2012; Kauhala and Kurkilahti, 2019). Specifically, Kauhala et al. (2019) demonstrated a clear association between the frequency of reproductive signs in female grey seal necropsy samples and the WAA of herring in the Baltic proper, the Gulf of Finland, and the Gulf of Bothnia. This association is reasonable, since grey seals prefer older and larger herring (Lundström et al., 2007; Gårdmark et al., 2012) and the status of herring stocks in the central Baltic is correlated with the status of sprat and cod (*Gadus morhua*) stocks (Margonski et al., 2010) which together form the majority of the diet of grey seals in that region (Scharff-Olsen et al., 2019). However, the impact of herring, or other fish prey, on the population dynamics of Baltic grey seals has not been assessed. Due to ongoing changes in the Baltic Sea ecosystem, it is important to understand their effect on the grey seal population when planning policy actions and predicting population development under alternative future scenarios. Such predictions are possible only with mechanistic models capturing essential life history processes and demographic parameters – as well as variation in them – trained with observational data.

As the grey seal has long been a recognised indicator of the health of the Baltic ecosystem (HELCOM, 2023a), extensive data collection has been carried out on them for decades. These efforts have provided annual census counts and necropsy data from hunted and by-caught seals, which contain information on the growth rate of the population, population demography, and fertility rates. These monitoring data, when combined together into integrative analysis, provide a unique possibility to update our understanding on the drivers of one of the top predators of the Baltic Sea ecosystem. Hence, the methodological aim of this work was to build a Bayesian IPM capable of answering these questions. We then specifically aimed to estimate the current carrying capacity of Baltic grey seals and assess the effect of Baltic herring WAA on the development of the grey seal population. We also aimed at providing an updated estimate for many life history parameters of relevance to management, as well as for the proportion of seals counted during the aerial censuses. Moreover, to evaluate the uncertainties and risks associated with the future of Baltic grey seals, we predicted the population development under alternative hunting and herring WAA scenarios.

2. Materials and methods

2.1. Data

The available data on Baltic grey seals consist of annual aerial census counts, records of the number of hunted seals, and necropsy data of bycaught and hunted seal samples. For this study, we compiled all these data for the years 2003–2024.

2.1.1. Aerial grey seal surveys

To estimate the total population size of Baltic grey seals, coordinated annual aerial census surveys have been carried out in a systematic manner since 2003 (HELCOM, 2023a). The census counts are carried out over all known haul-out sites during the moulting period of juvenile and adult grey seals between mid-May and early June, when seals are expected to be out of the water and visible on terrestrial haul-outs in large numbers (Fig. 1A). Survey flights are conducted two to three times during a two-week annual census period, and the highest number obtained from the repeated survey is used as a census count

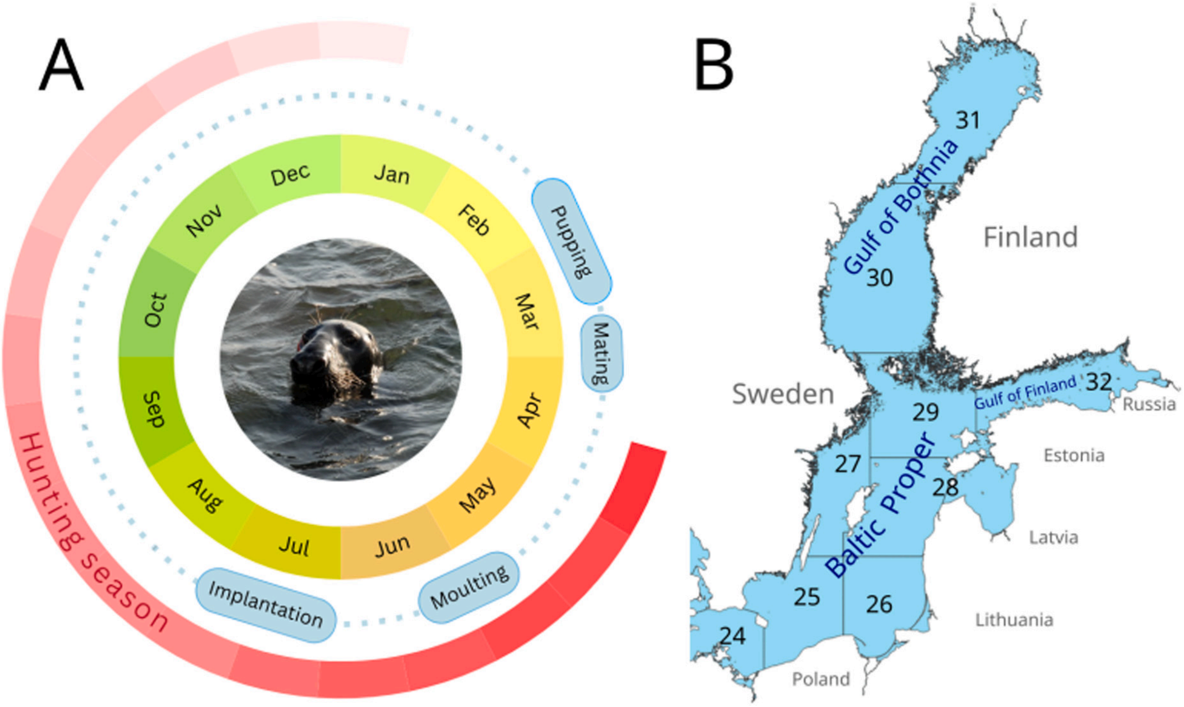


Fig. 1. (A) Important yearly processes of the Baltic grey seal and the corresponding hunting season. (B) The ICES subdivisions covering the Baltic Sea.

in each area (Galatius et al., 2014). To reduce randomness in survey counts, which could arise from variation in seal haul-out behaviour between different weather conditions (Galatius et al., 2014), surveys are carried out under standard dry weather conditions when seals are expected to haul out in the largest numbers.

2.1.2. *Grey seal hunting statistics*

In Finland and Sweden, hunters have had to report each hunted seal to the national authorities, providing access to the yearly hunting quota and the size of the total harvest. These data are compiled and stored by, respectively, the Finnish Wildlife Agency and the Swedish Environmental Protection Agency. In addition, small-scale grey seal hunting has also been allowed in Estonia since 2015 (Suuronen et al., 2023). However, the Estonian hunting statistics were not included in our analysis, as they were negligible compared to the Swedish and Finnish hunting, with annual harvests not exceeding 50 seals (Keskkonnaportaal, 2024).

Since its reintroduction, seal hunting practices in the Baltic Sea have changed over the years. First, seal hunting was heavily regulated; in Finland, seal hunters had to acquire a special licence for each seal, and seal hunting was restricted to protective hunting near fishing gear in Sweden (Kauppinen et al., 2005; Vanhatalo et al., 2014; Eschbaum et al., 2021; Lundström et al., 2025). Since 2014, licensed seal hunters in Finland have been allowed to freely hunt seals until the yearly quota is filled, and in 2020, Sweden also legalised recreational quota hunting. Since its reintroduction, hunting quotas in Finland and Sweden have been steadily increasing, reaching a total quota of 3050 grey seals per year by 2023. The hunting season starts on 16 April in Finland and 20 April in Sweden. It ends 31 December in Finland and 15 January in Sweden.

2.1.3. *Grey seal necropsy samples*

To collect information on grey seal population demography, necropsy samples have been collected from hunted (n = 3933) and bycaught (n = 1042) seals in Sweden and Finland since 2003. In Finland, hunters send the lower jaw and reproductive organs of a set number of seals to the Natural Resources Institute Finland (Luke) each year. In Sweden, jaws and all internal organs are collected from hunted animals and bycaught carcasses. The species and their age are then determined from growth layer groups in the cementum of the teeth, and reproductive organs are used to determine the sex and reproductive status of females.

Adult female seals have been examined for the presence of placental scars and a corpus albicans (CA) in the ovary, and a fetus to obtain information on the reproductive success status of the population (HELCOM, 2023b). Placental scars and CA are present if the seal gave birth that year. However, as scars fade over time, they are often not detectable after summer; therefore, we used placental scar and CA data from samples taken between April and June only. A fetus is detectable in pregnant seals after the implantation of the embryo, which occurs in mid-summer. Data from after the 1st of August were used for determining the annual pregnancy rate. In Finland, seal samples are mainly collected from spring to early summer, while in Sweden, most seal samples are collected after the beginning of August. Hence, reproductive scar data (n = 661) were obtained from Finland, and pregnancy rate data (n = 312) from Sweden.

2.1.4. *Baltic herring weight-at-age*

To assess the impact of herring body condition on the Baltic grey seal population, we compiled data on WAA of Baltic herring (i.e., the mean weight, in grams, of herring over five years old) in the Baltic Proper combined with the Gulf of Finland (ICES sea subdivisions 25–29 and 32, Fig. 1B) and the Gulf of Bothnia (ICES sea subdivisions 30 and 31). These data were obtained from the annual reports of the Baltic Fisheries Assessment Working Group (WGBFAS) of the International Council for the Exploration of the Sea (ICES, 2023).

2.2. *Bayesian integrated population model*

We built a stochastic, discrete-time, age-structured state–space model, to analyse the underlying dynamics of the Baltic grey seal population. Seals were categorised into six different age groups and divided by sex, resulting in 12 demographic classes. While the population reproduction is assumed to be limited only by the number of females, the model includes both sexes, since mortality rates can vary between males and females. Zero-year-old seals were considered pups, 1–4 year olds were categorised as sub-adults, and seals of age five and above as adults, as the majority of female grey seals start to reproduce at the age of five (Hewer, 1964; Bowen et al., 2006). The demographic composition of the population in year t was, hence, represented by

$$\mathbf{n}_t = \left(n_{0,f,t}, \dots, n_{4,f,t}, n_{5+,f,t}, n_{0,m,t}, \dots, n_{4,m,t}, n_{5+,m,t}\right), \tag{1}$$

where $n_{a,s,t}$ is the population size of the demographic group with age a and sex s in year t just after seals have given birth, which happens from February to March (Coulson, 1981; Kauhala et al., 2019). The changes in the population throughout the year were modelled via three subsequent processes: survival, ageing, and reproduction. The general structure of our IPM follows the model developed by Ersalman et al. (2025) (see their Figure 3 for a graphical description). Next, we specify the details of the temporal dynamics and observation models.

2.2.1. *Survival and aging*

Baltic grey seals are subject to mortality through hunting and other causes, including natural mortality and bycatch. Therefore, the survival process was modelled as a stochastic transition where each seal can move to one of the four states: it can survive (S) the year, be hunted in Sweden (H^{sw}) or Finland (H^{fi}), or die from *other causes* (D), such as death due to natural mortality and incidental by-catch in fishing gear. By-catch is a significant mortality source for the Baltic grey seals (Vanhatalo et al., 2014) but was not explicitly modelled in this work due to the lack of sufficient data on the annual numbers of by-caught seals. Then the total population – including both dead and alive individuals – after the process of survival in demographic class $\{a, s\}$ can be expressed as a vector

$$\mathbf{u}^1_{a,s,t} = \left(u^{1,S}_{a,s,t}, u^{1,H_{\text{sw}}}_{a,s,t}, u^{1,H_{\text{fi}}}_{a,s,t}, u^{1,D}_{a,s,t}\right), \tag{2}$$

where $u^{1,I}_{a,s,t}$ is the number of seals of age a and sex s who transitioned to state I in year t. The different mortality sources are assumed to act independently; therefore, the stochastic transition can be modelled by a multinomial distribution:

$$\mathbf{u}^1_{a,s,t} \sim \text{Multinomial}\left(n_{a,s,t}, \left(\rho^S_{a,s,t}, \rho^{H_{\text{sw}}}_{a,s,t}, \rho^{H_{\text{fi}}}_{a,s,t}, \rho^D_{a,s,t}\right)\right), \tag{3}$$

where $\rho_{a,s,t} = \left(\rho^S_{a,s,t}, \rho^{H_{\text{sw}}}_{a,s,t}, \rho^{H_{\text{fi}}}_{a,s,t}, \rho^D_{a,s,t}\right)$ is the vector of sex and year-specific transition rates to the four different states and n_a, s, t is the number of seals of age a and sex s in year t. Seals that survive year t age deterministically so that seals younger than five transition to the next age class, whereas seals of age five and older remain in their class. Hence, the aged population at the end of the year can be expressed as $\mathbf{u}^2_t = A\mathbf{u}^{1,S}_t$ where A is the ageing matrix.

We treated the mortality rate $\mu_{a,s}$ combining the causes of death other than hunting as constant in time but varying between different demographic groups. It was assumed to be highest for the pups and decreasing until maturity, after which it remained constant (Harding et al., 2007). Therefore, we defined the mortality rates for the pups, $\mu_{0,s}$, and adults, $\mu_{5+,s}$, and interpolated the sub-adult mortality rates using a logarithmic regression

$$\log(\mu_{a,s}) = \log(\mu_{0,s}) + \left(\frac{a}{5}\right)^c \left(\log(\mu_{5+,s}) - \log(\mu_{0,s})\right), 1 \le a \le 4, \tag{4}$$

where c is a parameter that describes how steeply the mortality rate decreases. We gave informative priors for the female pup and adult mortality rates, whereas those of the males were modelled by their deviation from the female mortality rates (see Appendix D).

