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Integrated population model reveals human- and environment-driven changes in Baltic ringed seal *Pusa hispida botnica* demography and behavior

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ABSTRACT: Integrated population models (IPMs) are a promising approach to test ecological theories and assess wildlife populations in dynamic and uncertain conditions. By combining multiple data sources into a unified model, they enable the parametrization of versatile, mechanistic models that can predict population dynamics in novel circumstances. Here, we present a Bayesian IPM for the ringed seal *Pusa hispida botnica* population inhabiting the Bothnian Bay in the Baltic Sea. Despite the availability of long-term monitoring data, traditional assessment methods have faltered due to dynamic environmental conditions, varying reproductive rates, and recently re-introduced hunting, thus limiting the quality of information available to managers. We fit our model to census and various demographic, reproductive, and harvest data from 1988 to 2023 to provide a comprehensive assessment of past population trends, and predict population response to alternative hunting scenarios. We estimated that 20 000–36 000 ringed seals inhabited the Bothnian Bay in 2024, increasing at a rate of 3–6 % yr^{-1}. Reproductive rates have increased since 1988, leading to a substantial increase in the growth rate up until 2015. However, the re-introduction of hunting has since reduced the growth rate, and even minor quota increases are likely to reduce it further. Our results also support the hypothesis that a greater proportion of the population hauls out under lower ice cover circumstances, leading to higher aerial survey results in such years. In general, our study demonstrates the value of IPMs for monitoring wildlife populations under changing environments and for supporting science-based management decisions.

KEY WORDS: Integrated population model · IPM · State-space model · Bayesian · Pinniped · Environmental change · Haulout · Long-term monitoring · Wildlife management

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1. INTRODUCTION

The rapid pace of environmental change presents unprecedented challenges for monitoring and managing wildlife populations (Berkes et al. 2008, Waltner-Toews et al. 2008, Chapin et al. 2009). Conventional approaches often rely on long-term historical trends, and are increasingly insufficient as populations are exposed to novel conditions that result in unfamiliar dynamics (Chapin et al. 2009, Marolla et al. 2021). Management actions in response to changing conditions are frequently delayed until a more complete

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understanding is achieved through research, yet the urgency of these problems seldom allows for lengthy deliberation (Chapin et al. 2009, Dietze et al. 2018).

There is thus a growing need for versatile, mechanistic population models capable of testing alternative hypotheses on the development of natural populations and accommodating uncertainties in population assessments. The integration of such models with long-term monitoring data can lead to efficient generation of explanatory and anticipatory predictions (Mouquet et al. 2015, Maris et al. 2018, Marolla et al. 2021). The repeated application of short-term predictions, combined with informed management decisions and continuous monitoring, can facilitate testing and refining model assumptions and accelerate the pace of research — a process that is at the heart of adaptive management (Holling 1978, Lahoz-Monfort et al. 2014, Dietze et al. 2018).

The demand for mechanistic, data-driven population models was among the key motivations behind the development of integrated population models (IPMs), which combine multiple data sources in a single, unified model to simultaneously infer key demographic parameters and population processes (Besbeas et al. 2002, Buckland et al. 2004, Schaub & Abadi 2011, Zipkin & Saunders 2018). This is in contrast to traditional approaches where independent empirical estimates for model parameters are typically incorporated into a population projection matrix such as a Leslie matrix (Caswell 2001). The main advantages of IPMs include their flexibility, their ability to separate process variability from observation error, and their ability to more precisely estimate a larger number of parameters by leveraging synergies between multiple data sources (Abadi et al. 2010, Schaub & Abadi 2011, Zipkin & Saunders 2018). Additional information can also be incorporated under the Bayesian framework in the form of prior distributions, which can be determined based on previous empirical work on similar species or expert opinions (Buckland et al. 2004). Sufficiently developed IPMs could potentially function as ‘digital twins’ of their target populations, where the data are continuously updated and the model recalibrated in a way that enables managers to swiftly respond to changing conditions (de Koning et al. 2023, Trantas et al. 2023, Lecarpentier et al. 2024). Despite the great promise of IPMs as digital twins of wild animal populations, their potential has yet to be fully realized.

To demonstrate the value of IPMs in monitoring and managing animal populations in dynamic and uncertain conditions, we developed a Bayesian IPM for the Baltic ringed seal *Pusa hispida botnica* population inhabiting the Bothnian Bay, the northernmost region of the Baltic Sea and home to over 75% of all Baltic ringed seals (Härkönen et al. 1998, Sundqvist et al. 2012, Halkka & Tolvanen 2017). We adopted a state-space formulation for our model (Buckland et al. 2004) and parametrized it using count data obtained from aerial transect surveys, demographic data from hunted and bycaught seals, hunting records from Finland and Sweden, and assessments of reproductive status in sampled females. The ringed seal population in the Bothnian Bay is a notable example of an ice-dependent pinniped population for which long-term monitoring data are available. However, despite the abundance of data, uncertainties stemming from a multitude of changing conditions have precluded assessments of population size and growth for over a decade (HELCOM 2023a).

The population size of Baltic ringed seals had plummeted from an estimated 100 000–450 000 in the year 1900 to about 5000 by the late 1970s, driven largely by unsustainable bounty hunting practices and extremely low reproductive rates caused by organochlorine contamination (Helle et al. 1976, Durant & Harwood 1986, Härkönen et al. 1998, 2008, Harding & Härkönen 1999, Kokko et al. 1999). Both seal hunting and the use of PCB and DDT were subsequently prohibited, and the Bothnian Bay population has shown signs of recovery since the late 1980s. Aerial transect surveys conducted in 1988–2012 suggested an annual growth rate of approximately 5% (Sundqvist et al. 2012). However, more recent census estimates have shown unusually high variability and systematic deviations from historical trends, casting uncertainty over the current status of the population (HELCOM 2023a).

In the Bothnian Bay, aerial transect surveys are conducted annually around the third week of April, and ringed seals are counted when they are visible while molting on the sea ice (i.e. ‘hauled out’) after having abandoned their subnivean lairs (Härkönen & Lunneryd 1992). Aerial survey results have traditionally been used as an index of population size and trend, based on the assumption that approximately the same proportion of the population hauls out on ice during the surveys each year (Härkönen & Lunneryd 1992). It has been speculated, however, that a substantially larger fraction of seals may haul out when aerial surveys coincide with low ice cover or early ice breakup, resulting in extremely large population counts that are not comparable to typical results (HELCOM 2023a). Moreover, previous analyses of survey estimates have often assumed constant population growth, implying constant demographic rates (Sundqvist et al. 2012). However, reproductive rates of Baltic ringed seals have likely been improving since the use of PCB and DDT was banned (Helle 1980b, Kauhala et al. 2019, HELCOM 2023b). Unsurprisingly, the population growth rate may have been increasing as well (HELCOM 2023a). Thus, we hypothesized that the atypical aerial survey estimates observed over the past decade stem from a combination of improvements in reproductive rates and a higher visibility of seals on ice following mild winters.

The challenges of managing the ringed seal population in the Bothnian Bay are amplified by the recent re-introduction of seal hunting in Finland and Sweden in an attempt to mitigate the rising tension between fisheries and the growing seal population. The effectiveness of hunting as a strategy for alleviating seal—fishery conflicts hinges on achieving a compromise between conservation goals and the interests of coastal fisheries (Oksanen et al. 2014, Cummings et al. 2019). This requires reliable assessments of population size, growth rate, and demography, an understanding of seal—human interactions, and the ability to predict population responses to alternative management decisions. However, due to the ongoing difficulties with monitoring ringed seals in the Bothnian Bay, the impact of hunting on ringed seal demography is unknown.

The growing conflict between seals and fisheries, and the dynamic and uncertain conditions brought on by climate change, improving reproductive rates, and the re-introduction of hunting highlight the need for mechanistic models of ringed seal population dynamics, and an increasingly holistic analysis of the available data. Using a Bayesian IPM, we provide a solution to the challenges that have crippled ringed seal monitoring efforts in the Bothnian Bay throughout the last decade. In addition to the population size and growth rate, we estimate a large number of ecologically important parameters and make short-term predictions regarding population response to changes in hunting quotas.

2. MATERIALS AND METHODS

2.1. Study population

The Baltic ringed seal is a subspecies of ringed seal endemic to the Baltic Sea (Rice 1998; but see Palo et al. 2001). Recognized sub-populations inhabit the Bothnian Bay, the Archipelago Sea, the Gulf of Riga, and the Gulf of Finland (Härkönen et al. 1998, Halkka & Tolvanen 2017). Our study focused on the Bothnian Bay population, which comprises over 75% of all Baltic ringed seals (Sundqvist et al. 2012). The Bothnian Bay is the northernmost region of the Baltic Sea, with a surface area of approximately 37 000 km^2 (Fig. 1). Since the southern sub-populations in the Archipelago Sea, the Gulf of Finland, and the Gulf of Riga are small (Sundqvist et al. 2012), and ringed seals show high breeding site fidelity (Härkönen et al. 2008, Kelly et al. 2010), we treated the dynamics of the Bothnian Bay population independently of the other sub-populations.

Ringed seals are among the smallest and most strongly ice-associated pinnipeds in the world (Smith et al. 1991). Their annual life cycle has been classified into 3 main 'ecological seasons' (Fig. 2): the foraging period, the subnivean period, and the molting period (Born et al. 2004, Kelly et al. 2010, Oksanen et al. 2015b).

During the foraging period between June and January, Baltic ringed seals spend over 90% of their time in the water, hauling out on land primarily at night for resting (Oksanen et al. 2015b). This phase is marked by intense feeding activities, as ringed seals seek to accumulate blubber reserves in preparation for the approaching winter (Oksanen et al. 2015b, Kauhala et al. 2019). Interactions with coastal fisheries are therefore most common between late spring and late fall. During this period, bycatch mortality is most typical for young ringed seals (Oksanen et al. 2015a, Jounela et al. 2019).

During the winter, ringed seals spend most of their time out of the water in subnivean lairs built on sea ice (Kelly et al. 2010). Around February—March, a single pup is born inside the snow lair and is nursed for 5—8 wk (Helle 1979, Lydersen & Hammill 1993). The snow lair provides shelter to pups against harsh weather conditions and predators. Therefore, pups born without the protection offered by a stable lair are unlikely to survive (Smith & Stirling 1975, Ferguson et al. 2005, Sundqvist et al. 2012). Because whelping and nursing require sufficient ice and snow conditions, adult seals are often associated with stable pack ice during the breeding season, whereas juveniles are more commonly observed in productive foraging areas near the ice edge or in the open water (Crawford et al. 2012, Oksanen et al. 2015b). Mating is thought to take place within 1 mo of parturition (McLaren 1958, Stirling 1983), although the implantation of the embryo is delayed until around July (McLaren 1958). If females do not have enough blubber reserves, implantation may not occur (Boyd et al. 1999).

The molting period begins as the snow cover starts to melt and subnivean lairs collapse, typically in April.