Since its reintroduction, the monthly harvest numbers have typically been highest in early season and tend to decrease towards the end of the hunting season (see Appendix A). Hence, national hunting efforts were assumed to be proportional to the national quota (see Appendix D) and decrease linearly with time from the start to the end of the hunting season. Combining the different sources of mortality, the expected numbers of dead and surviving seals during a year can be described by the following system of ordinary differential equations (ODEs):

$$\frac{dH^{\text{sw}}_{a,s,t}}{d\tau} = \begin{cases} \tilde{n}_{a,s,t}(\tau)E^{\text{sw}}_{a,s,t}(k-\tau) & \text{if } 0 < \tau < k \\ 0 & \text{otherwise} \end{cases} \tag{5}$$

$$\frac{dH^{\text{fi}}_{a,s,t}}{d\tau} = \begin{cases} \tilde{n}_{a,s,t}(\tau)E^{\text{fi}}_{a,s,t}(k-\tau) & \text{if } 0 < \tau < k \\ 0 & \text{otherwise} \end{cases} \tag{6}$$

$$\frac{dD_{a,s,t}}{d\tau} = \mu_i \tilde{n}_{a,s,t}(\tau) \tag{7}$$

$$\frac{d\tilde{n}_{a,s,t}}{\tau} = \begin{cases} -\tilde{n}_{a,s,t}(\tau)\sum_C E^C_{a,s,t}(k-\tau) - \mu_{a,s}\tilde{n}_{a,s,t}(\tau) & \text{if } 0 < \tau < k \\ -\mu_{a,s}\tilde{n}_{a,s,t}(\tau) & \text{otherwise.} \end{cases} \tag{8}$$

where $H^{\text{C}}_{a,s,t}$ is the number of hunted seals in country $C \in \{\text{sw}, \text{fi}\}$, $E^{\text{C}}_{a,s,t}$ is the corresponding hunting effort, and $\tilde{n}_{i,t}(\tau)$ is the expected population size in the demographic group i time τ after the beginning of the hunting season in year t, and $k \approx 3/4$ is the length of the hunting season. First, solving for $\tilde{n}_{i,t}$ analytically (Appendix B) provides an expression for the probability $\rho^S_{a,s,t}$ that a seal in group a, s survives year t. Then the expected number of seals hunted at the end of the year in each group, $H^C_{i,t}(k)$, was calculated using a numerical ODE solver, from which the probability of being hunted $\rho^{H_C}_{a,s,t}$ was solved (Appendix B). The probability of death due to other causes than hunting is then $\rho^D_{a,s,t} = 1 - \rho^{H_{\text{sw}}}_{a,s,t} - \rho^{H_{\text{fi}}}_{a,s,t} - \rho^S_{a,s,t}$.

2.2.2. *Reproduction*

Since Baltic grey seals give birth to at most one pup at a time, and the sex ratio at birth is assumed to be equal (Harwood and Prime, 1978), the birth of pups in year t was modelled as

$$(n_{0,f,t+1}, n_{0,m,t+1}, \cdot) \sim \text{Multinomial}\left(u^2_{5+,f,t}, \left(\frac{b_t}{2}, \frac{b_t}{2}, 1 - b_t\right)\right), \tag{9}$$

where b_t is the probability that an adult female gives birth at year t and $\cdot$ denotes a dummy variable, representing the number of adult females who have not given birth in year t. As seals compete for a finite amount of resources, their population size cannot grow without limit. Hence, we assumed that the fecundity of Baltic grey seals is limited by the total population size, following the model of Ersalman et al. (2025). Moreover, to link herring WAA to reproductive success, we regressed the intrinsic birth rate (i.e., birth rate at zero seal density) along a covariate vector $h_t = [h^{\text{GoB}}_t, h^{\text{BP+GoF}}_t]^T$ where h^{GoB}_t denotes the normalised WAA of Gulf of Bothnia herring stock and $h^{\text{BP+GoF}}_t$ that of the Baltic Proper combined with the Gulf of Finland stock. This resulted in the model for the probability of birth as

$$b_t(n_{t-1}, h_{t-1}) = b^t_0(h_{t-1})e^{-\theta_0\left(e^{\theta_1 n_{t-1}} - 1\right)}, \tag{10}$$

where $b^t_0(h_{t-1})$ is the intrinsic birth rate, θ_0 is the average failure rate of pregnancies at zero population density, and θ_1 is a parameter that governs the density dependent increase in pregnancy failures (see Appendix C). We modelled the intrinsic birth rate as

$$b^t_0(h_{t-1}) = b^0_{min} + \frac{b^0_{max} - b^0_{min}}{1 + e^{-\left(\alpha + \beta(w h^{\text{BP+GoF}}_{t-1} + (1-w)h^{\text{GoB}}_{t-1})\right)}}, \tag{11}$$

where b^0_{min} and b^0_{max} are the lowest and highest attainable intrinsic birth rates, and parameters α and β determine the shape of the logistic curve interpolating between these values. Moreover, $w \in [0, 1]$ is a weight parameter that describes the relative importance of WAA of herring in the Baltic Proper combined with the Gulf of Finland on reproductive success. Detailed derivation of the model and effect of the reproduction model parameters on carrying capacity are given in Appendix C.

2.3. *Observation model*

2.3.1. *Aerial survey*

The probability of observing a seal during the annual aerial counts depends on the proportion of seals hauled out, which is assumed to vary

Table 1
Simulated scenarios for harvest size, hunting selectivity, and WAA of herring. We predicted the population dynamics of Baltic grey seals with all combinations of the three scenario parameters, leading to in total $6 \times 5 \times 5$ simulations.

Harvest	Hunting selectivity	WAA of herring
0	Historical (2003–2024) selectivity	Historical mean
1311	Towards pups	+0.2g/year starting from the historical mean
2400	Towards adults	−0.2g/year starting from the historical mean
3050	Toward males	+4 g to the historical mean throughout the simulation
3600	Toward females	−4 g to the historical mean throughout the simulation
4800		

stochastically throughout the years. Therefore, the yearly count can be modelled with a negative binomial distribution with mean μn^{tot} and variance $\mu n^{\text{tot}} + \frac{(\mu n^{\text{tot}})^2}{r}$, where μ is the average observation probability across age and sex groups, excluding the pups of the year, $n_t^{\text{tot}} = \sum_i n_{i,t}$ is the total population size in year t, and r is an overdispersion parameter

$$y_t^{\text{count}} \sim \text{Neg-Bin}\left(\mu n_t^{\text{tot}}, r\right). \tag{12}$$

2.3.2. Hunted seals

The total number of harvested seals is reported each year, but it can still deviate slightly from the actual number of hunted seals due to misreporting or illegal hunting. Hence, the observation of the total harvest was modelled stochastically, with a small variance,

$$y_t^{hb} \sim N(H_t^{tot}, 0.05(H_t^{tot})^2). \tag{13}$$

2.3.3. Hunting samples

The samples acquired from hunters provide the yearly demographic composition of the sampled hunted seals represented as $\mathbf{y}_t^{\text{hs}} = \left(y_{0,f,t}^{\text{hs}}, \dots, y_{5+,m,t}^{\text{hs}}\right)$, where $y_{a,s,t}^{\text{hs}}$ is the number of sampled seals of age a and sex s in year t. This composition is drawn from a multinomial distribution, with probabilities for each demographic class equal to the proportion of hunted seals in that class:

$$\mathbf{y}_t^{hs} \sim \text{Multinomial}\left(\sum_{a,s} y_{a,s,t}^{hs}, \frac{H_t}{H_t^{tot}}\right), \tag{14}$$

where $H_t = \left(H_{0,f,t}, \dots, H_{5+,m,t}\right)$ and $H_{a,s,t}$ is the number of seals of age a and sex s hunted in year t. Seals hunted in Sweden and Finland are drawn separately through this model.

2.3.4. Bycatch samples

The observation model for the bycatch samples is defined similarly as for the hunting samples, except that since the number of bycaught seals is not directly modelled, the samples are drawn from $\mathbf{u}_{a,s,t}^D$, which includes all seals that died from causes other than hunting. To account for the differences between the demographic compositions of seals that die from bycatch and from other causes, $\mathbf{u}_{a,s,t}^D$ is weighed by a selectivity vector Ψ^{bc}

$$\mathbf{y}_t^{\text{bc}} \sim \text{Multinomial}\left(\sum_{a,s} y_{a,s,t}^{\text{bc}}, \frac{\Psi^{\text{bc}} \odot \mathbf{u}_{a,s,t}^D}{(\Psi^{\text{bc}})^T \mathbf{u}_{a,s,t}^D}\right). \tag{15}$$

2.3.5. Reproduction

The number of pregnant adult females past the preimplantation period (after July) can be described with a binomial model.

$$y^{\text{pregnant}} | p_t(\tau_s) \sim \text{Binomial}\left(y^{\text{pregnant}} + y^{\text{not pregnant}}, p_t(\tau_s)\right), \tag{16}$$

where y^{pregnant} are all the seals that could possibly be detectably pregnant (adult, female, past preimplantation period), and $p_t(\tau_s)$ is the probability of a seal being pregnant in year t, τ_s time after implantation, which is the approximated time that passes between implantation and sample collection (Appendix C).

Other indicators of reproductive success are the presence of a placental scar or a corpus albicans (CA). These scars can fade after summer. Therefore, only seals collected before August were included in the observation model for placental scar and CA. Let z_t^{ij} represent the number of sampled seals in year t who had composition ij of placental scar and CA, where $i, j \in \{0, 1\}$ and i corresponds to the presence of placental scar, j to the presence of a CA. Then

$$z_t = (z_t^{00}, z_t^{10}, z_t^{01}, z_t^{11}) \sim \text{Multinomial}(\gamma_t = (\gamma_t^{00}, \gamma_t^{10}, \gamma_t^{01}, \gamma_t^{11})), \tag{17}$$

where γ_t^{ij} are the probabilities of observing outcome ij on a (female, adult) seal (Appendix C).

2.4. Posterior inference

We treated the different observation data types as mutually independent, given the model parameters. We gave prior distributions for all model parameters, incorporating earlier knowledge on their possible values (Appendix D). We sampled from the joint posterior distribution for the parameters and state variables using Stan (v2.32.2; Team 2024). For the sampling algorithm of Stan to work, the model parameters and their distributions need to be continuous. Therefore, following Ersalman et al. (2025), we approximated the multinomial survival process by a logit-Gaussian distribution and the multinomial birth process with two consecutive Gaussian distributions. Moreover, all discrete-valued parameters in our model were approximated with continuous numbers. Within MCMC sampling, we used the ODE solver of Stan to solve the expected numbers of hunted seals in (5) and (6). The posterior results were analysed in R Statistical Software (v4.4.2; R. Core Team 2025). Prior and likelihood sensitivity analyses were performed with the *priorsense* package (Kallioinen et al., 2024).

To draw samples from the posterior distribution and evaluate the posterior medians and 95% credible intervals, four MCMC chains were simulated, each with 4000 samples, of which the first 2000 were discarded as warm-ups. The visual inspection of the four chains suggested suitable mixing and convergence, and $\hat{R}$ values were found to all deviate from one with less than 0.01, further indicating that the chains have converged. Posterior predictive checks comparing the simulated and observed data indicate a good model fit (Appendix E).

2.5. Hunting scenario predictions

To assess how the population would change in the future if current conditions were sustained and how it would react to changes in WAA of herring or hunting pressure, we simulated the population size and structure until 2080 under alternative hunting and WAA of herring scenarios (see Table 1). To quantify the uncertainty related to these scenario simulations, we used samples from the posterior distribution of the model parameters.

For hunting scenarios, we examined total harvests ranging from 0 to 4800 individuals, including the 2024 total harvest of 1311 seals. To assess how the distribution of the hunted seals among the demographic and age classes affects the population trends, we simulated five different hunting selectivity scenarios: historical selectivity (estimated by the posterior distribution), selectivity towards pups, selectivity towards adults, selectivity towards males, and selectivity towards females. Here, selectivity towards a demographic group means that there is a 50% higher chance of being hunted for individuals in the selectivity group

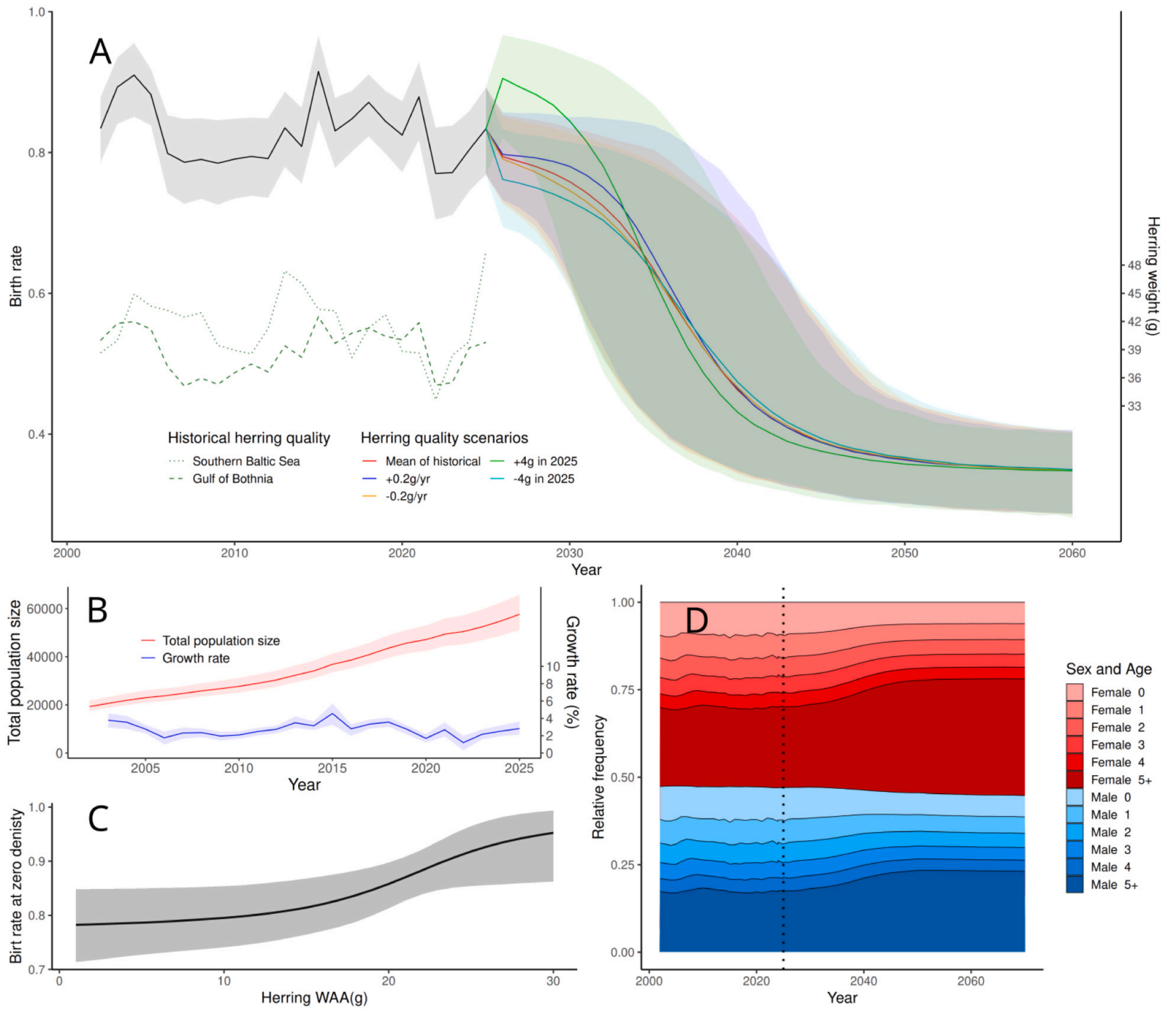


Fig. 2. (A) Estimated historical birth rate (median and 95%CI) of the Baltic grey seal and its future projections with varying weight-at-age of herring overlaid with the yearly mean herring weights in the Gulf of Bothnia and in the Baltic Proper combined with the Gulf of Finland. (B) Estimated historical total population size and growth rate (median and 95%CI). (C) $b_0(h)$: Birth rate (median and 95%CI) at zero density as a function of weight-at-age of herring. (D) Relative frequency of demographic groups throughout the observed period and predicted until 2060, assuming the 2024 harvest for the simulated years (the dotted line represents 2024).

than individuals in other demographic groups. For these simulations, we assumed the WAA of herring to be the historically observed mean for the years 2003–2024.