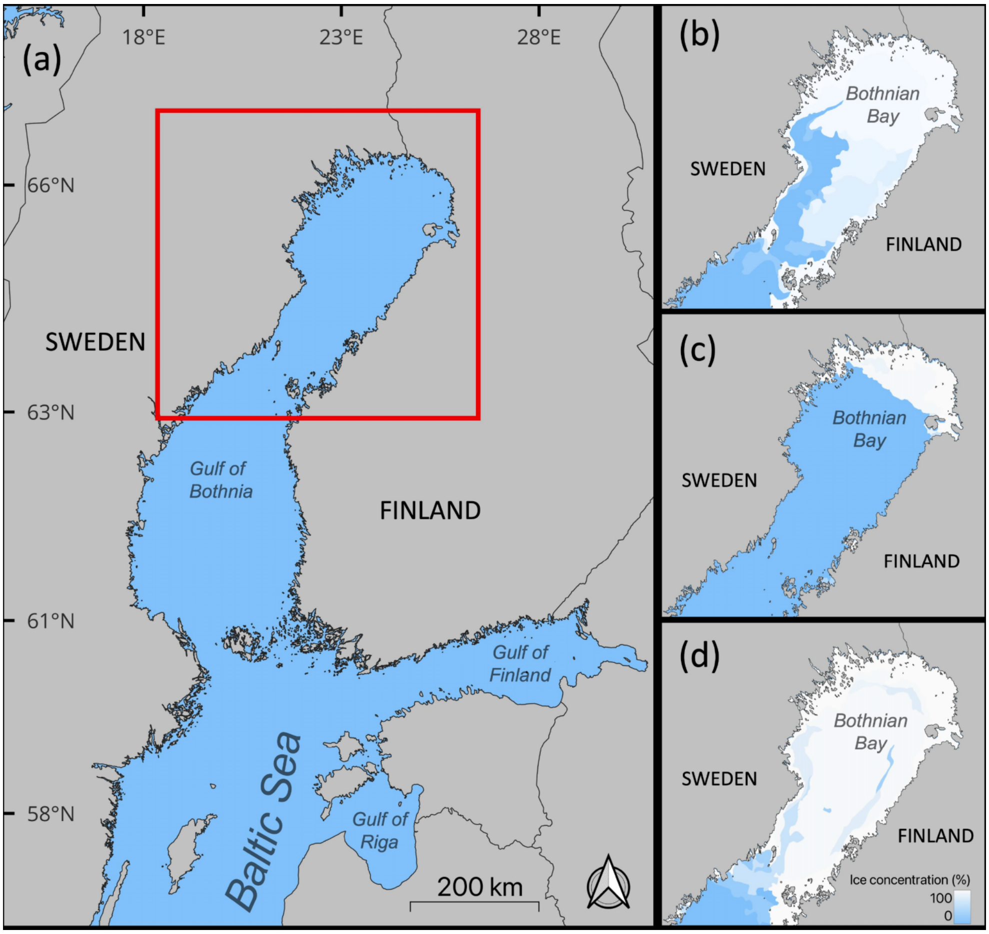

Fig. 1. (a) Study area (red square) and the extent of ice cover in (b) 2004, (c) 2015, and (d) 2018 around the third week of April. These 3 years respectively illustrate the median, minimum, and maximum ice extents observed during the study period

Molting ringed seals spend a significant portion (50–80%; Härkönen & Lunneryd 1992, Born et al. 2002, Kelly et al. 2010) of their time basking on the sea ice in order to increase blood flow to the skin and maintain elevated skin temperatures (Feltz & Fay 1966, Thometz et al. 2021). Sub-adults and adults often continue molting until the ice melts, typically around late May in the Bothnian Bay (Helle 1980a, Härkönen et al. 2008), whereas pups typically complete their natal hair molt in lairs (Smith 1973, Lydersen & Hammill 1993).

The molting period also marks the beginning of the ringed seal hunting seasons in Sweden and Finland, which were re-introduced in 2015 and in 2016, respectively. Some small-scale hunting took place earlier, mainly for research purposes (Nyman et al. 2003, Routti et al. 2009). Annual hunting quotas were initially set to about 100 seals in each country and were gradually raised to 420 seals in Sweden and 375 seals in Finland as of 2022 (Section 2.2.2). Sweden then reduced quotas to 350 seals in 2023, whereas the Finnish quota was kept the same.

Hunting of ringed seals in Sweden is legal between 1 May and 15 January, although the actual distribution of hunting activities is bimodal, with distinct spring and autumn seasons (Fig. 2). Sweden practices 'protective' hunting, which largely restricts hunting to within 200 m of fishing sites where seals have previously caused damage to gear or taken catch. Protective hunting is also allowed within the vicinity of fish farms, fish conservation areas, and fish release sites. Hunting in Sweden is therefore likely to be opportunistic.

Hunting of ringed seals in Finland is legal between 16 April and 31 December. Finland allows recreational hunting of ringed seals, and hunters are therefore more likely to actively seek out seals. Hunting in Finland almost exclusively takes place on sea ice, and the hunting season effectively ends once sea ice melts (Fig. 2). The total harvest in Finland is influenced by the sever-

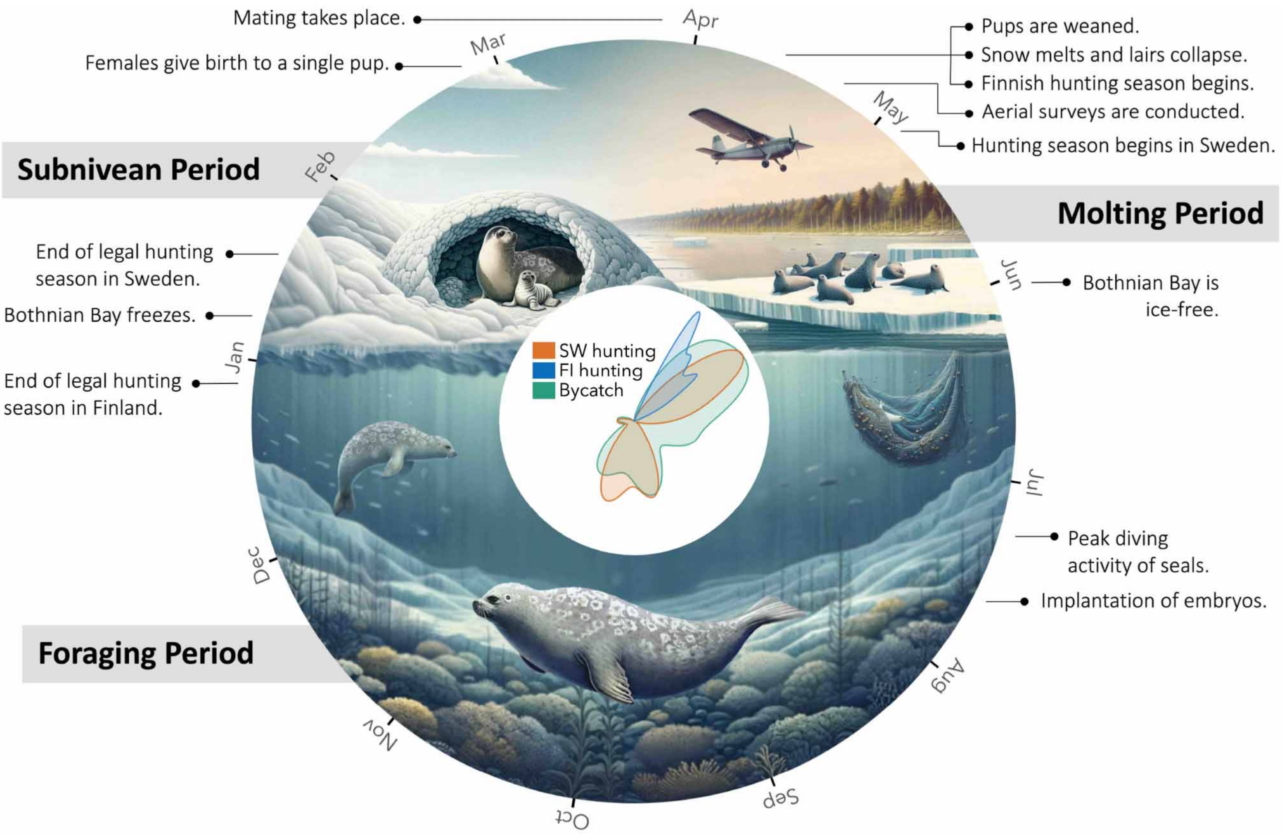

Fig. 2. Baltic ringed seal annual life cycle. The density plots at the center show, in polar coordinates, the temporal distribution of hunting and bycatch based on sampled seals (SW: Sweden; FI: Finland). The illustration was created with the aid of DALL-E 3 (https://openai.com/index/dall-e-3/)

ity of winter. For example, following mild winters, seals tend to congregate in smaller areas of stable ice closer to land, making them more accessible to hunters (Härkönen & Lunneryd 1992, Harding & Härkönen 1999, Ministry of Agriculture and Forestry 2007).

2.2. Data

2.2.1. Aerial surveys

The basking population size of ringed seals during the peak molting season was estimated by the Swedish Museum of Natural History (SMNH) using aerial strip surveys conducted in the Bothnian Bay in mid- to late April each year between 1988 and 2023. The 800 m wide strips were placed evenly over the study area, and the number of observed seals was recorded from an aircraft flying at 90 m altitude (Härkönen & Lunneryd 1992, Härkönen et al. 1998). The proportion of the total ice area covered by the surveys ranged from 13 to 53%, except for 2016, when only 7% of the total ice area was surveyed. The average density of seals over the surveyed transects was extrapolated over the whole ice-covered area to estimate the total size of the basking population, which is thought to account for 50–80% of the overall population (Härkönen & Lunneryd 1992, Born et al. 2002, Kelly et al. 2010). The precision of the estimates improves with increasing coverage, although the gain in precision begins to diminish beyond a coverage of about 13% (Härkönen & Lunneryd 1992).

2.2.2. Harvest totals and quotas

Finnish hunting quotas and harvest totals from 2016–2022 were provided by the Finnish Wildlife Agency. Hunting records, quotas, and sampling protocols from Sweden between 2015 and 2022 were provided by the SMNH.

2.2.3. Demographic and reproductive data

Demographic age and sex data on the ringed seal population and data on the reproductive status of female seals were obtained from the Natural Resources Institute Finland (Luonnonvarakeskus, or Luke) and SMNH. These data were compiled from samples taken from hunted (2016–2021 for Finland and 2015–2021 for Sweden) and bycaught (years 1988–2021) seals sent to Luke or SMNH by hunters and fishermen. Age determination was done by counting the growth layer groups in the cementum of either canines or molars from the lower jaw (Stewart et al. 1996). We assumed that misidentifications of sex or age were negligible, and samples that were missing information on both age and sex were excluded from our analysis. The resulting number of samples per year ranged between 46 and 240 for Finland, and between 28 and 80 for Sweden. Among those, the number of samples missing either age or sex information ranged from 1 to 10 per year for Finland, and 1 to 9 per year for Sweden.

Female ringed seals were examined for the presence of a visible fetus and placental scar in the uterine horn, and a corpus albicans (CA) within the ovary. Because the implantation of embryos does not occur until July (McLaren 1958, Boyd 1991), we relied on evaluations of a visible fetus in samples obtained between August and January. Placental scars and CA may both fade with time (Boyd 1984, HELCOM 2023b). In our samples, the proportion of seals with placental scars in recent years was nearly 20% lower in May than in April. In contrast, the proportion of seals with CA was similar between April and June. To minimize observation errors associated with fading in post-partum signs, we relied on placental scar data from April, and CA data from April through June.

We used only samples of females that were 5+ yr old for the post-partum signs, and 4+ yr old for a visible fetus (see Section 2.3.1). Samples that were not evaluated for any reproductive sign were excluded, resulting in yearly sample sizes ranging from 0 to 18 for visible embryos, 0 to 62 for placental scars, and 0 to 83 for CA (Fig. S2 in Supplement 1; all Supplements are available at www.int-res.com/articles/suppl/m764p213_supp.pdf).

From here on, we define the pregnancy rate as the proportion of 4+ yr old females carrying a fetus during the fall. To account for possible pregnancy losses, post-partum signs of pregnancy were modeled separately. We define the birth rate as the proportion of 4+ yr old females that remained pregnant long enough to have a placental scar at the time of parturition, as this is thought to be the closest measure available to assess the percentage of adult females that produced a live pup. Our definition of birth may include some late-term abortions and stillbirths, which are potentially common in pinnipeds (McKenzie et al. 2005, Stenson et al. 2016) and treated as pup mortality in our analysis.

2.2.4. Sea ice extent data

Weekly raster maps of ice concentration across the Baltic Sea between 1988 and 2023 were acquired from the Finnish Meteorological Institute. We used ice concentration data from north of 63° N latitude around the third week of April, when both aerial surveys and most of Finnish hunting take place (Härkönen & Lunneryd 1992). The ice cover was calculated by multiplying the total sea area with the proportion of raster cells containing an ice concentration >0.

2.3. Population dynamics model

2.3.1. Structure of the population dynamics model

We modeled the population dynamics of ringed seals using an age- and sex-structured model with demographic stochasticity in births and deaths. Because female ringed seals typically begin reproducing at the age of 5 yr (McLaren 1958, Lydersen & Gjertz 1987, Kauhala et al. 2019, Reimer et al. 2019), and reproductive senescence is rare (McLaren 1958, Ellis et al. 2018), we included 6 age classes in our model, grouping 5+ yr old individuals in a single age class. We refer to 0 yr old individuals as pups, 1–4 yr olds as sub-adults, and 5+ yr olds as adults. Note that while 4 yr old sub-adults can become pregnant in our model, they do not give birth until reaching adulthood at age 5. As hunting quotas do not discriminate between males and females, and the sex ratio of the harvests does not necessarily reflect the sex ratio of the population, we included males in our population model but assumed that females were the limiting sex in reproduction.

We assumed a post-breeding census, and formulated the dynamics of the population between each census in terms of 3 successive sub-processes: mortality, aging, and birth (Fig. 3). Aging was assumed to occur immediately before parturition. We denote the state of the population at the census of year t by the vector $\mathbf{n}_t$. The elements of $\mathbf{n}_t$, denoted by $\mathrm{n}_{s,a,t}$, correspond to the number of seals of sex $s \in \{\mathrm{f,m}\}$ and age $a \in \{1,\ldots, 5+\}$ in the population immediately after parturition. The states of the population after the mortality and aging sub-processes are denoted respectively by the intermediate state vectors $\mathbf{u}_t^{(1)}$ and $\mathbf{u}_t^{(2)}$. Nota-

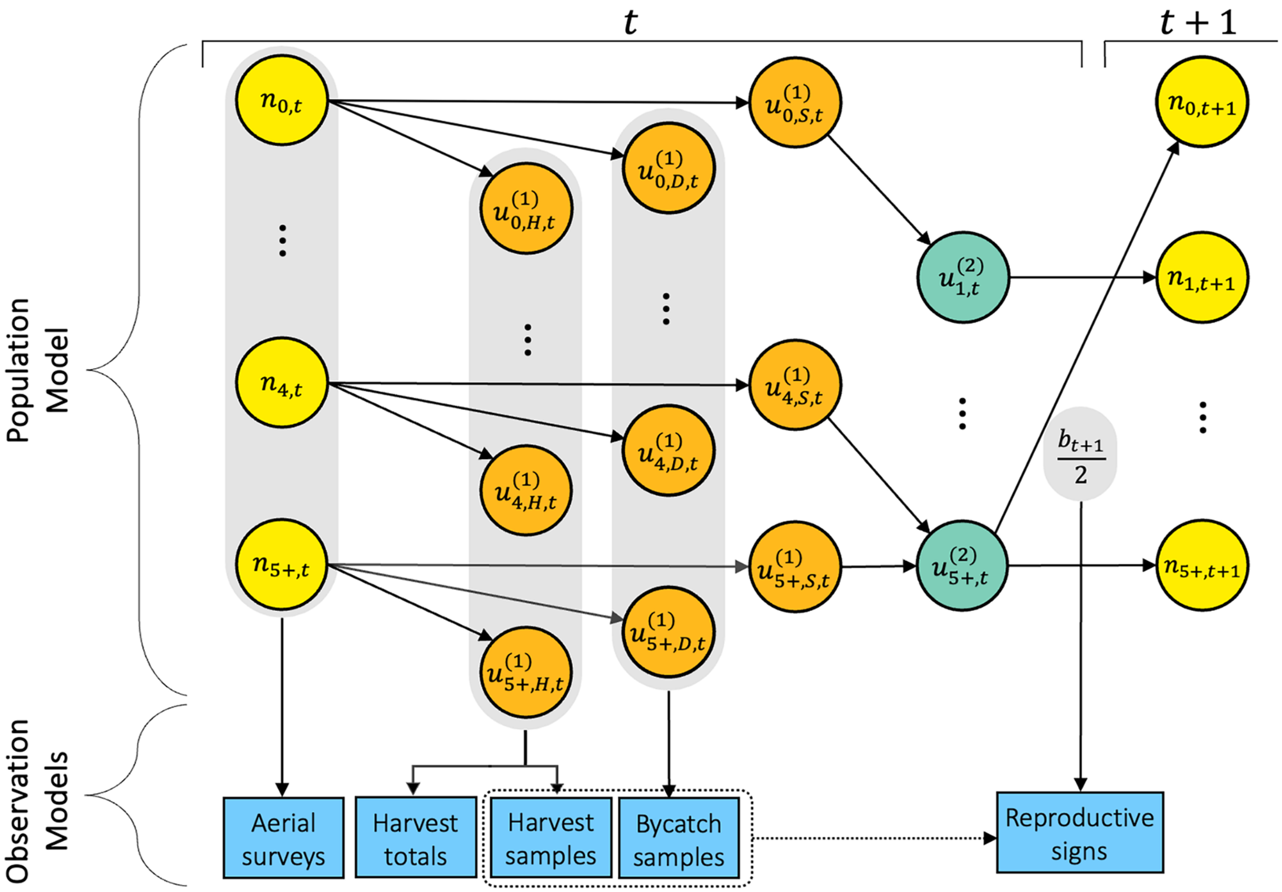

Fig. 3. Simplified model structure for female ringed seals. Colored circles represent unobserved state variables and blue squares represent observed data sources. Vertical ellipses indicate continuation across age classes. Arrows denote dependencies, with grey shading indicating groups of variables on which observations are conditioned. The dotted arrow indicates that reproductive signs are derived from harvested and bycaught seal samples. The dynamics of the population state between census points (yellow circles) are decomposed into three sub-processes: (1) individuals transition to mortality states (orange circles) based on whether they survive (S), are harvested (H), or die from other causes (D), with harvested individuals further grouped based on whether they were harvested in Finland, in Sweden during the spring, or during the fall (not shown); (2) survivors age into the next class (green circles); and (3) adult females produce new pups, forming the population state at the next census. All variables are defined as in Table 1 and Section 2

tions for commonly referenced parameters are summarized in Table 1.

2.3.2. Survival and mortality

In each year, the mortality sub-process was described as a multi-state transition model, where seals are assigned to 1 of 5 states: those that survived (S), were harvested in Finland (H^{fi}), were harvested in Sweden either during the spring ($H^{\mathrm{sw}(1)}$) or during the fall ($H^{\mathrm{sw}(2)}$), or died due to other causes (D). Due to a lack of data on the magnitude of bycatch, it was included with other sources of mortality.

Assuming mortality depends on sex and age and is mutually independent among seals, this process can be modeled stochastically using a multinomial distribution:

$$\mathbf{u}^{(1)}_{s,a,t} \,|\, \mathbf{n}_t \sim \mathrm{Multinomial}(n_{s,a,t}, \boldsymbol{\rho}_{s,a,t}) \tag{1}$$

where $n_{s,a,t}$ is the total number of seals of sex s and age a at the census of year t;

$$\boldsymbol{\rho}_{s,a,t} = \left\{\rho^{S}_{s,a,t}, \rho^{D}_{s,a,t}, \rho^{H^{\mathrm{sw}(1)}}_{s,a,t}, \rho^{H^{\mathrm{sw}(2)}}_{s,a,t}, \rho^{H^{\mathrm{fi}}}_{s,a,t}\right\} \tag{2}$$

is a vector of transition probabilities; and

$$\mathbf{u}^{(1)}_{s,a,t} = \left\{u^{(1)}_{s,a,S,t}, u^{(1)}_{s,a,D,t}, u^{(1)}_{s,a,H^{\mathrm{sw}(1)},t}, u^{(1)}_{s,a,H^{\mathrm{sw}(2)},t}, u^{(1)}_{s,a,H^{\mathrm{fi}},t}\right\} \tag{3}$$

is a vector of the number of seals that transition to each state.

We modeled the mortality rates in the absence of hunting, $\mu_{s,a}$, as constant throughout the years. We explicitly modeled only the mortality rates of female pups and adults. The mortality rates of sub-adult females were interpolated between the mortality rates of pups and adults, so that:

Table 1. Notation for commonly referenced parameters

Symbol	Description
$n_{s,a,t}$	Number of seals of sex s and age a at the start of year t
N_t	Total population size at the start of year t
$\rho^X_{s,a,t}$	Probability that a seal of sex s and age a transitions to mortality state X
$u^{(1)}_{s,a,X,t}$	Number of seals of sex s and age a that transition to mortality state X
$u^{(2)}_{s,a,t}$	Number of seals of sex s and age a at the end of year t
H^i_t	Harvest totals of country i in year t
$\mu_{s,a}$	Mortality rate of seals of sex s and age a in the absence of hunting
$\phi_{s,a}$	Survival probability of seals of sex s and age a in the absence of hunting
$\omega_{s,a,t}$	Haul out probability of seals of sex s and age a in year t
$\hat{\omega}_{s,a}$	Haul out probability of seals of sex s and age a when sea ice is abundant
C_t	Ice extent in the Bothnian Bay in late April
b_t	Probability that an adult female gives birth at the start of year t

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

where $\mu_{f,a}$ is the mortality rate of female seals of age a, and c is a parameter that determines how quickly the mortality rate approaches that of adults as the seals age. Male survival rates were modeled in terms of deviations from female survival rates, so that *a priori* mortality rates were expected to be identical between the sexes, while allowing the data to inform us on potential differences (Supplement 2). The probability, $\phi_{s,a}$, that a seal survives all sources of mortality other than hunting throughout the year is then given by the exponential function:

$$\phi_{s,a} = e^{-\mu_{s,a}} \tag{5}$$

To be able to predict future population responses to alternative management decisions, we explicitly modeled the within-year dynamics of hunting as a function of hunting quotas. We assumed all Finnish hunting takes place in April and May when ringed seals are basking on sea ice, and that the harvest rate is proportional to the density of seals hauled out on ice. We estimated the density of seals along the Finnish coast, in each age and sex group, as $\omega_{s,a,t} n_{s,a,t}/C_t$, where $\omega_{s,a,t}$ denotes the proportion of seals expected to be hauled out on sea ice in year t (see Section 2.3.3), and C_t is the ice extent across the Bothnian Bay during peak molting. We further assumed that the number of active hunters in Finland is proportional to the number of unused hunting licenses, implying a Holling Type I functional response in the absence of a quota (Holling 1959). The within-year dynamics of hunting in Finland can therefore be expressed as a system of 2 ordinary differential equations:

$$\frac{dH^{\mathrm{fi}}_{s,a,t}}{d\tau} = E^{\mathrm{fi}}_{s,a,t}\left(Q^{\mathrm{fi}}_t - H^{\mathrm{fi}}_t(\tau)\right)\frac{\omega_{s,a,t}\tilde{n}_{s,a,t}(\tau)}{C_t} \tag{6}$$

$$\frac{d\tilde{n}_{s,a,t}}{d\tau} = -\mu_{s,a}\tilde{n}_{s,a,t}(\tau) - E^{\mathrm{fi}}_{s,a,t}\left(Q^{\mathrm{fi}}_t - H^{\mathrm{fi}}_t(\tau)\right)\frac{\omega_{s,a,t}\tilde{n}_{s,a,t}(\tau)}{C_t} \tag{7}$$

where $H^{\mathrm{fi}}_{s,a,t}$ denotes the expected number of seals of sex s and age a that have been harvested in Finland, Q^{fi}_t is the hunting quota for year t, $H^{\mathrm{fi}}_t(\tau) = \sum_{s,a} H^{\mathrm{fi}}_{s,a,t}(\tau)$ is the total harvest in Finland at time τ after the onset of the hunting season, $\tilde{n}_{s,a,t}(\tau)$ is the number of seals that are alive at time τ, and $E^{\mathrm{fi}}_{s,a,t}$ is the per capita harvest rate directed towards each demographic group in year t.

We assumed that there was stochastic variation in per capita harvest rates across the years, without any temporal trends:

$$E^{\mathrm{fi}}_{s,a,t} = \hat{E}^{\mathrm{fi}}_{s,a} e^{\epsilon_t} \tag{8}$$

Here, $\hat{E}_{s,a}$ is the median per capita harvest rate, and $\epsilon_t \sim \mathrm{N}(0, \sigma^2_{E^{\mathrm{fi}}})$ is a noise term. Setting the initial harvest to 0, an approximate closed-form solution to Eqs. (6) and (7) can be obtained to estimate the expected composition of the harvests, and hence the probability, $\rho^{H^{\mathrm{fi}}}_{s,a,t}$, that a seal of sex s and age a is harvested in Finland during year t (Supplement 3). Swedish hunting during both the spring and the fall were modeled similarly to Finnish hunting. However, unlike hunting in Finland which takes place almost entirely on sea ice, protective hunting in Sweden is likely to be opportunistic. We therefore assumed that the harvest rate in Sweden was proportional to the total number of ringed seals in the Bothnian Bay, rather than to the density of ringed seals on sea ice (Supplement 3). Spring hunting in Sweden was assumed to take place during May and June, and fall hunting during September and October (Fig. 2).