To assess the risk of the Baltic grey seal population under each scenario, we calculated the probability that the population goes (virtually) extinct by 2080, defined as the percentage of the simulated populations that consist of less than 100 seals by 2080 (hence, a population under 100 individuals is deemed unrecoverable). To assess the Baltic grey seal population response to changes in WAA of herring under different hunting pressures, we modelled the population under the same hunting pressure scenarios as above, with five different weights at age of herring scenarios: mean observed weight in 2003–2024, an assumed yearly increase or decrease of 0.2 grams in weight, and under constant herring weights of plus or minus 4 grams compared to the average weight in 2003–2024. For these scenarios, we assumed the hunting selectivity to be the historical one. All the posterior predictive simulations were done with R Statistical Software (v4.4.2; R. Core Team 2025).

2.6. Comparison to the matrix population model of Carroll et al.

Since the parameter estimates and future projections from our analysis deviated to some extent from the estimates by the recent Baltic grey seal population analysis of Carroll et al. (2024), we compared our model and its results with theirs. We compared the population parameter estimates of Carroll et al. (2024) and ours. Then we ran the future scenario predictions of Carroll et al. (2024) using their model (and code), but the posterior parameter estimates of our Bayesian model, to assess the magnitude of difference induced by the different parameter estimates. Moreover, we compared how the undisturbed population size grows with time under the two models, starting from the same initial population and compared the growth rate as a function of population size in an undisturbed population.

3. Results

3.1. Current state of the population

The posterior estimate for the total Baltic grey seal population size in 2025 was 57,000 (posterior median with 95% posterior credible interval of (51,000; 66,000)) individuals whereas the population size in 2002 was around 19,000, corresponding to average yearly growth rate of 4.9% (Fig. 2). Adult female survival was 0.91 (0.89; 0.94), and female pup survival was 0.78 (0.52; 0.89). The respective estimates for

Table 2
Prior and posterior median (and 95% credible intervals) of key Baltic grey seal population parameters.

	Parameter description		Posterior median and 95% CI	Prior median and 95% CI
Survival	Female survival probability for adults	$\phi_{f,5+}$	0.91 (0.89; 0.94)	0.9 (0.805; 0.995)
	Female survival probability for pups	$\phi_{f,0}$	0.78 (0.52; 0.89)	–
	Shape parameter of the logarithmic curve of mortality from natural death and bycatch	c	0.08 (0.00; 0.95)	0.5 (0.025; 0.975)
	Male survival probability for adults	$\phi_{m,5+}$	0.88 (0.79; 0.93)	–
	Male survival probability for pups	$\phi_{m,0}$	0.79 (0.56; 0.92)	–
Birth	Minimal birth rate at zero density	b^0_{min}	0.78 (0.42; 0.84)	–
	Maximum birth rate at zero density	b^0_{max}	0.99 (0.88; 1.00)	0.5 (0.025; 0.975)
	Midpoint of the logistic curve along weight-at-age of herring	α/β	−0.80 (−1.9; 3.6)	0 (−7.8; 7.8)
	Shape parameter of the logistic curve that indicates herring dependency	β	2.1 (0.30; 5.5)	0 (−5.8; 5.8)
	Relative weight the Baltic Proper combined with the Gulf of Finland on the effect of weight-at-age of herring	w	0.09 (0.00; 0.47)	0.5 (0.025; 0.975)
	Carrying capacity	$\bar{K}$	120,000 (83,000; 190,000)	81,000 (45,000; 150,000)
	Mean observation probability in aerial censuses (excluding pups of the year)	μ	0.84 (0.74; 0.91)	0.79 (0.64; 0.89)

males were 0.88 (0.79; 0.93) and 0.79 (0.56; 0.92) (Table 2). The current carrying capacity of the population in the absence of hunting, and under average WAA of herring, was estimated to be around 120,000 (Table 2 and Fig. 3). The mean observation probability of seals other than pups of the year in aerial censuses was estimated to 0.84 (0.74; 0.91).

Female adults made up around 23% of the total population, male adults 17%, and female and male pups each contributed approximately 9% of the total population in 2025 (Fig. 2.D). The composition varied but there were no trends in demographic composition from 2003 to 2025. The grey seal birth rate was predicted to decrease significantly in the coming decades, due to density dependent effects, and the demography of the population to shift towards adults (Fig. 2).

3.2. Effect of herring weight-at-age on reproduction and population dynamics

The WAA of herring (i.e., the mean weight of herring over 5 years old) was estimated to have positive effect on grey seal birth rate so that the intrinsic birth rate with low WAA of herring (b^0_{min}) was 0.78 (0.42; 0.84) and with high WAA of herring (b^0_{max}) was 0.99 (0.88; 1.00) (Table 2). Herring in the Gulf of Bothnia had approximately nine times larger role in the variation in the grey seal birth rate than the herring in the Baltic Proper combined with the Gulf of Finland, as indicated by the weight parameter w that was estimated to be 0.09 (0.00; 0.47). As a result, the birth rate b showed a visible variation due to the WAA of herring during the past 20 years.

The future simulations with varying WAA of herring showed that the effect of herring on the birth rate is expected to decrease as the population increases near the carrying capacity (Figs. 2, 4.A, see also the next section).

3.3. Hunting scenario predictions

With the three smallest total harvest scenarios – no hunting, 1311 individuals (realised hunting in 2024), and hunting of 2400 individuals – the grey seal population was predicted to survive and grow to the respective stable population sizes (Fig. 3). When the total harvest was further increased to the current quota of 3050 individuals, the viability of the population was predicted to become uncertain and depend on the hunting selectivity. The population was predicted to continue to increase and be viable with virtual certainty if the hunting selectivity was the same as currently or weighted towards pups or males. However, with hunting selectivity towards adults, the uncertainty in predicted population growth was high and if hunting targeted female seals, the population was predicted to go extinct by 2080 with a 19% chance.

With scenarios of yearly harvest of 3600 seals, the fate of the population depended on hunting selectivity. The population was predicted to be viable with hunting selectivity towards males (with 99% probability) and its fate was uncertain with historically observed hunting selectivity, hunting selectivity towards pups, and hunting selectivity towards adults. However, the population was predicted to go extinct with hunting selectivity towards females (Fig. 3). With a total harvest of 3600 seals, the WAA of herring also significantly affected the viability of the population (Figs. 2, 4.B).

Total harvest of 4800 seals was predicted to lead to a quick extinction of the population under all hunting selectivities. Increasing the WAA of herring did not save the population from extinction with this large hunting, but a constantly high WAA of herring delayed extinction by approximately 10 years.

3.4. Prior and likelihood sensitivity

Posterior estimates were generally robust to the prior choice (Appendix E) and clearly differed from the respective prior estimates for the most essential biological parameters (Table 2). An exception was the estimate for the deviation of male pup mortality rate from the mortality rate of female pups (Fig. 13). The carrying capacity parameter also showed moderate sensitivity to the prior so that narrower prior shifted the posterior distribution to the left but the posterior still differed considerably from the prior with all reasonable prior choices (Fig. 11).

3.5. Comparison to the matrix population model of Carroll et al.

Both the birth rate at zero density and the survival probability for adults were estimated to be higher by Carroll et al. than our study, while our IPM estimated higher pup survival (Table 3). When simulating the population size under different hunting quota scenarios with the model of Carroll et al., we observed similar trends with their lower and upper carrying capacity estimates as well as with our posterior median for the carrying capacity (Fig. 5A). However, when starting from the same initial population size, our IPM predicted a quicker increase in population size than the model of Carroll et al. (Fig. 5A, B). When

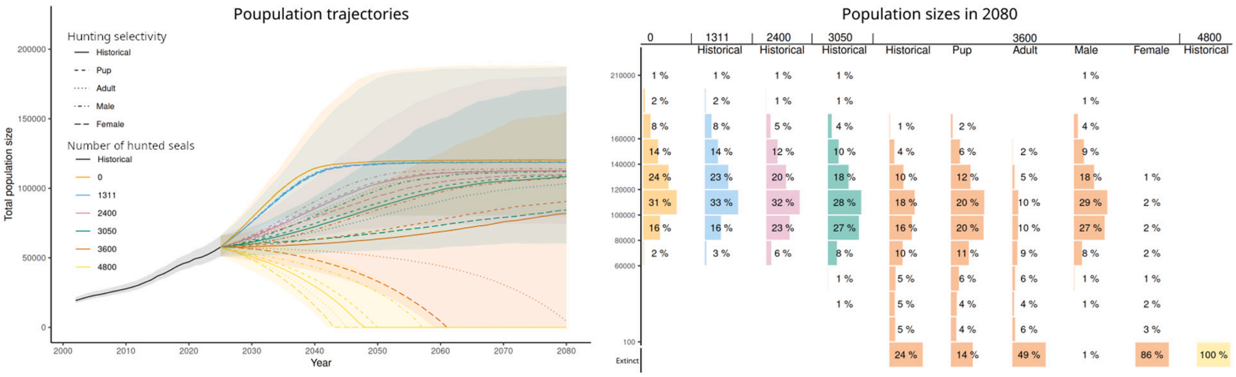
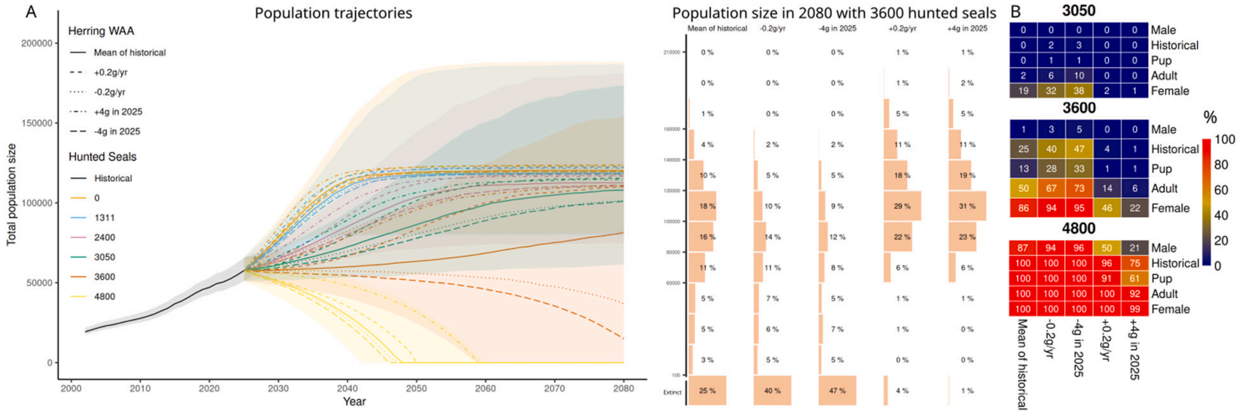


Fig. 3. Simulated population size (median and 95%CI) of the Baltic grey seal under different scenarios for hunting effort and selectivity and the posterior probability density for the population size in 2080 under the respective scenarios.



3050

	Mean of historical	-0.2g/yr	-4g in 2025	+0.2g/yr	+4g in 2025
Male	0	0	0	0	0
Historical	0	2	3	0	0
Pup	0	1	1	0	0
Adult	2	6	10	0	0
Female	19	32	38	2	1

3600

	Mean of historical	-0.2g/yr	-4g in 2025	+0.2g/yr	+4g in 2025
Male	1	3	5	0	0
Historical	25	40	47	4	1
Pup	13	28	33	1	1
Adult	50	67	73	14	6
Female	86	94	95	46	22

4800

	Mean of historical	-0.2g/yr	-4g in 2025	+0.2g/yr	+4g in 2025
Male	87	94	96	50	21
Historical	100	100	100	96	75
Pup	100	100	100	91	61
Adult	100	100	100	100	92
Female	100	100	100	100	99

Fig. 4. (A) Simulated population size (median and 95%CI) of the Baltic grey seal under different scenarios for total harvest and weight-at-age of herring, and the posterior probability density for the population size in 2080 under a harvest of 3600. (B) Probability of virtual extinction (population size less than 100) by 2080 when 3050 (current quota), 3600 and 4800 seals are shot under varying WAA (i.e., mean weight-at-age of herring older than five) and hunting selectivity scenarios.

Table 3
Population parameter estimates from Carroll et al. (2024) compared to those from our model (median and 95% CI).