Once estimates for $\rho^{H^{\mathrm{sw(1)}}}_{s,a,t}$, $\rho^{H^{\mathrm{sw(2)}}}_{s,a,t}$, and $\rho^{H^{\mathrm{fi}}}_{s,a,t}$ are obtained, the probability that a seal survives all sources of mortality is given by:

$$\rho^S_{s,a,t} = \left(1 - \rho^{H^{\mathrm{sw(1)}}}_{s,a,t} - \rho^{H^{\mathrm{sw(2)}}}_{s,a,t} - \rho^{H^{\mathrm{fi}}}_{s,a,t}\right)\phi_{s,a} \tag{9}$$

Note that while the expected harvests, as implied by Eqs. (6) and (7), are constrained by the hunting quotas, the realized harvests given by the stochastic model in Eq. (1) may exceed these quotas. This formulation not only simplifies the model considerably but also accounts for the possibility of illegal or unrecovered hunting.

2.3.3. Haul-out probability

The proportion of seals that are visible on ice during the molting period depends on the frequency with which seals move into and out of the water. We assumed that during the molting period, seals of sex s and age a move onto the ice at a per capita rate of $\zeta^1_{s,a,t}$, and move back into the water at a per capita rate of $\zeta^0_{s,a,t}$. The proportion of seals hauled out on ice is then given by:

$$\omega_{s,a,t} = \frac{\zeta^1_{s,a,t}}{\zeta^1_{s,a,t} + \zeta^0_{s,a,t}} \qquad (10)$$

Although our assumption of constant movement rates implies exponentially distributed haul-out and foraging durations, Eq. (10) remains valid for any distribution with a finite expectation (Janssen & Manca 2006).

Deteriorating ice conditions may force seals to spend longer periods of time in the water or on land, as suitable haul-out sites on ice become increasingly less accessible (Härkönen et al. 1998, Thometz et al. 2021). We therefore assumed that the per capita rate at which seals move onto the ice follows a sigmoid function of ice availability, obtaining a value of 0 when no ice is present, and saturating at a maximum value when sea ice is abundant:

$$\zeta^1_{s,a,t} = \frac{C_t^2}{f^2 + C_t^2} \qquad (11)$$

Here, f is a half-saturation constant. The value of $\omega_{s,a,t}$ in Eq. (10) is determined solely by the relative magnitudes of $\zeta^0_{s,a,t}$ and $\zeta^1_{s,a,t}$. Consequently, we have chosen to scale $\zeta^1_{s,a,t}$ such that it asymptotically approaches 1 for all sex and age classes.

To account for the possibility that a larger fraction of seals hauls out during low ice cover, we modeled the per capita rate at which hauled-out seals move into the water as a logistic function that decreases as ice cover approaches 0. In other words, we assumed that on average, seals remain on the ice for longer periods of time when sea ice is scarce:

$$\zeta^0_{s,a,t} = \frac{1-\hat{\omega}_{s,a}}{\hat{\omega}_{s,a}}\left[d + \frac{1-d}{1+e^{-(\alpha_0+\alpha_1 C_t)}}\right] \qquad (12)$$

Here, $\hat{\omega}_{s,a}$ is the expected proportion of seals hauled out when sea ice is abundant, α_0 and α_1 are parameters that determine the shape of the logistic curve, and d is the ratio between the lower and upper asymptotes of $\zeta^0_{s,a,t}$. A non-0 lower asymptote for $\zeta^0_{s,a,t}$ accounts for the fact that the maximum amount of time seals can spend on ice may be constrained by the need to forage or cool off.

We assumed that on average, sub-adult and adult seals haul out with the same probability (i.e. $\hat{\omega}_{s,a} = \hat{\omega}, \forall a > 0$), but note that during the time of aerial surveys, sub-adults are typically thought to be underrepresented on ice compared to adults (Smith 1973). Hence, $\hat{\omega}$ should be regarded as the average haul-out probability across sub-adults and adults. Pups largely complete molting by the time aerial surveys are conducted, and are significantly less likely to be on ice (Smith 1973, Lydersen & Hammill 1993). Thus, we assumed that the baseline haul-out probability of pups is a constant fraction $\delta \in [0,1]$ of that for sub-adults and adults (i.e. $\hat{\omega}_{s,0} = \delta\hat{\omega}$), with the effect of sea ice modeled in the same way as for sub-adults and adults using Eqs. (10) – (12).

2.3.4. Reproduction

To account for the diminishing effects of organochlorine contamination on the reproductive rates of ringed seals, we modeled the probability that an adult female gives birth to a single pup in the absence of density-dependent effects as a time-varying logistic function increasing from a historic low of $b_{\min}$ to a theoretical maximum of $b_{\max}$, so that:

$$b_t^0 = b_{\min} + \frac{b_{\max} - b_{\min}}{1 + e^{-(\beta_0 + \beta_1 t)}} \qquad (13)$$

where $b_t{}^0$ is the expected birth rate in year t if population density were 0, and β_0 and β_1 are parameters that determine the shape of the logistic curve.

Little is known about the mechanisms that regulate population density in marine mammals, although DeMaster (1984) suggested that ringed seal populations in the Arctic may be predator-limited. Given the absence of large predators in the Baltic Sea, we assumed that Baltic ringed seals are resource-limited, with intra-specific competition primarily affecting fecundity. We assumed that fecundity would be more sensitive to changes in population size at high population densities, and modeled the rate at which pregnancies fail (e.g. due to abortions) as an exponentially increasing function of population size. The density-dependent birth rate, denoted by b_t, can then be modeled as:

$$b_t = b_t^0 e^{-\theta_0 (e^{\theta_1 N_{t-1}} - 1)} \qquad (14)$$

where $N_{t-1} = \sum_{s,a} n_{s,a,t-1}$ is the total population size during the previous year, θ_0 is the average failure rate of pregnancies at 0 population density, and θ_1 is the rate at which such failed pregnancies increase with population size (Supplement 4).

Pup production was then modeled using a multinomial distribution:

$$\begin{gathered}\{n_{f,0,t}, n_{m,0,t}, \bullet\} \mid \mathbf{u}_{t-1}^{(2)} \sim \\ \text{Multinomial}\left(u_{f,5+,t-1}^{(2)}, \left\{\frac{b_t}{2}, \frac{b_t}{2}, 1-b_t\right\}\right)\end{gathered} \tag{15}$$

where the sex ratio at birth is assumed to be at parity (McLaren 1958). Here, $u_{f,5+,t-1}^{(2)}$ denotes the number of adult females immediately before pupping, and $\bullet$ is a dummy variable for the number of mature females that do not give birth, which occurs with probability $1 - b_t$.

2.4. Observation models

2.4.1. Aerial survey estimates

We modeled the estimated basking population size resulting from the aerial strip surveys as a negative binomial distribution with expectation equal to the true basking population size:

$$y_t^{\text{survey}} \mid \tilde{\mathbf{n}}_t \sim \text{Negative}-\text{Binomial}(\boldsymbol{\omega}_t^{\mathbf{T}}\tilde{\mathbf{n}}_t, r) \tag{16}$$

Here, $\tilde{\mathbf{n}}_t$ is the expected population state at the time of the aerial surveys (Section 2.3.2), ω_t is a vector of haul-out probabilities (Section 2.3.3), and r is a variance parameter. The negative binomial distribution is commonly used to model biological count data and can be thought of as a Poisson distribution with a rate parameter that varies stochastically as a result of, e.g. changes in observability or demographic stochasticity on $\tilde{\mathbf{n}}_t$ that lead to overdispersion in the counts (Lindén & Mäntyniemi 2011).

2.4.2. Harvest totals and samples

The total harvests for both Finland and Sweden are known exactly in principle, but we nonetheless assumed a small (~5% CV) variation around them because, in addition to having computational benefits, it accounts for the possibility of unrecovered or illegally hunted seals, as well as rare instances of misreporting:

$$y_t^{\text{ht}} \mid \mathbf{u}_t^{(1)} \backsim N\left(H_t, (0.05H_t)^2\right) \tag{17}$$

where y_t^{ht} denotes the observed harvest totals and H_t denotes the actual harvest totals in either Finland or Sweden during year t. We used separate observation models for spring and fall hunting in Sweden, except in 2015 and 2016 when only the total harvest was known.

Assuming that sampling of seals from the harvests is independent, the age and sex composition of the sampled seals from Finland and Sweden can be modeled using a multinomial distribution:

$$\mathbf{y}_t^{\text{hs}} \mid \mathbf{u}_t^{(1)} \sim \text{Multinomial}\left(\sum_{s,a} y_{s,a,t}^{\text{hs}}, \frac{\mathbf{v} \odot \mathbf{u}_{H,t}^{(1)}}{\mathbf{v}^{\mathbf{T}}\mathbf{u}_{H,t}^{(1)}}\right) \tag{18}$$

where $\mathbf{y}_t^{\text{hs}}$ is the demographic composition of the recovered samples in year t, $\mathbf{u}_{H,t}^{(1)}$ is the composition of the harvests, $v_{s,a}$ is the relative probability that a seal of sex s and age a is sampled from the harvests, and $\odot$ denotes the element-wise, or Hadamard, product. We assumed that seals are sampled randomly from the harvests in Finland and in Sweden during the fall (i.e. $v_{s,a} = 1, \forall s, a$). However, sampling during the spring has not been random in Sweden since larger seals are specifically requested from hunters to assess reproductive health. The observation model to estimate $\mathbf{v}$ for spring hunting in Sweden is described in Supplement 5. Observation models for samples that were missing either sex or age information are described in Supplement 6.

2.4.3. Bycatch samples

We assumed that bycaught seals were sampled randomly and independently. Because we included bycatch with other sources of mortality, we conditioned the observation model for bycaught samples on the number of seals that died due to causes other than hunting, and modeled the composition of bycaught samples using a multinomial distribution:

$$\mathbf{y}_t^{\text{bs}} \mid \mathbf{u}_t^{(1)} \sim \text{Multinomial}\left(\sum_{s,a} y_{s,a,t}^{\text{bs}}, \frac{\boldsymbol{\psi} \odot \mathbf{u}_{D,t}^{(1)}}{\boldsymbol{\psi}^{\mathbf{T}}\mathbf{u}_{D,t}^{(1)}}\right) \tag{19}$$

where $\mathbf{y}_t^{\text{bs}}$ is the demographic composition of the bycaught samples in year t, and ψ is a 12-simplex of weights accounting for possible deviations between the composition of bycatch and sources of mortality other than hunting (Supplement 2). Observation models for samples that were missing either sex or age information are presented in Supplement 6.

2.4.4. Observations of reproductive success

Given reports of significant late-term pregnancy losses in other pinniped populations and the increased energetic demands of late-stage gestation (Pitcher et al. 1998, McKenzie et al. 2005, Stenson et al. 2016), we assumed the rate of pregnancy losses increased linearly from zero at conception to a maximum at parturition. However, we note that there is little evidence of late-term pregnancy losses in Baltic ringed seals, and it has been suggested that the influence of nutritional factors on pinniped reproduction is greatest at the point of implantation (Boyd

1991). Hence, for sensitivity analysis, we also considered a model where the rate of pregnancy losses was assumed to decrease linearly (Supplement 4).

Assuming the reproductive status of sampled females is representative of the population as a whole, and there are no errors in the detection of fetuses, the number of observed pregnancies during the fall of year t can be modeled using a binomial distribution:

$$y_t^{\text{pregnant}} \mid p_t \sim \text{Binomial}\left(y_t^{\text{pregnant}} + y_t^{\text{not pregnant}}, p_t\right) \quad (20)$$

where:

$$p_t = b_{t+1} e^{\left(1-\tau_p^2\right)\theta_0 e^{\theta_1 N_t}} \quad (21)$$

is the pregnancy rate of the population, and $\tau_p \approx 0.5$ is the average time, in years, between mating and the sampling of pregnant females (Supplement 4).

In principle, all females that recently gave birth will possess both a placental scar and a CA. However, since both post-partum signs can fade with time, they might not always be identified (Boyd 1984, HELCOM 2023b). Moreover, the presence of a CA does not necessarily indicate recent birth. CA may also be present in females that had an infertile estrous cycle, and in some cases, it may even be a remnant of the previous reproductive season (Boyd 1984).

We denote by $z_{k,t}^{ij} \in \{0, 1\}$ whether a sampled seal k had a placental scar evaluation of i and a CA evaluation of j; for example, $z_{k,t}^{10} = 1$ if a placental scar, but not a CA, was observed in a seal. The outcome of the reproductive assessment for each adult female can then be modeled using a categorical distribution with probability vector γ_t:

$$\left\{z_{k,t}^{11}, z_{k,t}^{10}, z_{k,t}^{01}, z_{k,t}^{00}\right\} \mid \boldsymbol{\gamma}_t \sim \text{Categorical}\left(\left\{\gamma_t^{11}, \gamma_t^{10}, \gamma_t^{01}, \gamma_t^{00}\right\}\right) \quad (22)$$

The probabilities γ_t^{ij} for each assessment outcome will depend on the birth rate b_t, the probability κ that a seal that has not given birth has a CA, and the detection probabilities for placental scars (π_s) and CA (π_c), respectively. Hence, for a randomly sampled seal, both a placental scar and a CA are observed ($z_{k,t}^{11} = 1$) with probability $\gamma_t^{11} = b_t \pi_s \pi_c$, corresponding to sampling a seal that has recently given birth and successfully detecting both the placental scar and the CA. If a placental scar is observed without a corresponding CA ($z_{k,t}^{10} = 1$), it must be that a CA was present but not seen. Such an outcome will occur with probability $\gamma_t^{10} = b_t \pi_s (1 - \pi_c)$. Finally, if a CA is observed without a corresponding placental scar ($z_{k,t}^{01} = 1$), it means that either the female recently gave birth but the placental scar was not detected (i.e. because it faded), or the female did not recently give birth but nonetheless had a CA which was detected. Such an assessment will occur with probability $\gamma_t^{01} = b_t (1 - \pi_s) \pi_c + (1 - b_t) \kappa \pi_c$. The probability that neither a placental scar nor a CA is observed is then $\gamma_t^{00} = 1 - \gamma_t^{11} - \gamma_t^{10} - \gamma_t^{01}$.

Samples obtained in May and June, as well as those obtained before 2007, were only evaluated for the presence of CA. For these samples, we replaced the categorical distribution in Eq. (22) with the Bernoulli observation model:

$$z_{k,t}^{\bullet 1} \mid \boldsymbol{\gamma}_t \sim \text{Bernoulli}\left(\gamma_t^{11} + \gamma_t^{01}\right) \quad (23)$$

An extension of the observation model described in this section to handle incomplete data is presented in Supplement 6.

2.5. Posterior inference and model assessment

2.5.1. Posterior inference

Following standard practice in IPMs, we assumed the different data sources were independent and constructed the joint likelihood as a product of the individual data likelihoods presented in Section 2.4 (Abadi et al. 2010). Prior distributions for model parameters are given in Supplement 2. Posterior inference was conducted using Markov chain Monte Carlo methods implemented using Stan version 2.26.23 (Stan Development Team 2023), a probabilistic programming language that uses gradient-based methods to draw samples from the posterior distributions of the parameters. Because Stan relies on gradient information, it does not permit discrete valued parameters. As a result, all discrete valued parameters in our model, along with their corresponding probability distributions, were approximated using continuous numbers and distributions (Supplement 7).

We simulated 4 Markov Chains and drew 4000 posterior samples with each chain. The first 2000 samples drawn from each chain were treated as the warm-up period and were discarded. The resulting effective sample size (Stan Development Team 2023) was greater than 1500 for all model parameters. Convergence checks were performed using the R-hat diagnostic (Stan Development Team 2023) as well as visual inspection of trace plots. All R-hat values were less than 1.01, and the trace plots for each parameter appeared to be well-mixed, indicating that the model had converged. Model fit was assessed using posterior predictive checks (Supplement 1). A visual comparison of the observed distribution of data with the distribution of simulated data showed no signs of model misfit.

2.5.2. Sensitivity analyses

To examine how different data sources influenced posterior estimates of individual parameters, we refitted our model using various subsets of the available data (Gelman et al. preprint doi.org/10.48550/arXiv.2011.01808). We focused on aerial survey data, reproduction data, harvest totals, and dead samples. For each of the 4 data types, we refitted the model using only data from odd years. For aerial survey data, we also ran models with only pre- and post-2012 data, corresponding respectively to periods with low and high variability in the observed counts. For reproduction data, we ran an additional model with only post-2007 data to determine if long-term reproductive trends could be estimated without direct observations of reproductive signs. In total, we fit our model to 8 different data sets: the full data set and 7 reduced versions. For all models, we created prior–posterior comparison plots of key parameters and calculated prior–posterior overlaps (Figs. S5–S9 in Supplement 1). For models using the reduced data sets, we also computed overlaps of posteriors with those from the full model (Table S1 in Supplement 1).

Additionally, we computed Pareto-*k* statistics for each data type using Pareto smoothed importance sampling, implemented via the R package 'loo' (Vehtari et al. 2022), in order to assess their relative influence on overall model fit (Vehtari et al. 2017). The results of these analyses are presented in Supplement 1.

We also ran prior sensitivity analyses for the baseline haul-out probability parameter $\hat{\omega}$, which plays a key role in estimating total population size and was assigned an informative prior in our model due to a lack of direct data (Section 2.3.3). We refitted our model with 2 alternative priors, each shifted by 0.1 to the left and right from the original, and compared the resulting estimates for key model parameters.

All models were fitted and their sampling convergence assessed as described in Section 2.5.1. In 4 of the sensitivity analyses, 1 of the chains showed poor mixing and was therefore removed from consideration.

2.5.3. Demographic analysis

Since asymptotic demographic analysis is of interest to practical management of Baltic ringed seals, we applied analytical methods for matrix population models to our demographic parameter estimates to calculate key asymptotic quantities, such as the intrinsic population growth rate, stable stage structure, and critical harvest levels that would lead to population decline (Caswell 2001, Ersalman 2024). All demographic analyses were performed in R Statistical Software version 4.2.0 (R Core Team 2022).

2.5.4. Predictive simulations

Using posterior samples of the model parameters, we projected the population dynamics of Baltic ringed seals in the Bothnian Bay over the next 15 yr. Since our model lacked an explicit link between demographic parameters and sea ice conditions, we chose not to include climate change projections in future simulations to avoid drawing misleading conclusions. Instead, we focused on comparing the effects of alternative hunting quota scenarios. We considered 4 management scenarios: Scenario 1 maintains current hunting quotas; Scenarios 2 and 3 implement annual increases of 15 and 35 licenses, respectively, for both Finland and Sweden; and Scenario 4 introduces a one-time reduction of 270 licenses in each country, equivalent to a decrease of approximately 75%. These scenarios were applied starting from 2024. For each simulated year, the ice extent in April was randomly sampled from historically observed results. We ran 8000 simulations of each scenario, corresponding to each posterior sample of the model parameters, using R Statistical Software version 4.2.0 (R Core Team 2022).

3. RESULTS

Posterior median estimates from our model indicate that the total number of ringed seals in the Bothnian Bay has increased from 4700 (95% CI: 3500–6600) in 1988 to 26 700 (20 200–36 300) in 2023 (Fig. 4a). Driven by an estimated rise in ringed seal birth rates from 0.32 (0.13–0.53) to 0.74 (0.66–0.81) (Fig. 4b), we estimated that the population growth rate increased from 1.7% (−1.7 to 4.5%) in 1988 to a peak of 6.8% (5.6–8.1%) in 2015 before declining to as low as 4.0% (2.5–5.5%) in 2021 due to the re-introduction of seal hunting (Fig. 4c). The dominant eigenvalue of the population projection matrix suggests that under ideal conditions, the Bothnian Bay population can achieve a maximum growth rate of about 7.0% (5.9–8.8%) (Fig. 4c), with a corresponding net reproduc-

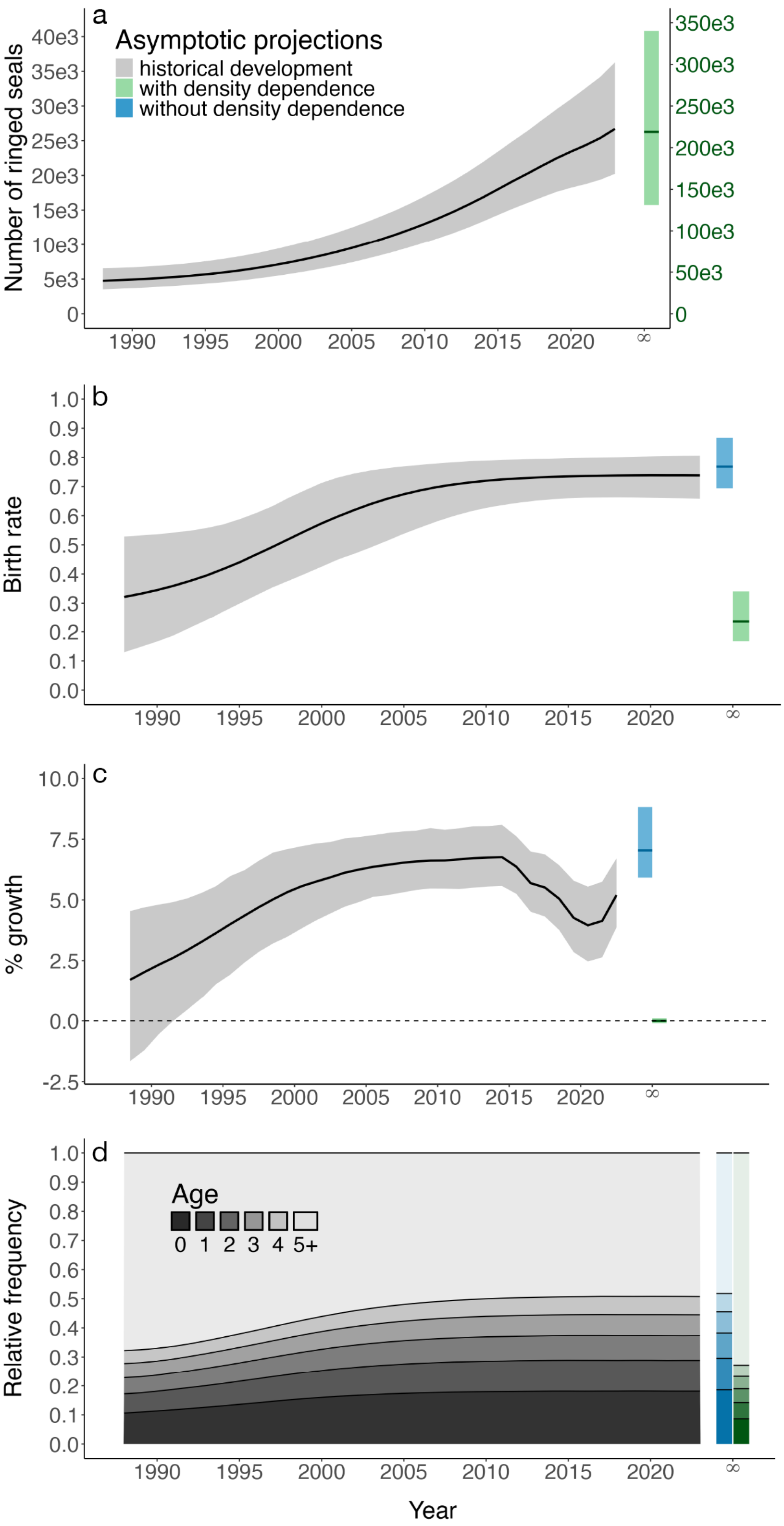

Fig. 4. Estimated (a) population size, (b) birth rate, (c) population growth rate, and (d) age structure for ringed seals in the Bothnian Bay. The rightmost segments show the expected asymptotic values for an unexploited population with and without density-dependent effects

tion rate of 3.3 (2.3–4.6) female pups produced per lifetime (Section 2.5.3).