Baltic grey seal parameter description	Carroll et al. (2024)	Bayesian IPM in this study
Birth rate at zero density	$b_{9:25}(K = 88000) = 0.895$ $b_{9:25}(K = 100000) = 0.905$	$b^0_{min} = 0.78(0.42 - 0.84)$ $b^0_{\text{mean WAA of herring}} = 0.82(0.76 - 0.87)$ $b^0_{max} = 0.99(0.88 - 1.00)$
Survival probability	$(\phi_U)_0 = 0.709$ $(\phi_U)_{1:3} = 0.952$ $(\phi_U)_{4+} = 0.96$	$\phi_{0,f} = 0.78(0.52 - 0.89)$ $\phi_{1,f} = 0.89(0.87 - 0.94)$ $\phi_{2,f} = 0.90(0.88 - 0.94)$ $\phi_{3,f} = 0.91(0.89 - 0.94)$ $\phi_{4,f} = 0.91(0.89 - 0.94)$ $\phi_{5+,f} = 0.91(0.89 - 0.94)$

comparing the growth rates under the two models as a function of population size, in the model of Carroll et al. growth rate decreased linearly with the population size, while our IPM showed a minimal decrease in growth rate until the population was near the carrying capacity, after which it declined fast (Fig. 5C).

4. Discussion

4.1. Baltic grey seal population size

Estimating the size of the Baltic grey seal population is an important starting point for assessing the state of the population. Our estimate of population size was smaller than the earlier estimates. For example, Carroll et al. (2024) estimated the 2020 population size at 55,000, significantly higher than our estimate of 47,000 for the same year. This difference can be attributed to the difference between the value of the mean observation probability of seals, excluding pups of the year, in aerial census counts (μ), which our IPM estimated to be higher than the fixed value used by Carroll et al. (84% vs. of 70%) that was based on the only previous study estimating the observation probability by Hiby et al. (2007). While this previous estimate of observation probability in census counts was included in our model through the prior distribution, our posterior estimate was driven by the joint information from the complementary data sets used to fit our model. Specifically, the total harvest combined with information on population growth rate, estimable from the aerial census counts, together informs about the total population size – for a given growth rate, a larger total harvest needs to be paired with a larger population size – and through that about the observation probability (Ersalman et al., 2025). Hence, in addition to being a population management measure, hunting statistics also provide information on population

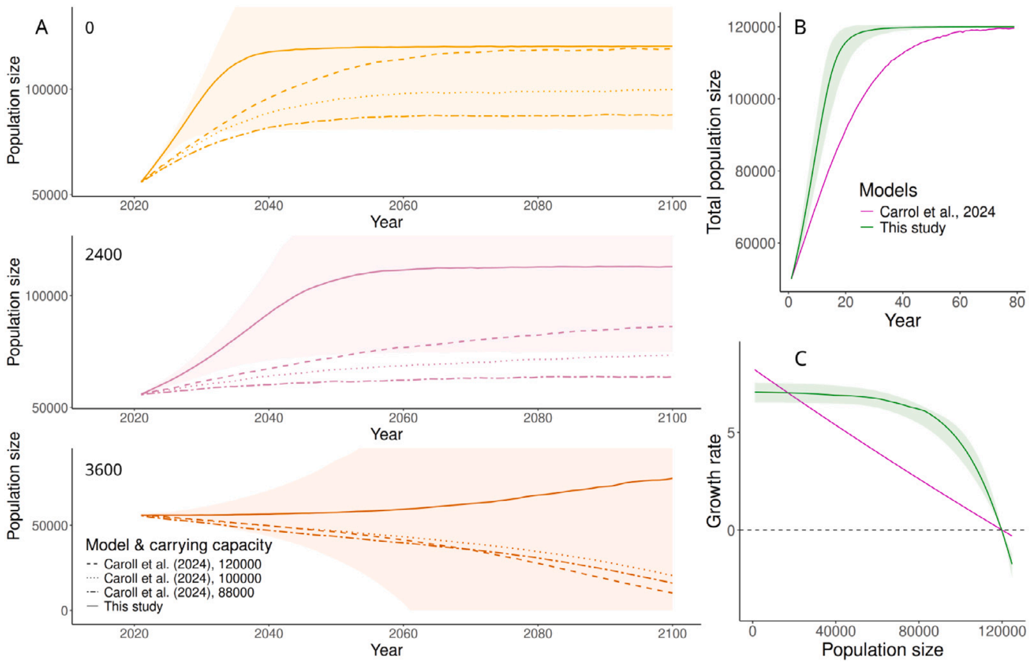


Fig. 5. (A) Predicted population size of the Baltic grey seal under different harvest scenarios (0,2400, and 3600 hunted seals per year) with the model of Carroll et al. under three different carrying capacity scenarios, and with the model of this study (95% CI added for our model). The population size (B) and growth rate (C) simulated under the model of this study and the model of Carroll et al. starting from the same initial population.

parameters when combined with other data. However, the information provided by hunting statistics is expected to decrease with decreasing total harvest, since then its effect on the growth rate would be smaller. It is also important to note that newborn pups do not moult during the aerial census in May–June, and the timing of the moult for juveniles and adults – and thus the observed proportion of seals during census surveys – varies between age and sex classes and is also influenced by the environment and breeding (Cronin et al., 2014; Schop et al., 2017; Ersalman et al., 2025). Therefore, if there is a shift in the demographic composition of the population, such as a change in sex or age ratios, it could impact how many seals are observed during the surveys. For example, a change in the number of pups in the population will only affect the census count of the next year.

4.2. Carrying capacity of baltic grey seals

Another example showcasing how the Bayesian framework combined with an IPM can provide information on parameters that would be otherwise difficult to estimate is our result on Baltic grey seal carrying capacity. Acquiring an accurate estimate for a carrying capacity is vital to developing suitable conservation strategies, and it can have a great impact on population management and, particularly, on hunting regulation. So far, there has been no research aiming at estimating the current carrying capacity of Baltic grey seals; instead, existing studies have used the estimate for historical maximum population size in the early 1900s made by Harding and Härkönen (1999). The estimate provided by our study (approximately 120,000) is somewhat larger than the historical one. This increase in carrying capacity could arise from changes in the state of the Baltic Sea ecosystem, which has become much more productive in the past century due to eutrophication (Andersen et al., 2017). The difference between these two estimates could also simply arise from uncertainties related to historical carrying capacity estimates. Moreover, it could be that our estimate underestimates the potential carrying capacity since grey seals currently do not occupy all the same areas that they historically used to occupy (Galatius et al., 2020).

Estimating carrying capacity and density dependent factors, and how they depend on environmental conditions and resources, is difficult when the population size has not stabilised. For example, Nelson et al. (2023) estimated the carrying capacity of harbour seals in British Columbia using data from 135 years and multiple population fluctuations and Tinker et al. (2026) estimated the carrying capacity of Northwest Atlantic harp seals (*Pagophilus groenlandicus*) using data from seven decades. Since we had only 20 years of data during which the Baltic grey seal population has increased from its historical low, our carrying capacity estimate can be sensitive to model assumptions, specifically when – relative to the carrying capacity – the model predicts the population growth rate to bend. Thus, the carrying capacity estimate could change if the form of the density dependence was changed (see also Section 4.6 for more discussion on this). It should also be noted that the carrying capacity parameter in our model corresponds to the carrying capacity in the presence of the mean WAA of herring (i.e., the mean weight of herring over 5 years old) during the study period. We then analysed the effect of the WAA of herring on the realised carrying capacity of grey seals by estimating the stabilising population size in the future.

4.3. Effects of prey on grey seal population

The modelling of the dependence of the birth rate on the WAA of herring was motivated by studies showing that herring is among the most important items in the diet of grey seals (Scharff-Olsen et al., 2019) and the findings of Kauhala et al. (2019), who reported a positive correlation between the birth rate of Baltic grey seals and the mean weight of herring over the age of five. Our results show a similar dependency to that found by Kauhala et al. (Figs. 2 A, C) and suggest that the intrinsic birth rate can be up to 30% higher with the highest compared to the lowest herring WAA observed between 2003 and 2024. However, our results suggest that the carrying capacity changes along with the WAA of herring only little (Fig. 4A). Even though this seems contradictory to how prey availability is understood to affect the carrying capacity of an environment (Washington State Academy of Sciences, 2022), it should be noted that our model does not assume changes in prey availability but only in prey quality. Other prey species and environmental factors, such as annual temperature and spring ice cover, could also affect the carrying capacity, for example, through availability of reproduction habitats (Tinker et al., 2021).

Reports suggest Baltic grey seals are capable of travelling long distances and can forage over the entire Baltic Sea (Oksanen et al., 2014). Our results suggest that the WAA of herring in the Gulf of Bothnia better explains the fluctuations in grey seal birth rate than that in the Baltic proper and the Gulf of Finland. This could indicate that grey seals are more dependent on herring in the north, possibly because they spend more time foraging northern areas, or they visit those areas at a time of year with the highest demand for high-quality food resources. Note also that, since herring dependency is expressed through the birth rate, the model can only inform us about the foraging habits of females.

Our model linking prey quality and reproductive success aims to serve as the first step to help develop an ecosystem-based approach to the Baltic grey seal population management as opposed to single-species management. Even though the effect of WAA of herring on grey seal population dynamics was small near the carrying capacity, where the density-dependent decline in birth rate became dominant, at smaller population sizes, it had a significant impact on population viability. For example, at a yearly harvest of 3600, decreasing herring WAA by 4 grams from its average value led to a 22 percentage-unit increase in the probability of extinction by 2080. These findings suggest that a healthy herring population is more important when the size of the seal population is small. The results also emphasise the need to apply a comprehensive approach to seal management and to acknowledge the changing environmental conditions of the Baltic Sea. In general, the WAA of Baltic herring has decreased substantially in recent decades, the decline occurring in the southern Baltic much earlier than in the north (ICES, 2023). These shifts are driven by, for example, changes in salinity, zooplankton communities, and sprat abundance (Casini et al., 2010; ICES, 2024) — all factors that are not possible to manage, at least not in the short-term. Hence, grey seal management should emphasise factors that can be controlled, such as hunting and bycatch mitigation.

4.4. Annual survival

Estimates on female grey seal adult survival probabilities for Atlantic grey seals range from 0.935 to 0.97, while for pups, there is a high variety in the estimates, ranging from 0.4 to 0.875 (Harwood and Prime, 1978; Baker and Baker, 1988; Harding et al., 2007; Thomas et al., 2019). We estimated a slightly lower adult female survival of 0.91 (0.89; 0.94), while our estimate for the female pup survival probability, 0.78 (0.52; 0.89), was on the higher end of the range of estimates for other grey seal populations. The adult female survival probability corresponds to adult stage life expectancy of 11 years, when a seal would be 16 years old. This seems a bit low since grey seals are known to be able to live up to 25–35 years. However, in our model it is to some extent confounded with the pup survival probability and birth rate. Our estimate for pup survival is also on the higher end of the corresponding estimate for Baltic ringed seals (Ersalman et al., 2025). This may be explained by the different breeding habits of the two species. While grey seals can breed on ice or land, ringed seal pups are nursed exclusively on ice (Jüssi et al., 2008; Sundqvist et al., 2012). Moreover, since ringed seals build snow lairs for their pups, they may be more vulnerable to changes in ice and snow conditions. While our model did not include environmental covariates for pup survival, changes in climate can be expected to also affect the Baltic grey seals (Jüssi et al., 2008). For grey seals in the Sable Islands in Canada, den Heyer and Bowen (2017) also estimated the difference between adult male and female survival rates (0.943 versus 0.976). We used this ratio in defining the prior for the deviation in mortality rate between males and females. However our posterior estimate for the ratio indicated smaller difference between males and females in the Baltic Sea than in Sable Islands (Fig. 13).

While our model captured well that the survival probability increases as seals age into adulthood, the shape of the survival probability as a function of age was not well identified by our model. This is not surprising, as while the aerial count data contain information on the growth rate of the population, we have a very limited understanding of the age structure of the population. This information would be needed to identify how the survival probabilities for different ages are related to each other. Data on age come from sampling hunted and bycaught seals, which do not represent the structure of the entire population, as there can be significant selectivity towards certain age groups both for hunting and bycatch — for example, pups have been found to be much more likely to be bycaught in fishing gear than older seals (Bjørge et al., 2002; Luck et al., 2022) and male seals are more common to raid fishing gear than females (Königson et al., 2013; Oksanen et al., 2014). Acquiring a reliable estimate of the magnitude of bycatch could also provide valuable information about its significance to the grey seal population. However, obtaining accurate data on this is difficult since fishers tend not to report them (Vanhatalo et al., 2014). While legislations in Finland and Sweden require fishers to report each bycaught seal since 2016 and 2022, respectively, they are not well enforced (L. C. and M. K. personal communication).

4.5. Hunting scenario predictions

The hunting quotas in Sweden and Finland have been rising, and the realised total yearly harvest grew from 304 seals in 2002 to 1699 in 2019. From 2020 onward, the yearly total harvest has stagnated, with only 1311 seals being shot in 2024, even though the quota permitted the hunt of 3050 seals. Our results indicate that under the current hunting pressure, the population would continue to grow and stabilise at the carrying capacity before 2060 — assuming that environmental conditions remain the same. However, if total harvest was increased significantly, the viability of the population would first depend on the hunting selectivity and with further increase of hunting the population would become unviable. For example. if the current hunting quota of 3050 seals was filled, the population would most likely continue to grow towards the carrying capacity in all other hunting scenarios except if hunting was selective towards females, in which case there would be a considerable probability (19%) for extinction. If as many as 3600 seals were shot each year, the population would become uncertain, with a high possibility of extinction by 2080. If the yearly harvest were raised to 4800, extinction is predicted to be inevitable by 2080.

The impact of hunting on the Baltic grey seal population thus depends on how hunters target each demographic group. Adult male grey seals are known to be particularly prone to damaging fishing gear (Königson et al., 2013; Oksanen et al., 2014); hence, when hunters target problem seals, it may lead to a higher proportion of males shot than under recreational hunting. This could mean that a shift from mainly protective hunting towards more recreational hunting in the future could further alter the effects and consequences of hunting, even if the number of harvested seals remained unchanged. Moreover, with a large total harvest, the combined effect of hunting selectivity and the state of the ecosystem can lead to further deviations. For example, at a harvest size of 4800, most scenario predictions led to fast grey seal extinction with virtual certainty, but under a combination of high WAA of herring and a male-selective hunting, the population had an 79% chance of survival until 2080 (Fig. 4B). Nater et al. (2024) showed similar relationship with hunting and ice for ringed seals in Svalbard and Tinker et al. (2026) studied the combined effects of multiple hazards for Northwest Atlantic harp seals.