We estimated that pregnancy rates may have been as low as 0.27 (0.02–0.56) during the 1970s and could reach a maximum of 0.83 (0.75–0.93) in a healthy Bothnian Bay population. Reproductive rates were primarily informed by direct data on reproductive signs, but the aerial survey data also provided some indication of an increasing trend in reproduction over time (Fig. S7 in Supplement 1). The current pregnancy rate was estimated to be 0.82 (0.74–0.89) (Fig. S2 in Supplement 1), although the birth rate in the spring was 0.74 (0.66–0.81). It is therefore possible that about 9% (1–21%) of pregnancies are aborted between the fall and spring. However, the pregnancy estimates were somewhat sensitive to assumptions about the importance of late-term abortions. When late-term abortions were assumed to be relatively rare, corresponding to the model with decreasing rate of pregnancy losses (Supplement 4), the estimated current pregnancy rate was 0.78 (0.72–0.84), with 4% (0–8%) of pregnancies failing between fall and winter. The choice of the model for the pregnancy losses was insignificant for other results.

The reproductive status of ringed seals is commonly assessed using placental scars and CA. We estimated that by late April, approximately 7% (1–15%) of placental scars from births may have already faded sufficiently to become undetectable. In contrast, we estimated that most CA were easily visible between April and June, and were correctly identified 97% (91–100%) of the time. In addition to seals that had recently given birth, our estimates indicate that between April and June, CA can also be found in 9% (0–26%) of seals that had not given birth.

Our model was not informative on the carrying capacity of the population, indicating that density-dependent effects were not detectable at the present population size. Hence, the posterior distribution of the carrying capacity corresponded to our prior assumptions based on historical estimates of the population size (Supplement 2). Assuming density dependence primarily affects fecundity, birth rates may eventually decline to as low as 0.24 (0.17–0.34) (Fig. 4b). It is worth noting that this latter result is independent of the estimated carrying capacity (Caswell 2001).

Improvements in reproductive rates have implied a substantial change in the age structure of the population (Fig. 4d). Our estimates suggest that the proportion of pups in the population may have increased from 11% (5–15%) in 1988 to 18% (16–21%) in 2023. During the same period, we estimated a decline in the proportion of adults from 67% (54–84%) to 50% (43–55%). Assuming density dependence primarily affects fecundity, the age structure at carrying capacity can be expected to consist of 9% (6–11%) pups, 18% (12–29%) sub-adults, and 74% (61–82%) adults.

We did not find evidence for a skewed sex ratio which, driven by our prior assumptions, was reflected in similar mortality rates between the sexes in the absence of hunting (Supplement 2). The probability that pups survive all mortality sources other than hunting during their first year was estimated to be 0.63 (0.42–0.87), which increased to 0.86 (0.77–0.95) at age 1 and to 0.95 (0.91–0.97) by maturity (Fig. 5a). However, the large negative posterior correlation between juvenile and adult survival probabilities suggested that the model had limited capacity to estimate age-specific mortality rates (Fig. S11 in Supplement 1). Refitting the model with different subsets of the data confirmed that survival probabilities were primarily informed by pre-2012 aerial survey and the reproduction data, both of which lack information on age-specific mortality (Fig. S5 in Supplement 1).

We found significant juvenile bias in bycatch from small-scale fisheries, with pups nearly 8 (4–16) times more likely to be bycaught than 1 yr olds (Fig. 5b). Male pups were also about 40% (1–88%) more likely to be bycaught than female pups. We estimated that Swedish hunting during the spring was representative of population demography (Fig. 5c). In contrast, the fall hunt was heavily aimed at adults of both sexes, with a slight bias towards males (Fig. 5d). We estimated that pups were the most vulnerable age group to hunting in Finland (Fig. 5e). Sub-adults were also generally underrepresented in the Finnish harvest.

We estimated that about 60% (48–74%) of sub-adult and adult seals and 35% (12–60%) of pups may be visible on ice during aerial surveys that coincide with extensive ice cover. Historical ice conditions in the Bothnian Bay suggest that approximately 51% (39–65%) of the total population may be visible during aerial surveys carried out in typical ice conditions (Fig. 6b). We found that as ice cover diminishes, the fraction of hauled-out seals may gradually decline to as low as 44% (30–62%). However, this proportion was found to increase dramatically to as much as 91% (70–99%) when the ice cover declined below a critical threshold of about 13 000 km^2 (Fig. 6). Although our mechanistic haul-out probability model was relatively complex, all parameters appeared to be well informed, largely by the aerial survey data. The exception was the baseline haul-out probability $\hat{\omega}_{s,a}$, which was given an informative prior (Supplement 2) and was only weakly informed by data. Nonetheless, posterior estimates were generally robust to prior choice. Only estimates of total population size, and consequently population growth rate under harvesting, showed moderate sensitivity, with estimates varying by less than 10% under sensible prior choices (Table S1 in Supplement 1).

An analysis of the impact of hunting on population growth revealed that at present, hunting 1200 seals per year may be sufficient to cause population decline (Fig. 7a), although the uncertainty around this estimate was high (1200–2600). Achieving a growth rate of 7%, the benchmark set by the Baltic Marine Environment Protection Commission (HELCOM) for designating good status, might prove challenging with any level of hunting activity (Fig. 7b), especially if more than 380 seals are hunted annually. Posterior predictive simulations suggested that maintaining hunting quotas at their current levels of 350 and 375 seals per year in Sweden and Finland, respectively, may allow for a slight improvement in the population growth rate over the next 10–15 yr (Fig. 7b). In contrast, increasing quotas by 15 licenses per year in each of Sweden and Finland may cause a slight decline in the growth rate, and an increase of 35 licenses per year in each country may significantly slow down population growth, and may even lead to population decline within the next 15 yr.

4. DISCUSSION

So far, different sources of long-term monitoring data on Baltic ringed seals have been analyzed separately to assess population growth, reproductive health and other relevant metrics of population status. A major limitation of this approach is its inability to leverage all available information, as the

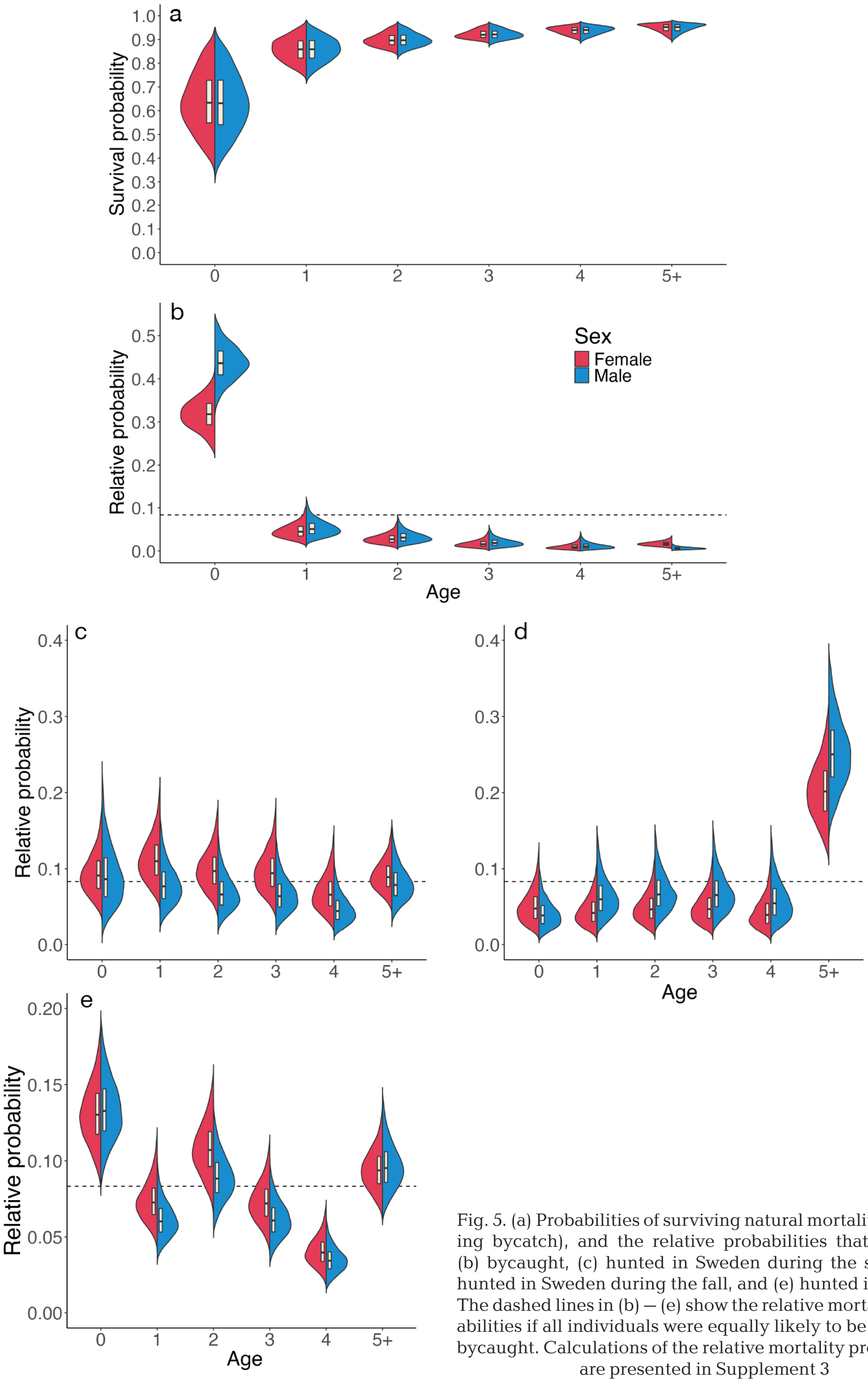

Fig. 5. (a) Probabilities of surviving natural mortality (including bycatch), and the relative probabilities that seals are (b) bycaught, (c) hunted in Sweden during the spring, (d) hunted in Sweden during the fall, and (e) hunted in Finland. The dashed lines in (b) – (e) show the relative mortality probabilities if all individuals were equally likely to be hunted or bycaught. Calculations of the relative mortality probabilities are presented in Supplement 3