Throughout the analysis of the forecasted population scenarios, it is important to note that even extension risks of a few percentage points are considered non-negligible. In conservation biology and risk analysis, acceptable extinction risk is often defined as a 5% to 10% probability of extinction over a 100-year timeframe (Wilhere, 2024). As our model forecasts the population only 55 years into the future, our extinction probabilities should be even more strictly evaluated.

4.6. Model criticism and comparison to previous modelling approaches

The prior and likelihood sensitivity analyses suggested that our model estimates and predictions were not sensitive to the choices of prior distributions. Moreover, when comparing our parameter estimates for the Baltic grey seals with the estimates from the matrix population modelling approach of Carroll et al. (2024), we did not find significant deviations in general (Table 3). The only considerable difference was the estimate of the carrying capacity, which was estimated to be 30% larger in our work than with the approach of Carroll et al. (2024). Our parameter estimates compared well with those reported for other grey seal populations as well (see Section 4.4).

Certain aspects of population predictions were sensitive to the choices of the model equations though. The clearest example of this is how the density dependence is incorporated into the model. The density dependence equation of our model induces qualitatively different growth rate at low and high population sizes compared to, for example, the Beverton–Holt model. At a small population size, the grey seal population grew considerably faster under our model than with the Beverton–Holt model of Carroll et al. (Fig. 5A, B). However, in the latter, the growth rate decreased linearly with population size, while with our formulation, the growth rate stayed nearly constant until close to the carrying capacity and declined sharply thereafter (Fig. 5C). While the intrinsic growth rates are similar in both models, the Beverton–Holt model induces a much smaller growth rate for medium-range population sizes than our model, resulting in greater vulnerability to hunting under the former assumption. This then partially explains also the qualitative differences in the predicted effects of hunting between the two studies. Our scenario predictions were somewhat more optimistic than the previous analysis by Carroll et al. (2024), who predicted a slower growth rate and certain extinction already when 3600 seals are shot each year.

One could thus argue that using the Beverton–Holt density-dependent growth model would be a more precautionary option. However, its parameters cannot be directly linked to grey seal biology. Our model, on the other hand, was built so that all its parameters have a biological interpretation at the individual level. Since scenario predictions were sensitive to the description of density dependence, gaining a better understanding of the environmental and demographic processes impacting grey seal reproduction would be important in the future. For example, it is debatable whether the abortion rate of grey seals increases or decreases from early to late pregnancy (see also, Ersalman et al., 2024). Late-term abortions are reported to occur for some pinniped species (Pitcher et al., 1998; McKenzie et al., 2005; Stenson et al., 2016), but signs of Baltic grey seal abortions have been very rarely seen on the necropsy table (S.P. personal communication). However, it should be noted that in our model, we separated the pre-implantation failures from post-implantation abortions. Another caveat in our model, and in the Beverton–Holt model, is that the birth rate is highest at zero population density, while it would be more realistic to assume birth rate to be highest at some low population size. However, even though Baltic seals have just recovered from very low population densities, estimating this Allee effect would be difficult due to the confounding from the pesticide induced reproduction impairment (Kauhala et al., 2014) that happened concurrently with the low population densities. It is also uncertain, through which processes environmental conditions and resources affect reproduction and survival. We included the effect of herring WAA into our model through intrinsic birth rate, which implicitly assumes that its relative effect is the same in small and big population size. However, some studies have described resource effects through density dependent mortality rates (Tinker et al., 2026) or carrying capacity parameter (Tinker et al., 2021).

Since the grey seal population is currently increasing, and this increase is predicted to slow down in the near future, it seems plausible that we can better learn about the drivers of density dependence in the future. This would also allow for better estimation of current carrying capacity. Although our model was able to provide an updated estimate for the carrying capacity (our posterior was clearly different from the prior), this estimate is dependent on the assumptions on density dependence in our model (see also Section 4.2).

Our model for annual hunting assumed that hunting effort decreases over the hunting season. While in Finland the decreasing trend in the harvest numbers over each year is rather clear (Fig. 6), there is more variation in this trend in Sweden (Fig. 7). Hence, we did a sensitivity test and tested also a model with constant hunting effort. Both models give virtually the same results. The most likely explanation for this is that our data are not very informative on population level effects of temporal distribution of hunting.

In addition to the differences between the density dependence assumptions, our model differed from the previous Baltic grey seal population models in other respects as well. All previous approaches have described the Baltic grey seal population via a deterministic matrix population model (Harding and Härkönen, 1999; Kokko et al., 1999; Carroll et al., 2024). They have also used a frequentist framework and estimated the parameters of the model in a stepwise manner.

5. Conclusion

This study used a Bayesian integrated population model to integrate multiple data sets for a comprehensive assessment of the Baltic grey seal population and its future prospects. Currently grey seal population is growing steadily at a population size of approximately 57,000 individuals and, under current conditions, is estimated to reach its carrying capacity of approximately 120,000 by 2050. If the total harvest of grey seals was increased from their current level, the growth rate of the population would decrease. Filling the current quota would decrease the growth rate considerably and could lead to population decline if the demographic composition of hunting changed towards females. Eventually, if the total harvest exceeded 3600 individuals and if hunting shifted from protective (targeting more males) to recreational (targeting more females and pups) hunting, the grey seal population would decline with high probability.

Our results also suggest that the mean weight of herring over 5 years old affects grey seal birth rate, implying population-level effects especially together with high total harvest. Prey quality should, thus, be considered if hunting quotas were to be increased considerably. Moreover, our results have direct implications for seal population management, for example, by providing an approach to quantify the precautionary approach, and target reference population levels for grey seal abundance as in the presence of the mean weight of herring over five years old during the study period (asked by HELCOM (HELCOM, 2019)) or estimating long-term sustainable reference levels for human-induced removal of grey seals. However, as there are several important factors, such as bycatch, prey stock size or climate factors that are not incorporated into this model, ongoing monitoring is essential for sustainable management and risk assessments in the changing environment.

CRediT authorship contribution statement

Milena Vanko: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Inari Helle:** Writing – review & editing, Resources, Data curation. **Mervi Kunnasranta:** Writing – review & editing, Resources, Data curation. **Markus P. Ahola:** Writing – review & editing, Resources, Data curation. **Britt-Marie**

Bäcklin: Writing – review & editing, Resources, Data curation. **Anja M. Carlsson:** Writing – review & editing, Resources, Data curation. **Linnea Cervin:** Writing – review & editing, Resources, Data curation. **Sara Persson:** Writing – review & editing, Resources, Data curation. **Jarno Vanhatalo:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Hunting

To understand how the hunting effort changes throughout the year, we analysed the distribution of recorded dates when seals were shot in Sweden and Finland, reported by the hunters. Detailed date information was incomplete for many of the years between 2003 and 2024, but there were 6 years in Finland (2016–2018 and 2021–2023) when the date was recorded trustworthily at least for 60% of the shot seals and 15 years in Sweden when the date was recorded trustworthily at least for 80% of the shot seals. In these years, the hunting effort showed a decreasing trend, supporting our assumption of a linearly decreasing hunting effort.

Appendix B. Survival

The ODE for the seal population during hunting season $0 < \tau < k$ is

$$\frac{dH^{\mathrm{sw}}_{i,t}}{d\tau} = \tilde{n}_{i,t}(\tau)E^{\mathrm{sw}}_{i,t}(k-\tau) \tag{18}$$

$$\frac{dH^{\mathrm{fi}}_{i,t}}{d\tau} = \tilde{n}_{i,t}(\tau)E^{\mathrm{fi}}_{i,t}(k-\tau) \tag{19}$$

$$\frac{dD_{i,t}}{d\tau} = \mu_i\tilde{n}_{i,t}(\tau) \tag{20}$$

$$\frac{d\tilde{n}_{i,t}}{\tau} = -\tilde{n}_{i,t}(\tau)\sum_C E^C_{i,t}(k-\tau) - \mu_i\tilde{n}_{i,t}(\tau). \tag{21}$$

This is solved for the number of alive seals by

$$\tilde{n}_{i,t}(\tau) = \tilde{n}^0_{i,t}\exp\left(-\sum_C E^C_{i,t}\left(k\tau - \tau^2/2\right) - \mu_i\tau\right), \tag{22}$$

where $\tilde{n}^0_{i,t} = \tilde{n}_{i,t}(0)$ is the total population size in demographic group i at the beginning of the hunting season. From this, the surviving population size at time $\tau = k$ can be evaluated as:

$$\tilde{n}_{i,t}(k) = \tilde{n}^0_{i,t}\exp\left(-\sum_C E^C_{i,t}k^2/2 - \mu_i k\right). \tag{23}$$

Throughout the rest of the year, when hunting is not allowed, the dynamics of the surviving population are simply

$$\frac{d\tilde{n}_{i,t}}{\tau} = \mu_i\tilde{n}_{i,t}(\tau), \tag{24}$$

solved by

$$\tilde{n}_{i,t}(\tau) = n^*_{i,t}\exp\left(-\mu_i\tau\right), \tag{25}$$

Hence, the population size at the beginning of the hunting season, $\tau_0 \approx 1.5/12$ time after seals gave birth, can be calculated as

$$\tilde{n}^0_{i,t} = \tilde{n}_{i,t}(\tau_0) = n_{i,t}\exp\left(-\mu_i\tau_0\right), \tag{26}$$

and the surviving population size right before seals give birth in the next year is

$$S_{i,t+1} = \tilde{n}_{i,t}(k)\exp\left(-\mu_i(1-\tau_0-k)\right) \tag{27}$$

$$= \tilde{n}^0_{i,t}\exp\left(-\sum_C E^C_{i,t}k^2/2 - \mu_i k\right)\exp\left(-\mu_i(1-\tau_0-k)\right) \tag{28}$$

$$= n_{i,t}\exp\left(-\mu_i\tau_0\right)\exp\left(-\sum_C E^C_{i,t}k^2/2 - \mu_i k\right)\exp\left(-\mu_i(1-\tau_0-k)\right) \tag{29}$$

$$= n_{i,t}\exp\left(-\sum_C E^C_{i,t}k^2/2 - \mu_i\right) \tag{30}$$

$$= n_{i,t}\exp\left(-\sum_C E^C_{i,t}k^2/2\right)\phi_i, \tag{31}$$

where $\phi_i = \exp\left(-\mu_i\right)$ is the probability that a seal in demographic group i survives all non-hunting mortality throughout the year. Hence the probability of survival in year t and group i is:

$$\rho^S_{i,t} = \frac{S_{i,t+1}}{n_{i,t}} = \exp\left(-\sum_C E^C_{i,t}k^2/2\right)\phi_i \tag{32}$$

Moreover, substituting (23) into the ODE system, we get that

$$\frac{dH^{\mathrm{C}}_{i,t}}{d\tau} = \tilde{n}^0_{i,t}E^{\mathrm{C}}_{i,t}\exp\left(-\sum_C E^C_{i,t}\left(k\tau - \tau^2/2\right) - \mu_i\tau\right)(k-\tau) \tag{33}$$

Since this equation is not analytically solvable, we used a numerical ODE solver to evaluate $H^C_{i,t}(k)$, from which we can express the probability of being hunted in country c as

$$\rho^{H_C}_{i,t} = \frac{H^C_{i,t}(k)}{n_i, t}, \tag{34}$$

and the probability of death not by hunting is

$$\rho^D_{i,t} = 1 - \rho^{H_{\mathrm{sw}}}_{i,t} - \rho^{H_{\mathrm{fi}}}_{i,t} - \rho^S_{i,t}. \tag{35}$$

Appendix C. Reproduction

C.1. Density-dependent mortality model

Grey seals mate in early spring, but, as for most pinnipeds, the implantation of embryo is delayed and only occurs approximately 3.5 months later (Atkinson, 1997). We denote by p^t_0 the probability that the implantation of the embryo occurs for a seal in year t and by $\theta(n_t, \tau)$ the failure rate of the pregnancy at time τ after implantation when the size of the population is n_t. Then the probability that a seal is still pregnant at time τ after implantation in year t can be expressed as

$$p_t(\tau, n_t) = p^t_0\exp\left(-\int_0^\tau \theta(n_t, \tau^*)d\tau^*\right). \tag{36}$$

We assumed the rate of pregnancy losses increases linearly from zero immediately after implantation to a maximum at parturition (but see Section 4 and Ersalman et al. (2025) for discussion of this assumption). The failure rate was assumed to increase exponentially along with the population density, so that

$$\theta(\tau, n_t) = \theta^{\mathrm{start}}_0 e^{\theta_1 n_t}\tau, \tag{37}$$

where $\theta^{\mathrm{start}}_0$ is the failure rate at zero grey seal density and θ_1 is the rate of density-dependent increase of pregnancy failures. Hence,

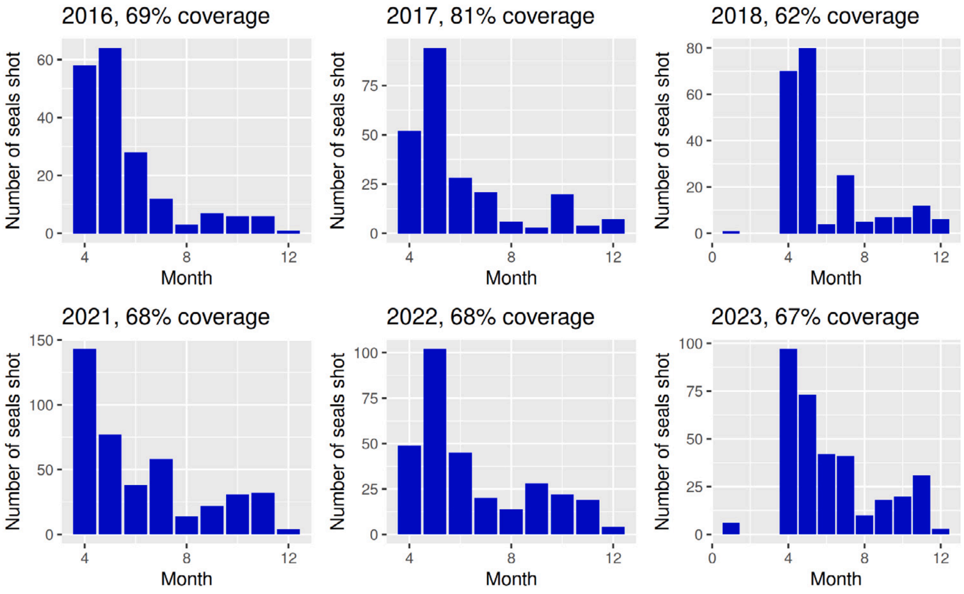

Fig. 6. Monthly number of hunted seals in Finland.

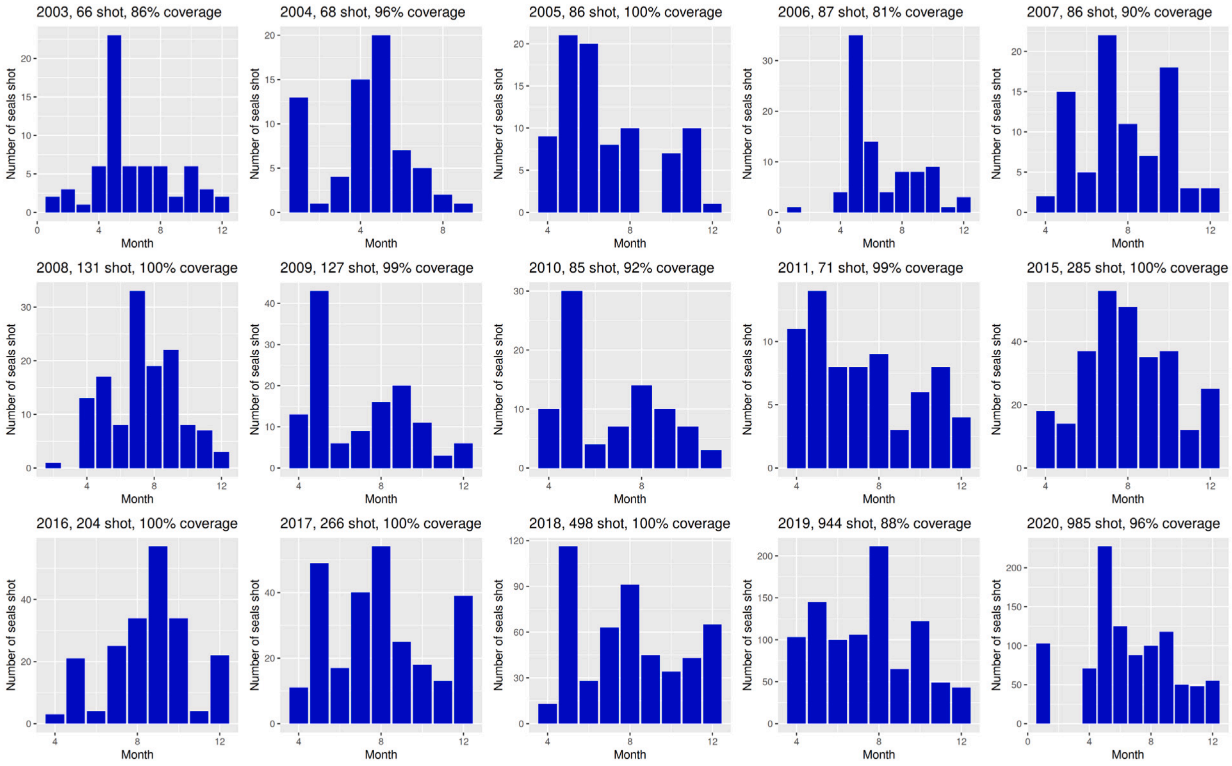

Fig. 7. Monthly number of hunted seals in Sweden.

plugging (37) into (36), the probability that a seal is still pregnant time τ after implantation in year t is

$$p_t(\tau, n_t) = p_0^t e^{-\theta_0^{\text{start}} e^{\theta_1 n_t} \tau^2/2}. \tag{38}$$

Now, the probability of giving birth, $b_t(n_{t-1})$, with given population density, is equal to the probability that a seal got pregnant in year $t-1$ and is still pregnant by the time of parturition in early spring, which is $\tau \approx 3/4$ years after implantation. Hence,

$$\begin{aligned} b_t(n_{t-1}) &= p_{t-1}(3/4, n_{t-1}) \\ &= p_0^{t-1} e^{-\theta_0^{\text{start}} \frac{9}{32} e^{\theta_1 n_{t-1}}} \\ &= p_0^{t-1} e^{-\theta_0 e^{\theta_1 n_{t-1}}}, \end{aligned} \tag{39}$$

where $\theta_0 = \frac{9}{32}\theta_0^{\text{start}}$. Then, at zero population density, the birth rate is

$$b_t(0) = b_0^t = p_0^{t-1} e^{-\theta_0}, \tag{40}$$

from which the initial probability of implantation of the embryo can be expressed as

$$p_0^{t-1} = b_0^t e^{\theta_0}. \tag{41}$$

When this is substituted into the equation for the birth rate in year t, it results in

$$b_t(n_{t-1}) = b_0^t e^{-\theta_0\left(e^{\theta_1 n_{t-1}}-1\right)}. \tag{42}$$

The parameter b_0^t can be called an intrinsic birth rate and was defined in Eq. (11) as

$$b_0^t = b_0^t(h_{t-1}) = b_{min}^0 + \frac{b_{max}^0 - b_{min}^0}{1 + e^{-\left(\alpha+\beta(wh_{t-1}^{\mathrm{BP+GoF}}+(1-w)h_{t-1}^{\mathrm{GoB}})\right)}}, \tag{43}$$

When this dependence is made explicit in Eq. (42), we get

$$b_t(n_{t-1}, h_{t-1}) = b_0^t(h_{t-1})e^{-\theta_0\left(e^{\theta_1 n_{t-1}}-1\right)}. \tag{44}$$

Thus, in our model the herring WAA, h_t, impacts reproduction similarly to the probability of implantation.

The previous equation can be rearranged to express θ_1 as

$$\theta_1 = n_{t-1}^{-1} \log\left(1 - \theta_0^{-1} \log\left(\frac{b_t(n_{t-1}, h_{t-1})}{b_0^t(h_{t-1})}\right)\right). \tag{45}$$

When the population has reached its carrying capacity $K(h)$ under WAA of herring h (and in the absence of hunting), this becomes

$$\theta_1 = K(h)^{-1} \log\left(1 - \theta_0^{-1} \log\left(\frac{b(K(h), h)}{b_0(h)}\right)\right). \tag{46}$$

The birth rate at carrying capacity can be expressed from the Euler–Lotka equation (Caswell, 2001; Ersalman et al., 2025)

$$\frac{b}{2}\frac{\lambda^{-5}\prod_{i=0}^{4}\phi_{f,i}}{1-\phi_{f,5+}/\lambda} = 1 \tag{47}$$

at growth rate $\lambda = 1$, which yields

$$b_K = 2\frac{1-\phi_{f,5+}}{\prod_{i=0}^{4}\phi_{f,i}}, \tag{48}$$

where $\phi_{f,i}$ is the survival probability of females in age group i. Note that this is independent of the value of K or h, hence

$$\theta_1 = K(h)^{-1} \log\left(1 - \theta_0^{-1} \log\left(\frac{b_K}{b_0(h)}\right)\right) \tag{49}$$

for all values of h and hence can be parameterised with any choice of h. At $h = 0$ (in the case of average WAA of herring), the expression for the birth rate at zero density simplifies to

$$\bar{b} = b_{min}^0 + \frac{b_{max}^0 - b_{min}^0}{1+\exp(-\alpha)}, \tag{50}$$

hence we introduced the parameter $\bar{K} = K(0)$ and expressed θ_1 as

$$\theta_1 = \bar{K}^{-1} \log\left(1 - \theta_0^{-1} \log\left(\frac{b_K}{\bar{b}^0}\right)\right). \tag{51}$$

C.2. Model for pregnancy observations

The number of pregnant adult females past the preimplantation period (after July) can be described with a binomial model

$$y^{\text{pregnant}}|p_t(\tau_s) \sim \text{Binomial}\left(y^{\text{pregnant}} + y^{\text{not pregnant}}, p_t(\tau_s)\right), \tag{52}$$

where $y^{\text{not pregnant}}$ are all the seals that could possibly be detectably pregnant (adult, female, past preimplantation period), and $p_t(\tau_s)$ is the probability of a seal being pregnant in year t, τ_s time after implantation, which is the approximated time that passes between implantation and sample collection. Then, from Eqs. (38) and (42), $p_t(\tau_s)$ can be expressed as

$$p_t(\tau_s) = b_0^{t+1} e^{-\theta_0\left(\frac{16}{9}\tau_s^2 e^{\theta_1 n_t}-1\right)}. \tag{53}$$

Pregnancy sample data were collected after the preimplantation in late July. As the majority of samples were collected in August and September, we included only these samples in the analysis, and set $\tau_s \approx 1.5/12$ (corresponding to 1.5 months after implantation). These data were available only from Sweden.

The observation probabilities γ_t^{ij} of reproductive scars can be expressed as (Ersalman et al., 2025):

$$\gamma_t^{10} = b_t\pi_t^s(1-\pi_t^C) \tag{54}$$

$$\gamma_t^{01} = b_t(1-\pi_t^s)\pi_t^C + (1-b_t)\kappa\pi_t^C \tag{55}$$

$$\gamma_t^{11} = b_t\pi_t^s\pi_t^C \tag{56}$$

$$\gamma_t^{00} = 1 - \gamma_t^{01} - \gamma_t^{10} - \gamma_t^{11}, \tag{57}$$

where κ is the probability that a seal that has not given birth in year t has a CA (which may be present from a pregnancy in the previous year or a late abortion Hewer and Backhouse, 1968; Kauhala et al., 2014; Ersalman et al., 2025) and π_t^s and π_t^C are the detection probabilities of placental scar and CA in year t, respectively. This depends on the probability of the reproductive scars being visible by the time of examination. Moreover, due to differences in sampling circumstances, we have assumed that there is a yearly random variation in the probability of reporting a visible scar. Hence, the detection probabilities are modelled as:

$$\pi_t^s = \pi_v^s \exp\left(-\epsilon_t^s\right) \tag{58}$$

$$\pi_t^C = \pi_v^C \exp\left(-\epsilon_t^C\right), \tag{59}$$

where π_v^s and π_v^C are the probabilities of the placental scar and the CA being visible at the time of examination and $\epsilon_t^s \sim N(0, \sigma_s^2) > 0$ and $\exp\left(-\epsilon_t^C\right) < 1$ represent the probabilities of reporting a visible placental scar or CA in year t, respectively, where $\epsilon_t^s \sim$ half-N$(0, \sigma_s^2)$ and $\epsilon_t^C \sim$ half-N$(0, \sigma_c^2)$. Reproductive scar data were available only from Finland.

Appendix D. Priors

D.1. Initial population size

Hiby et al. (2007) used photo-identification data to estimate the total Baltic grey seal population in 2000 to be 15,600 with a 95% confidence interval of 9600 to 19,000. Harding et al. (2007) carried out research using count data along the Swedish coast, independent from our aerial count data. They estimated the annual growth rate of the Baltic grey seal between 1990 and 2004 to be 7.5%. Combining these two results would estimate the 2002 total population size to be 18,000 with a 95% confidence interval of 11,000 to 21,100. Therefore, we chose the prior for the initial population size in 2002 to be $n_0 \sim$ log-N$(9.8, 0.1)$.

D.2. Survival

The survival probability for adult females (excluding death by hunting) was given a Uniform(0.8,1) prior, as by previous research, this parameter has been estimated to be well within this range (Harwood and Prime, 1978; Thomas et al., 2019; Carroll et al., 2024). The prior for the pup survival probability was defined through the ratio of $\frac{\phi_{0,f}}{\phi_{5+,f}}$ which was given a Uniform(0,1) prior. The mortality rate induced by other causes than hunting was thought to decline sharply after the first year of a seal's life, decline at a decreasing rate until maturity is reached at age 5, and then stay constant (Harding et al., 2007). This indicates that the shape parameter c, introduced in Equation (4), should be between 0 and 1, as $c < 0$ would indicate an increasing mortality rate with age and $c > 1$ would indicate an increasing decline in the mortality rate for older ages. Therefore, c was given a Uniform(0,1) prior.

For males, mortality rates are not modelled directly; they are only modelled by their deviation from the female mortality rates. For male pups,

$$\log(\mu_{0,m}) = \log(\mu_{0,f}) + \nu_0 \tag{60}$$

Table 4
Priors for model parameters.