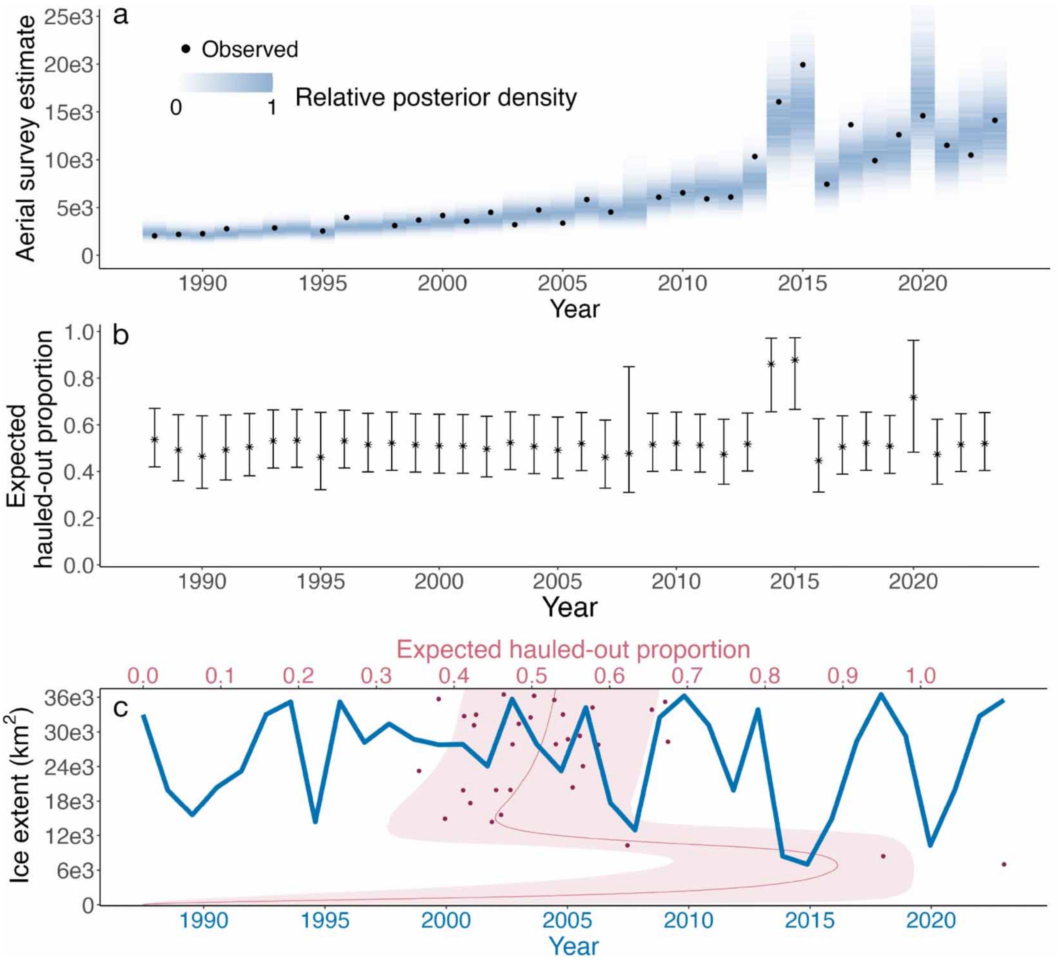

Fig. 6. (a) Posterior predictive distribution for aerial survey estimates. (b) Expected proportion of seals hauled out in each year. Error bars indicate the 95% posterior credible intervals. (c) Annual variation in the ice-covered area of the Bothnian Bay around the third week of April (blue line) and the expected proportion of seals hauled out during aerial surveys as a function of ice-covered area (red line). The points depict the median ratio of observed aerial survey estimates to the posterior estimates of total population size, and the red shaded region shows the 95% posterior credible interval for the expected proportion of seals hauled-out. Note that the overall proportion of seals hauled out depends on the population age structure, and panels b and c are based on the most recent estimate of the age structure

synergies between different data sources are not exploited (Schaub & Abadi 2011, Zipkin & Saunders 2018). This limitation has become more apparent than ever during the last decade, when unexpected trends and large fluctuations in population counts from aerial surveys made it impossible to obtain reliable estimates of population growth from survey data alone. Growth in closed populations, however, is ultimately a consequence of births and deaths. Thus, data related to reproduction and hunting also contain information on the growth rate. By incorporating all available information into a mechanistic IPM, we were able to address recent challenges in ringed seal monitoring in the Bothnian Bay. Our model showed a good fit to all available data (Supplement 1) and was able to estimate a large number of ecologically important parameters. Moreover, fitting our model in Stan (Stan Development Team 2023), while requiring some approximations, proved highly efficient, achieving convergence in under 1 h on a personal laptop computer despite the large number of parameters.

Earlier analyses of ringed seal population trends in the Bothnian Bay suggested that the population had been growing at a constant rate of approximately 5% per year since 1988 (Sundqvist et al. 2012), although more recent analyses showed that an increasing trend was likely (HELCOM 2023a). We estimated that improvements in reproductive rates may have led to a substantial increase in the growth rate between 1988

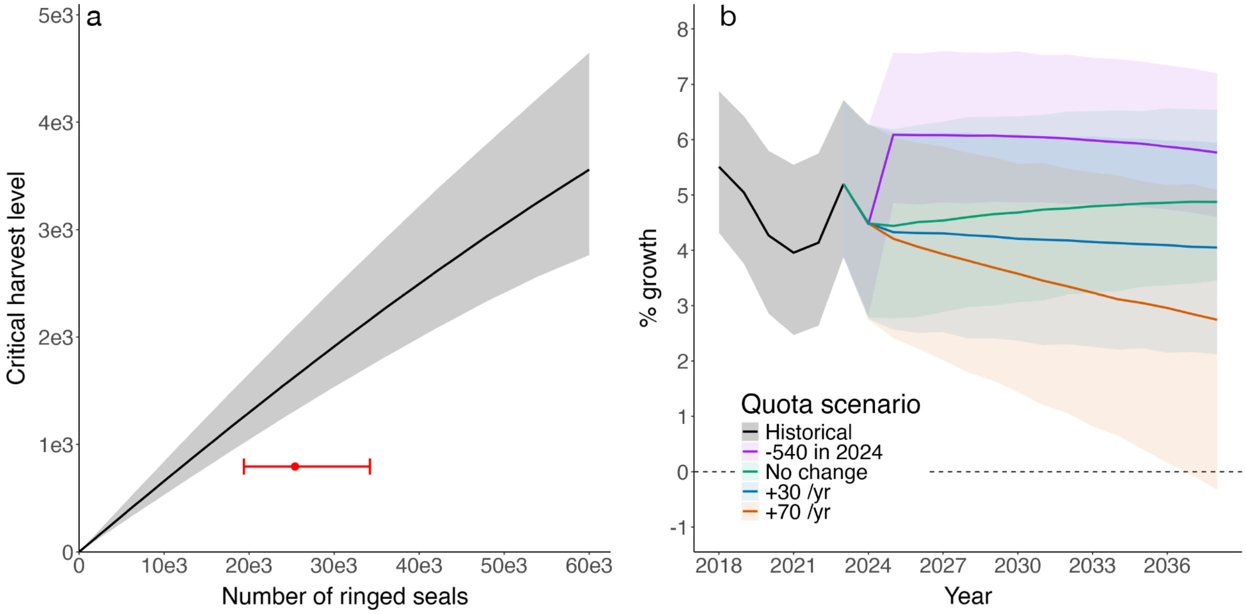

Fig. 7. (a) Critical harvest level for which the population growth rate is expected to be zero, as a function of total population size. The critical harvest level is calculated by setting the net reproduction rate equal to one. The red error bar shows the estimated population size and hunting quota (Finland and Sweden combined) in 2022. (b) Posterior predictions for future population growth rates under 4 different hunting quota scenarios: (1) quotas maintained at their current level of 350 and 375 ringed seals in Sweden and Finland, respectively, (2) quotas increased by a total of 30 licenses per year (15 in both Sweden and Finland), (3) quotas increased by a total of 70 licenses per year (35 in both Sweden and Finland) and (4) quotas reduced by a total of 540 in 2024 (270 in both Sweden and Finland) and kept constant thereafter

and the re-introduction of hunting in 2015, which accounted for much of the systematic deviation between recent population size estimates and earlier expectations based on historical trends.

On the other hand, a small number of unusually large population estimates obtained in recent years were explained surprisingly well by an increase in the fraction of seals hauling out during aerial surveys conducted in poor ice conditions, supporting earlier speculations (HELCOM 2023a). It is not clear why seals would haul out in significantly greater numbers under such circumstances. Sea ice conditions during the surveys likely correlate with air temperature, wind speed, and snow depth, which are known to affect ringed seal haul-out probability (Härkönen & Lunneryd 1992, Hamilton et al. 2018). Snow depth may additionally influence the proportion of seals that are hiding in lairs (Kelly et al. 2010). However, as surveys are conducted in late April, when most lairs have collapsed and seals are at the height of molting, and only on clear, calm days, the impact of these variables on population size estimates is likely limited. Another possibility is that the break-up of sea ice causes adult seals to relinquish territorial behavior typical of winter, allowing younger sub-adults to haul out in greater numbers (Härkönen & Lunneryd 1992, Härkönen et al. 1998, Kelly et al. 2010, Oksanen et al. 2015b). This may additionally result in large congregations of seals, potentially contributing to the high variability in survey estimates (Härkönen et al. 1998, Lindén & Mäntyniemi 2011).

Since the sub-adult age classes account for about a third of the total population, it seems unlikely that an increase in their visibility alone can account for a nearly 2-fold increase in population size estimates. Likewise, immigration from southern sub-populations, which are collectively believed to be nearly an order of magnitude smaller than the Bothnian Bay population (Sundqvist et al. 2012), also appears insufficient to explain the observed increase in counts. The increase in the proportion of visible seals during low ice cover could, in part, be attributed to an increase in the cost of foraging. During the molting period, ringed seals are likely to derive greater benefit from maintaining elevated skin temperatures than from consuming resources (Thometz et al. 2021). Diminishing sea ice will most likely result in increased distances between optimal haul-out sites and productive foraging areas, and the trade-offs associated with foraging could compel seals to decrease the frequency with which they venture out to sea. Moreover, seals may anticipate that the molting period could be interrupted prematurely, causing them to spend longer periods of time out of the water to ensure that they attain adequate levels of solar exposure before the ice melts completely.

While our findings demonstrate a clear effect of ice cover on aerial survey estimates, this conclusion was largely driven by 2 outliers that corresponded to unusually mild winters. Establishing haul-out behavior as the causal mechanism demands further investigations, including additional data and model comparisons to evaluate alternative hypotheses. Regardless of the mechanism, the number of seals on ice must be 0 when no sea ice is present. Extreme inter-annual variability in population counts from aerial surveys may therefore be expected following mild winters (Fig. 6c), which could pose additional challenges for future ringed seal monitoring efforts in the Bothnian Bay. As ice conditions in the Baltic Sea continue to deteriorate (Meier et al. 2004, Haapala et al. 2015), understanding the factors that affect ringed seal haul-out behavior will become increasingly important for reliable monitoring. Our study demonstrates that aerial surveys can be a valuable source of information to this end, and survey estimates that appear unreliable at first may provide important insights on ringed seal behavior. We therefore emphasize the need for continued monitoring efforts, as well as the need for detailed mechanistic models that go beyond simple analyses of trends. Future IPMs could also incorporate individual-level data collected from telemetry devices with dry/wet sensors, enabling direct estimation of haul-out probabilities (London et al. 2024).

Statements regarding the total population size of ringed seals require an estimate of the proportion of seals that are hauled out during the surveys. Haul-out behavior is likely to vary by age (Smith 1973, Lydersen & Hammill 1993, Crawford et al. 2012, Oksanen et al. 2015b), but little is known to quantify age-specific differences. Most studies have focused on sub-adult and adult ringed seals, which suggested that 50–84% of seals may be visible during surveys (Smith 1973, Härkönen & Lunneryd 1992, Born et al. 2002, Kelly et al. 2010). However, pups undergo their first molt and shed their lanugo hair before the molting season of older seals. Thus they spend most of their time in the water by the time they are 5 wk old (Smith 1973, Lydersen & Hammill 1993). Failing to account for their lower visibility during the surveys may lead to an underestimation of the total population size. We found that following typical winters, roughly half of the population may be visible on ice during surveys, which corresponds to the lower end of previous estimates, and is similar to what has been proposed by Smith (1973). The number of ringed seals in the Bothnian Bay may therefore be larger than previously expected (Sundqvist et al. 2012). However, our results were influenced by prior assumptions about haul-out probabilities in abundant ice conditions. Detailed studies on the molting behavior of Baltic ringed seals will be crucial for obtaining reliable estimates of total abundance.

Little is known about the survival probabilities of ringed seal pups, but previous estimates range from as low as 0.34 in Lake Saimaa, Finland, before active conservation efforts (Kokko et al. 1998) to 0.6–0.7 in the Arctic (Smith 1973, Kelly 1988). A survival probability as high as 0.8 has been suggested for unharvested Arctic populations (Smith 1973). For Baltic ringed seals, a pup survival probability of 0.65 has previously been assumed (Sundqvist et al. 2012), which is very similar to our posterior median estimate. However, the uncertainty around our estimate was high due to weak parameter identifiability (Fig. S11 in Supplement 1). Baltic ringed seal pups are safe from large predators that are common in the Arctic such as polar bears *Ursus maritimus* and Arctic foxes *Vulpes lagopus*, which might lead to comparably higher survival probabilities (Stirling & Smith 2004). On the other hand, higher bycatch mortality and greater chance of early snow and ice melt in the Baltic Sea could compensate for the limited presence of predators. Snow and ice conditions in the Baltic Sea are expected to decline in the future, which will most likely lead to increased pup mortality (Smith & Stirling 1975, Meier et al. 2004, Ferguson et al. 2005, Kelly et al. 2010, Sundqvist et al. 2012, Reimer et al. 2019).