Initial population size	n_0	log-N(9.8, 0.1)
Adult female survival probability	$\phi_{5+,f}$	Uniform(0.8,1)
Female pup vs adult survival probability ratio	$\frac{\phi_{0,f}}{\phi_{5+,f}}$	Uniform(0,1)
Shape parameter for age dependent survival	c	Uniform(0,1)
Deviation from female survival for male pups	ν_0	Cauchy(0,0.2)
Deviation from female survival for males	ν_{5+}	Cauchy(0.88,0.2)
Hunting selectivity in Sweden	g^{sw}	N(0,0.5)
Hunting selectivity in Finland	g^{fi}	N(0,0.5)
Bycatch selectivity	g^{bc}	N(0,0.5)
Standard deviation of Swedish hunting effort	σ_{sw}	Cauchy(0,0.1)
Standard deviation of Finnish hunting effort	σ_{fi}	Cauchy(0,0.1)
Maximum birth rate at zero density	b^0_{max}	Uniform(0,1)
Ratio of minimum and maximum limiting birth rates	$\frac{b^0_{min}}{b^0_{max}}$	Uniform(0,1)
Midpoint of the logistic birth rate curve	$\frac{\alpha}{\beta}$	N(0,4)
Herring dependency parameter in birth rate	β	N(0,3)
Weight for herring in Baltic Proper combined with the Gulf of Finland	w	Uniform(0,1)
Failure rate of pregnancies	$\exp\left(-\theta_0\right)$	Uniform($\max(b^t_0)$, 1)
Carrying capacity	K_{max}	log-N (11.3, 0.3)
Mean observation probability in census counts, excluding pups of the year	μ	Beta(32,9)
Overdispersion parameter	r	log-N(5.3, 1)
Probability of CA in non-pregnant seals	κ	Uniform(0,1)
Probability of visibility of placental scar	π^s_v	Uniform(0,1)
Probability of visibility of CA	π^C_v	Uniform(0,1)
Variance of reporting probability of placental scars	σ_s	N(0,0.1)
Variance of reporting probability of CA	σ_c	N(0,0.1)

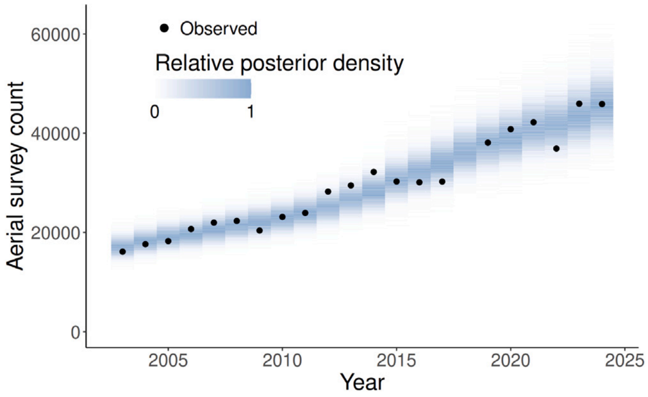

Fig. 8. Posterior predicted distribution of the yearly aerial count and the observed yearly aerial survey counts.

and for adults

$$\log(\mu_{5+,m}) = \log(\mu_{5+,f}) + \nu_{5+}, \tag{61}$$

from which we can express the male survival rate as

$$\phi_{i,m} = \phi_{0,f}^{e^{\nu_i}}, \tag{62}$$

for $i \in \{1, 5+\}$, and the deviations can be expressed as

$$\nu_i = \log\left(\frac{\log\left(\phi_{i,m}\right)}{\log\left(\phi_{i,f}\right)}\right). \tag{63}$$

For grey seals in the Sable Islands in Canada, den Heyer and Bowen (2017) estimated the adult male and female survival rates to be 0.943 (SE=0.003) and 0.976 (SE=0.001), respectively. This ratio would mean $\nu_{5+} = 0.88$. To account for the possible deviations between the Atlantic grey seals inhabiting the Sable Islands and the Baltic grey seal, we gave wider Cauchy(0.88, 0.2) prior for ν_{5+}, which would result in $\phi_{5+,m}$ having 80% of its probability density between 0.90 and 0.97 when $\phi_{5+,f} = 0.976$. For pups, following Thomas et al. (2019), we assumed that *a priori* the survival rate is equal for males and females and hence gave a Cauchy(0,0.2) prior to ν_0.

The yearly demographic group-specific hunting effort is expressed from the average hunting effort E^C_t as

$$E^C_{i,t} = \Psi^C_i E^C_t, \tag{64}$$

where Ψ^C_i is the hunting selectivity towards group i in country c.

Assuming that the total population size stays constant throughout the year, the equation for the harvest in group i simplifies to

$$\frac{dH^C_{i,t}}{d\tau} = \tilde{n}_{i,t} E^C_{i,t}(k - \tau), \tag{65}$$

hence the equation for the total harvest is

$$\frac{dH^C_t}{d\tau} = \sum_i \frac{dH^C_{i,t}}{d\tau} \tag{66}$$

$$= \sum_i \tilde{n}_{i,t} E^C_{i,t}(k - \tau) \tag{67}$$

$$= E^C_t(k - \tau) \sum_i \tilde{n}_{i,t} \Psi^C_{i,t}, \tag{68}$$

which can be solved analytically, leading to

$$H^C_t(\tau) = E^C_t(k\tau - \tau^2/2) \sum_i \tilde{n}_{i,t} \Psi^C_{i,t}. \tag{69}$$

Then the upper limit of the annual average hunting effort can be estimated by assuming that the quota is filled up, so at the end of the hunting season ($\tau = k$)

$$H^C_t(k) = Q^C_t = \frac{k^2}{2} E^C_t \sum_i \tilde{n}_{i,t} \Psi^C_{i,t}, \tag{70}$$

from which the maximal hunting effort can be derived as

$$E^C_t = \frac{2}{k^2} \frac{Q^C_t}{\sum_i \tilde{n}_{i,t} \Psi^C_{i,t}} \tag{71}$$

From this upper limit estimate of the hunting effort, we have expressed the true average hunting effort in year t via a stochastic reduction

$$E^C_t = \exp\left(-\epsilon^C_t\right) \hat{E}^C_t, \tag{72}$$

where $\epsilon^C_t \sim \mathrm{N}_+(\sigma^C)$ describes how much the year's hunting effort is lowered from filling the quota. The standard deviation σ^C is given a weekly informative $\mathrm{Cauchy}_+(0.1)$ prior, which induces the 95% CI of the reduction to fall between 0.14 and 0.99.

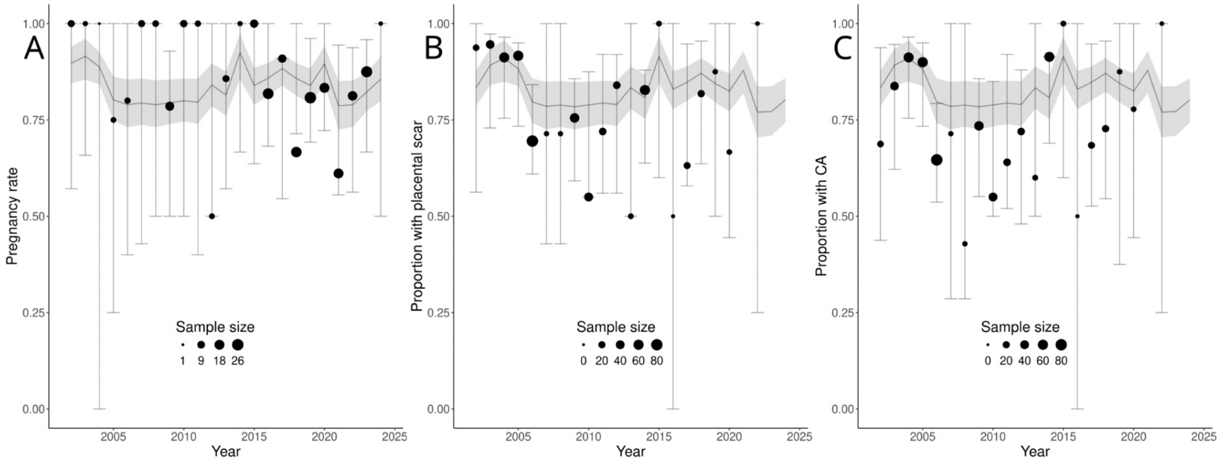

Fig. 9. Posterior predicted pregnancy (A) and birth (B, C) rate (median black line, 95% CI grey ribbon); observed proportions (dots) and posterior predicted 95% CI of the proportions (error bar) of pregnancy rate (A), reproductive scar (B) and CA (C).

The hunting selectivity is further expressed as

$$\Psi_i^C = \exp\left(g_i^C\right), \tag{73}$$

and similarly, the bycatch selectivity is expressed as

$$\Psi_i^{\mathrm{bc}} = \exp\left(g_i^{\mathrm{bc}}\right), \tag{74}$$

where g_i^C are given a $N(0, 0.5)$ prior, which induces density for the selectivity where 80% of the probability density falls within 0.5 and 1.9.

D.2.1. Reproduction

As derived in Equation (11), the birth rate at zero density in year t can be expressed as

$$b_0^t = b_{min}^0 + \frac{b_{max}^0 - b_{min}^0}{1 + \exp\left(-\alpha + \beta(w h_{t-1}^{\mathrm{BP+GoF}} + (1-w) h_{t-1}^{\mathrm{GoB}})\right)}. \tag{75}$$

Here, b_{min}^0 and b_{max}^0 are the limiting lowest and highest attainable birth rates with the variation in WAA of herring. b_{max}^0 was given a Uniform(0,1) prior and the prior for b_{min}^0 was induced from giving $\frac{b_{min}^0}{b_{max}^0}$ a Uniform(0,1) prior, which ensures $b_{min}^0 < b_{max}^0$.

The parameter β determines the shape of the logistic curve. For $|\beta| = 9$, an increase of 0.1 of the normalised WAA of herring at the midpoint of the logistic curve would result in a sudden increase of approximately $0.23(b_{max}^0 - b_{min}^0)$ in the birth rate. Such a sudden and sharp increase of such a small deviation in WAA of herring is very unlikely; hence, we have assumed that 95% of the prior probability density of β falls between −9 and 9, which corresponds to a $\beta \sim \mathrm{N}(0, 3)$ prior. The proportion $\frac{\alpha}{\beta}$ determines the midpoint of the logistic curve. As b_{min}^0 and b_{max}^0 are the lowest and highest attainable birth rates, the midpoint of the logistic curve should fall between the ecologically feasible values of the normalised WAA of herring. During the modelled period, the mean herring weight over age 5 ranged from 33 to 47. The historically observed maximum mean weight over age 5 was 75 g (ICES, 2023), which, after normalisation, would correspond to 11.5, and 0 g corresponds to −13. Hence, we have assumed that the prior for $\frac{\alpha}{\beta}$ should have 95% of its probability density between these boundaries and hence gave it a N(0,4) prior. The weight parameter w, measuring the importance of herring condition in different sea areas to birth rate, is given a Uniform(0,1) prior. The pregnancy failure rate θ_0 at zero density satisfies the equation

$$p_0^t = b_0^t \exp\left(\theta_0\right), \tag{76}$$

where p_0^t is a probability and hence cannot exceed 1. This then implies that

$$\exp\left(-\theta_0\right) > b_0^t \tag{77}$$

for all t, where b_0^t is the birth rate at zero density in year t. Moreover, as θ_0 is a failure rate, it must be larger than 0, implying $\exp\left(-\theta_0\right) < 1$. Hence the prior for θ_0 is expressed as

$$\exp\left(-\theta_0\right) \sim \mathrm{Uniform}(\max(b_0^t), 1). \tag{78}$$

The rate of density-dependent increase in pregnancy failures, denoted by θ_1, is expressed from the carrying capacity K_{max}, as described in Eq. (49). Therefore, we must set a prior for the K_{max} carrying capacity under ideal herring conditions. The only available estimate on the carrying capacity is derived from an estimate of the historical maximum population size, by Harding and Härkönen (1999). They estimated the population size to have peaked in 1914 and ranged from 88,000 to 100,000, which gives an estimate of the lower bound of K_{max}. Due to the high uncertainty of the estimate and a lack of information on the quality of the herring stock in the early 20th century, we gave K_{max} a wide log-N$(11.3, 0.3)$ prior.

D.2.2. Observation model parameters

By comparing the population size estimate based on photo-identification data and the number of counted seals at haul-out sites on the Swedish coast, Hiby et al. (2007) estimated that the proportion of all seals counted during their haul-out is 70%–85%. Thus, we defined $\mu \sim \mathrm{Beta}(32, 9)$, which includes approximately 90% of its mass between 0.7 and 0.85. Harding et al. (2007) have transformed the Swedish count data, assuming a zero growth rate, which resulted in the counts having a mean of 1770 and a standard deviation of 284. This would indicate that, at a minimum, r should be 40. Furthermore, it can be assumed that the variation in the yearly count should be at least as high as the variation in the mean observation probability, inducing an upper limit of 1250 on r. Therefore, we gave r a wide log-N(5.3,1) prior, which has 95% of its probability density between 40 and 1445.

The visibility probabilities of CA and placental scars, and the probability of CA present in non-pregnant seals, were all given uniform priors between zero and one. Underreporting of the reproductive scars is not common, so the standard deviations σ_s and σ_c, expressed in Eq. (58), were given N(0,0.1) priors. This induces a probability distribution for the reporting probabilities $\exp\left(-\epsilon_t^s\right)$ and $\exp\left(-\epsilon_t^C\right)$ that has 95% of its probability density between 0.81 and 0.99.

Appendix E. Model validation and prior sensitivity analysis

See Table 4 and Figs. 8–16.

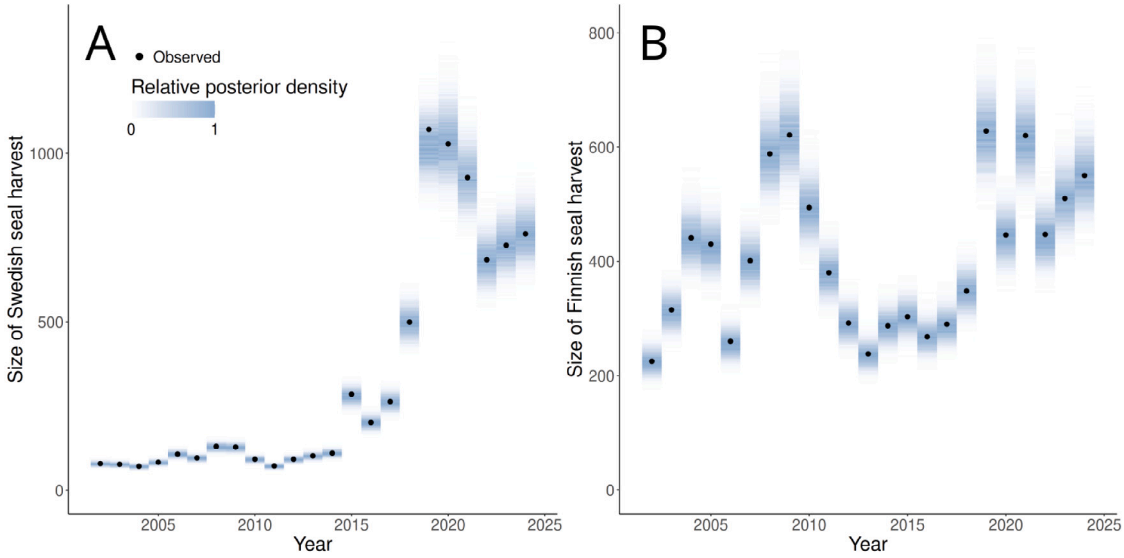

Fig. 10. Posterior predicted yearly distribution of total seal harvest size and observed yearly harvest in Sweden (A) and Finland (B).

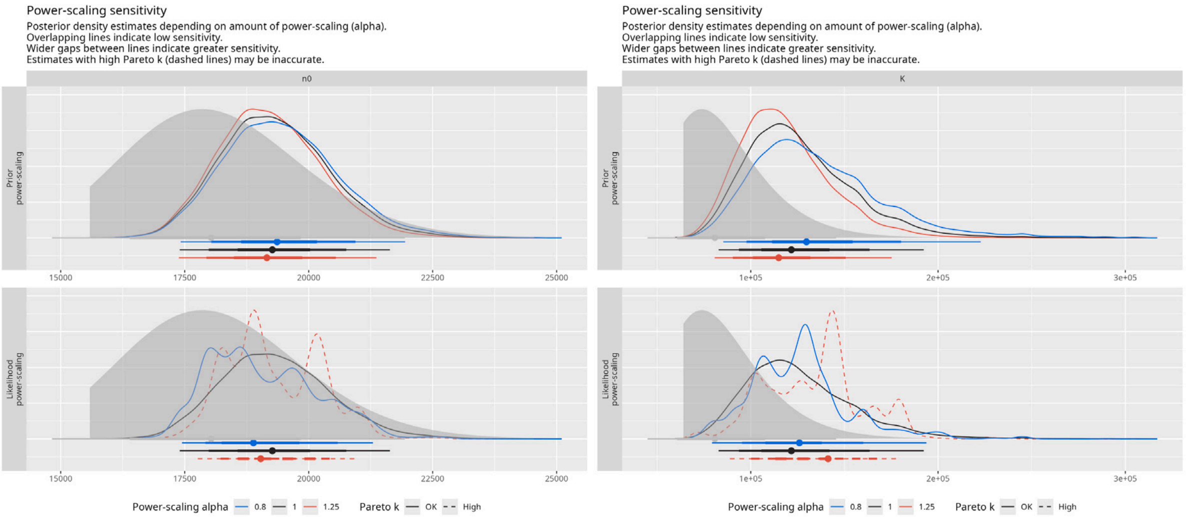

Fig. 11. Prior and likelihood sensitivity analysis for the initial population size n_0 (**On the left**) and carrying capacity $K_{\max}$ (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density function. The blue and red lines show the modified posterior density with power-scaling for prior ($p(n_0)$ on the left and $p(K_{\max})$ on the right; **upper figure**) and full likelihood for all data (**lower figure**).

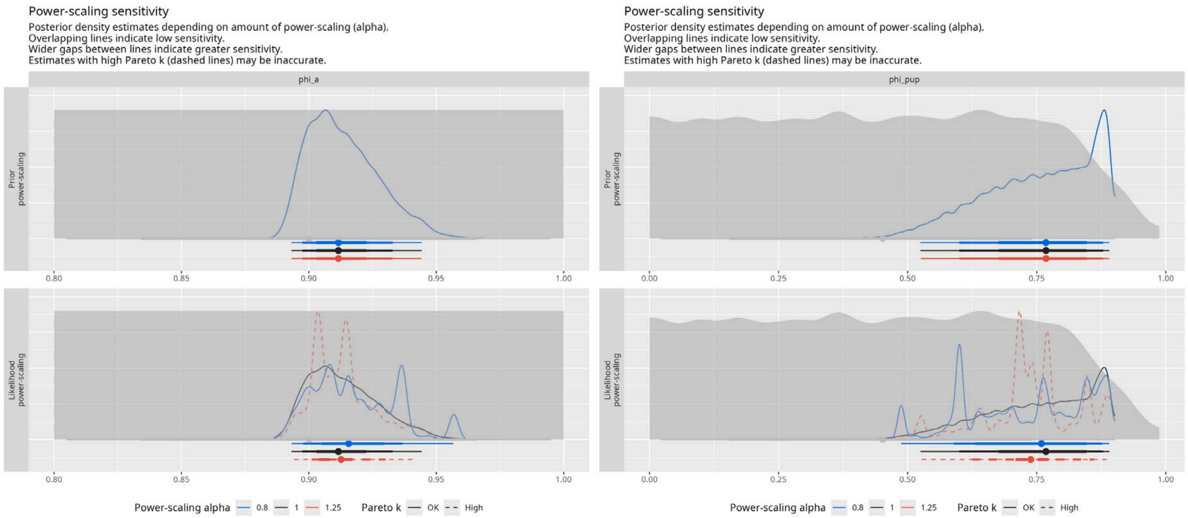

Fig. 12. Prior and likelihood sensitivity analysis for adult female mortality $\phi_{5+,f}$ (**On the left**) and pup mortality $\phi_{0,f}$ (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density function. The blue and red lines show the modified posterior density with power-scaling for prior ($p(\phi_{5+,f})$; **upper figure**) and full likelihood for all data (**lower figure**).

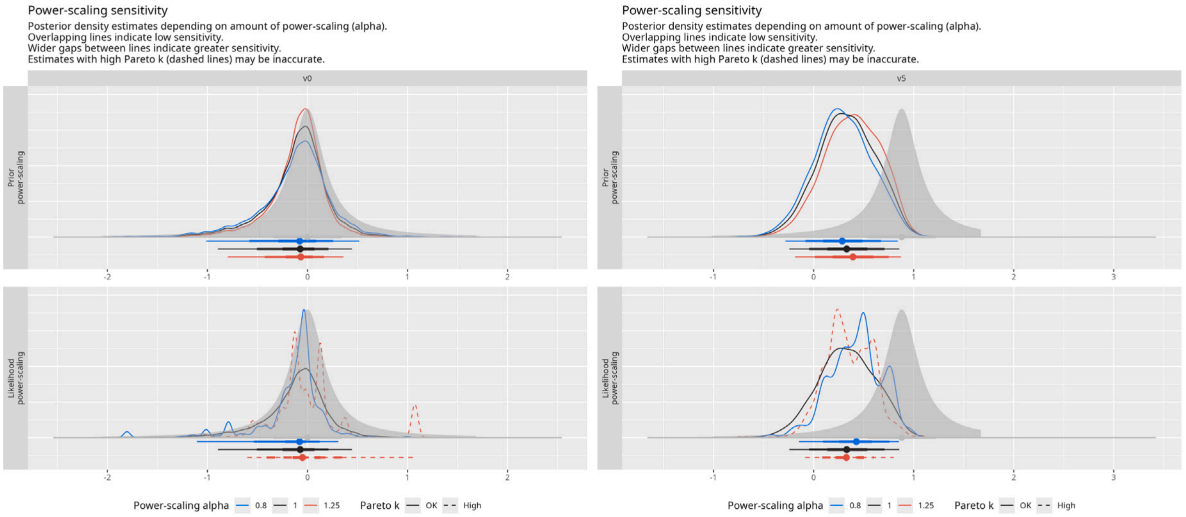

Fig. 13. Prior and likelihood sensitivity analysis for the deviation of male pup mortality rate from the mortality rate of female pups v_0 (**On the left**) and the deviation of male adult mortality rate from female adult mortality rate v_5 (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density functions. The blue and red lines show the modified posterior density with power-scaling for prior ($p(v_0, v_5)$; **upper figure**) and full likelihood for all data (**lower figure**).

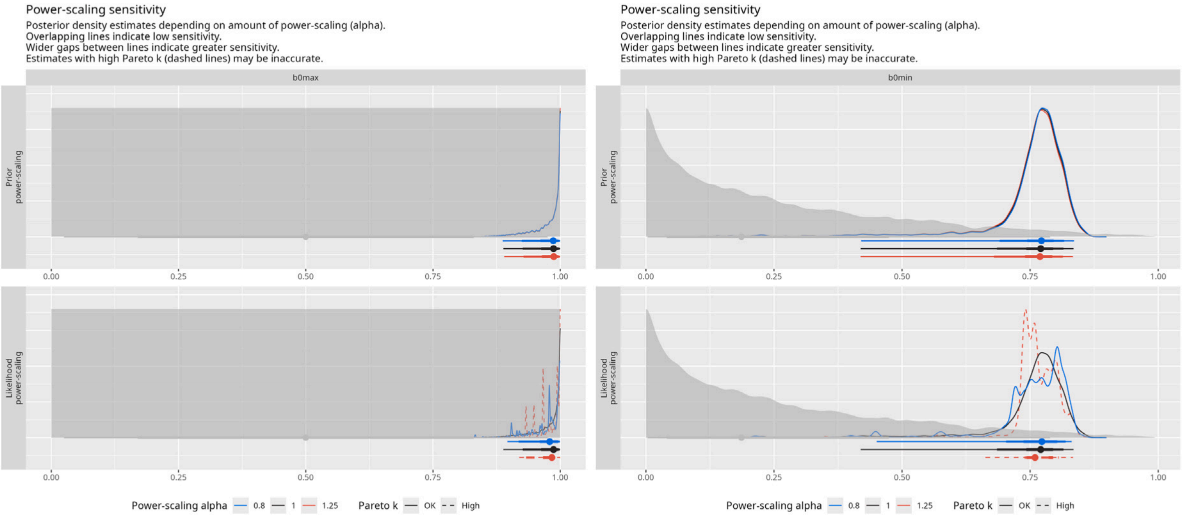

Fig. 14. Prior and likelihood sensitivity analysis for minimum intrinsic birth rate $b^0_{\min}$ (**On the left**) and maximum intrinsic birth rate $b^0_{\max}$ (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density function. The blue and red lines show the modified posterior density with power-scaling for prior ($p(b^0_{\min})$ on the left and $p(b^0_{\max})$ on the right; **upper figure**) and full likelihood for all data (**lower figure**).

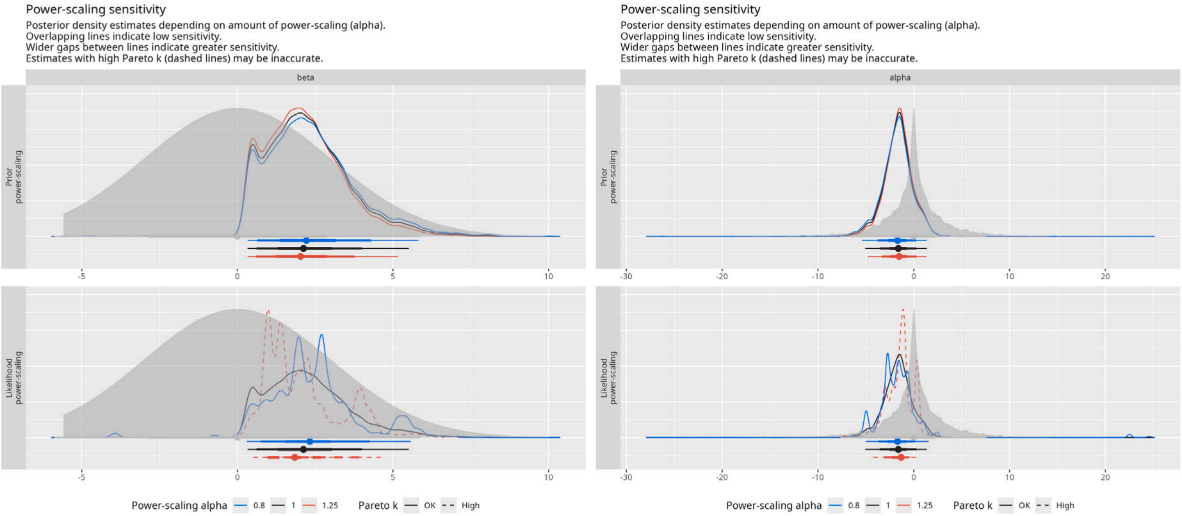

Fig. 15. Prior and likelihood sensitivity analysis for the parameters of the effect of herring WAA on birth rate: β (**On the left**) and α (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density function. The blue and red lines show the modified posterior density with power-scaling for prior ($p(\beta,\alpha)$; **upper figure**) and full likelihood for all data (**lower figure**).

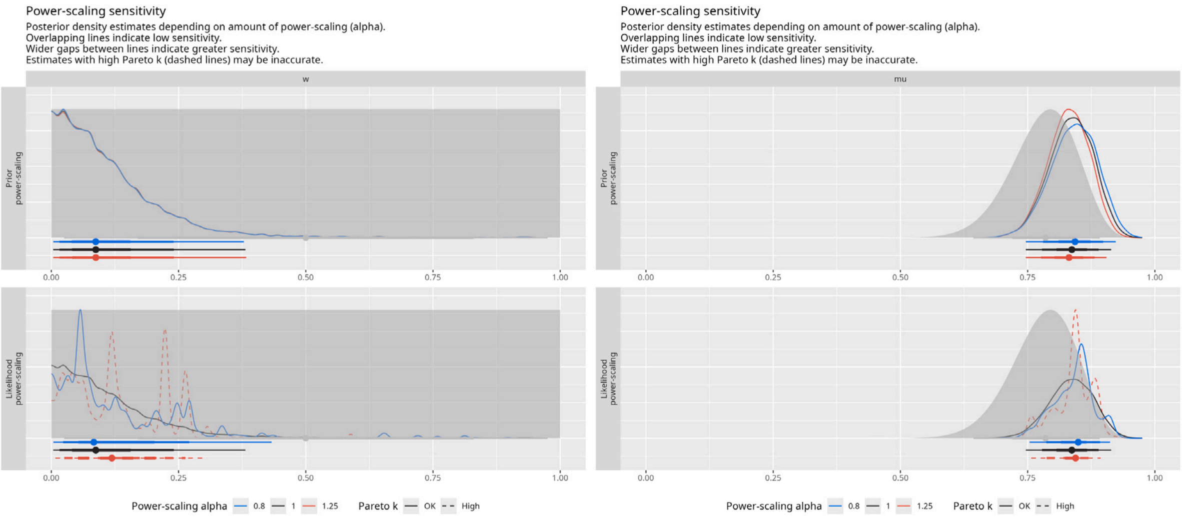

Fig. 16. Prior and likelihood sensitivity analysis for the relative weight of the Baltic Proper combined with the Gulf of Finland on the effect of WAA of herring w (**On the left**) and the average observation probability of seals, excluding the pups of the year, in the aerial census μ (**On the right**). The grey filled area shows the prior and the black line shows the posterior probability density function. The blue and red lines show the modified posterior density with power-scaling for prior ($p(w)$ on the left and $p(\mu)$ on the right; **upper figure**) and full likelihood for all data (**lower figure**).

Data availability

All the code and data are available on Zenodo at https://doi.org/10.5281/zenodo.20381625

Baltic grey seal IPM data (Original data) (Zenodo)

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