Although previous estimates of sub-adult survival probabilities are rare, our estimate aligns closely with the 0.81–0.93 range reported in earlier studies (Sundqvist et al. 2012, Koivuniemi et al. 2019). Our posterior median estimate of 0.95 for adult survival probability corresponds to the upper end of previous estimates for ringed seals, which range from 0.88–0.96 (Durant & Harwood 1986, Kelly 1988, Kokko et al. 1998, Sundqvist et al. 2012, Koivuniemi et al. 2019, Reimer et al. 2019), and is consistent with previous assumptions for Baltic ringed seals (Sundqvist et al. 2012). Similarly high adult survival probabilities have also been estimated for Saimaa ringed seals (Koivuniemi et al. 2019) and British grey seals *Halichoerus grypus* (Thomas et al. 2019). However, the high posterior correlation between juvenile and adult survival probabilities suggests that these parameters were not individually identifiable (Fig. S11 in Supplement 1). Direct data on survival, such as from mark–recapture studies, will be needed to obtain precise age-specific estimates. Such data can additionally support the estimation of overall abundance and, in turn, haul-out probabilities.

We estimated a historical minimum pregnancy rate that was strongly in agreement with some empirical estimates from the late 1970s (Helle 1980b). However, the uncertainty around our estimate was high due to limited data on female reproductive status during the initial years of our study period. Our estimates indicate that the current pregnancy rate may be nearly the same as the maximum attainable by a healthy Bothnian Bay population. Thus, the population appears to have almost fully recovered from the effects of organochlorine contamination. Assessments of the reproductive health of Baltic ringed seals are currently based on a tentative pregnancy rate threshold of 0.9 that was established by HELCOM based on studies of seal populations elsewhere (HELCOM 2023b). Our results suggest that this threshold may be too high even for a healthy Bothnian Bay population, possibly because the Bothnian Bay is a relatively unproductive environment (Kauhala et al. 2019). A threshold between 0.80 and 0.85 may be a more realistic target. As the population continues to grow, rising intra-specific competition may cause pregnancy rates to decrease. Body conditions of Baltic ringed seals may already be declining due to poor nutritional status (Kauhala et al. 2019), although it is unclear whether population density is a contributing factor. Our model did not provide information on density-dependent effects on reproductive rates, either because the current population size is substantially below carrying capacity, or because other demographic parameters, such as pup survival, were more strongly affected. Long-term predictions of ringed seal population dynamics will require detailed consideration of density-dependent mechanisms, which would greatly benefit from additional demographic data such as long-term mark—recapture studies (e.g. Hiby et al. 2007, Koivuniemi et al. 2019). Understanding seasonal patterns of reproductive failure and their links to population density and nutritional stress would also be valuable for both assessing current reproductive health and improving future population projections.

The most reliable assessments of reproductive rates will be based on the presence of embryos in female seals sampled in the fall. Unfortunately, the current sample size for this measure remains relatively small, with substantial inter-annual variability in the observed pregnancy rate. Assessments based on placental scars may underestimate the pregnancy rate, as our results indicate that some scars that were present during parturition may have already faded by the end of April. Many of these scars are likely to be from early births in February. Additionally, a small fraction of fetuses may be aborted in early pregnancy, and placental scars from these pregnancies may have also faded by spring. Accuracy of pregnancy rate estimates from placental scars can be improved either by using the earliest available samples in the spring, or by adjusting the estimates to account for the effect of fading. Assessments based only on CA may be more difficult to interpret since a CA could also be present in seals that had an infertile estrous cycle (Boyd 1984). However, we found that CA may yield very accurate estimates of the pregnancy rate when the pregnancy rate is high. An additional challenge when estimating pregnancy rates is accounting for potential sampling biases. Most assessments, including the present study, assume that reproductive signs in harvested or bycaught females are representative of the entire female population. This assumption may introduce bias if reproductive status affects a female's likelihood of being harvested or bycaught. For instance, preferential harvesting of pups can inflate reproductive rate estimates if their mothers are harvested with them. Similarly, if post-partum females forage differently due to reduced energy reserves or molt at different locations, their susceptibility to hunting or bycatch may differ. Detailed studies on seal and hunter behavior will be essential for addressing potential sampling biases.

Our results suggest that since its re-introduction, hunting has had a substantial impact on the population growth rate, possibly reducing it by more than 3 percentage points. An unexploited Bothnian Bay population could achieve a maximum growth rate of about 7%, satisfying HELCOM's current threshold for good status. However, this threshold is unlikely to be met in the presence of even a small amount of hunting, and a growth rate of 4—5% may be a more likely outcome from the current hunting practices (Fig. 7b).

It is possible that the quotas in 2022 were close to a critical threshold beyond which population growth could no longer be maintained. However, this threshold will increase in the near future provided that the population continues to grow (Fig. 7a). Current annual hunting quotas are established at 350 and 375 seals in Sweden and Finland, respectively. Our simulation study suggested that while increasing quotas by fewer than 35 licenses per year in each of Sweden and Finland is unlikely to cause population decline within the next 10—15 yr, increases in excess of 15 per year in each country may further decrease the population growth rate (Fig. 7b). Our model assumed that there is sufficient demand for seal hunting such that harvest rates will increase proportionally to hunting quotas. While this assumption will not hold for large quotas, it remains appropriate within a precautionary framework.

It should be emphasized that, due to the short time frame of available demographic data and the opportunistic nature of sampling, our model did not take into account likely effects of climate change and other environmental variables, such as prey availability, on demographic parameters like pup mortality and reproductive rates (Meier et al. 2004, Ferguson et al. 2005, Sundqvist et al. 2012, Reimer et al. 2019). Thus, our simulation results should be viewed as a comparison of the potential impact of different hunting quota decisions, rather than as forecasts of future population dynamics. As climate change is expected to lead to further declines in snow and ice cover in the Baltic Sea (Meier et al. 2004, Haapala et al. 2015), understanding its effects on ringed seal demography is essential for making longer-term predictions. Future IPMs could explicitly link ringed seal survival and reproduction to environmental variables such as snow and ice conditions to predict population responses to various climate change scenarios (e.g. Sundqvist et al. 2012, Reimer et al. 2019). However, estimating parameters of such models will likely require direct data on survival probabilities, such as from mark—recapture studies.

Our estimates suggest that the demographic composition of Swedish harvests may differ significantly between the spring and the fall. We found that hunting was largely aimed at adults during the fall, possibly because of the greater damage they cause to fishing gear and catch. Studies of grey seals have shown that some adults, typically males, may specialize in raiding fishing gear (Königson et al. 2013). In contrast, the adult bias was completely absent during the spring hunt. This is not particularly surprising considering that adult seals are molting on ice in large numbers during the spring, and seldom venture out at sea (Smith 1973, Härkönen & Lunneryd 1992, Born et al. 2002, Kelly et al. 2010). Younger seals may be much more likely to be foraging in open water during most of the molting period, and thus have more frequent interactions with fishermen (Smith 1973, Lydersen & Hammill 1993, Crawford et al. 2012, Oksanen et al. 2015b). In fact, we estimated that adult seals were generally more likely to be hunted than sub-adults during the spring in Finland, where hunting primarily takes place on sea ice. Pups were an exception and were overrepresented in Finnish harvests despite their relatively low presence on sea ice, although some late-born pups are often still with their mothers during the Finnish hunting season. Since hunting in Finland is recreational, hunters may specifically seek out inexperienced pups for their meat and fur (Kingsley & Byers 1998).

The response of a population to harvesting is strongly influenced by the age and sex composition of the harvest, with the removal of adult females typically having the greatest impact in long-lived mammals like ringed seals (Kokko et al. 1999, Heppell et al. 2000, Reimer et al. 2019). Hence, it is important to ensure that recovered samples are either selected randomly from the harvests or that any sampling biases are accounted for. In Sweden, hunter-reported data on the sex and body length of each seal, along with records of whether or not each harvested seal was recovered as a sample, allowed us to quantify size- and sex-related sampling biases. Although such biases are unlikely in Finland, similar data could help ensure accurate and unbiased estimates of harvest compositions.

We were not able to estimate the overall magnitude of bycatch mortality due to a lack of data. Such data could be obtained through interviews with fishermen (Vanhatalo et al. 2014, Tubbs & Berggren 2024). However, consistent with findings from many other seal populations, we found that pups were significantly more at risk of getting bycaught in small fisheries than older seals (Sipilä et al. 1990, Bäcklin et al. 2011, Niemi et al. 2013, Vanhatalo et al. 2014, Jounela et al. 2019, 2024). As pups tend to favor shallow waters for foraging, and are generally curious and inexperienced, it is probable that they frequently engage with coastal fisheries and become caught in fishing gear (Kelly et al. 2010, Niemi et al. 2013, Cronin et al. 2014). Their relatively small body sizes may also make them more likely to enter smaller fishing gear and make escaping more difficult once they are caught (Cronin et al. 2014). The juxtaposition between the substantial juvenile bias in bycatch and the pronounced adult bias in protective hunting by fishermen may reflect the fact that young, inexperienced seals are inclined towards exploration, whereas experienced adults prioritize exploitation (Sjöberg & Ball 2000). On the other hand, larger seals may be more likely to detach from fishing nets, and fishermen often report the difficulty of lifting out larger seals from the water (Cronin et al. 2014). Older seals may therefore be underrepresented in the samples compared to the actual bycatch.

5. CONCLUSIONS

Amid the dynamic and uncertain conditions brought on by climate change, varying reproductive rates, and the re-introduction of seal hunting, our Bayesian IPM succeeded in providing a comprehensive assessment of the Baltic ringed seal population in the Bothnian Bay — a task that has not been possible for over a decade. In addition to estimating population size and growth, we inferred key demographic parameters including survival probabilities, reproductive rates and the relative vulnerabilities of different demographic groups to hunting and bycatch. Moreover, our model revealed possible changes in ringed seal haul-out behavior in response to changing sea ice patterns. The mechanistic nature of our model additionally enabled near-term predictions of population response to changes in hunting quotas, informing management decisions.

Wildlife populations across the globe are increasingly exposed to novel conditions that fundamentally alter their dynamics. The recent difficulties in monitoring and managing ringed seals in the Bothnian Bay may foreshadow similar challenges elsewhere. Our study demonstrates the value of mechanistic IPMs for monitoring populations in uncertain and rapidly changing environments, testing ecological hypotheses regarding mechanisms of change, and supporting science-based management decisions. IPMs such as ours could be developed into digital twins of their target populations (de Koning et al. 2023, Trantas et al. 2023). Embedding these models and Bayesian inference software within a user-friendly interface could substantially streamline research and monitoring efforts, as well as hasten management responses. We believe that the modeling approach presented here will pave the way towards the embrace of IPMs as digital twins of wildlife populations, which could prove to be a critical component of the adaptive management toolkit in a rapidly changing world. Given the accelerating pace of anthropogenic change, we anticipate increasing adoption of IPMs in studies of wild animal populations.

Data availability. Code and data are available on Zenodo at https://doi.org/10.5281/zenodo.14243458.

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LITERATURE CITED

Abadi F, Gimenez O, Arlettaz R, Schaub M (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology 91:7–14

Bäcklin BM, Moraeus C, Roos A, Eklöf E, Lind Y (2011) Health and age and sex distributions of Baltic grey seals (*Halichoerus grypus*) collected from bycatch and hunt in the Gulf of Bothnia. ICES J Mar Sci 68:183–188

Berkes F, Colding J, Folke C (2008) Navigating social-ecological systems: building resilience for complexity and change. Cambridge University Press, Cambridge

Besbeas P, Freeman SN, Morgan BJ, Catchpole E (2002) Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547

Born E, Teilmann J, Riget F (2002) Haul-out activity of ringed seals (*Phoca hispida*) determined from satellite telemetry. Mar Mamm Sci 18:167–181

Born EW, Teilmann J, Acquarone M, Riget FF (2004) Habitat use of ringed seals (*Phoca hispida*) in the North Water area (North Baffin Bay). Arctic 57:129–142

Boyd I (1984) Development and regression of the corpus luteum in grey seal (*Halichoerus grypus*) ovaries and its use in determining fertility rates. Can J Zool 62: 1095–1100

Boyd I (1991) Environmental and physiological factors controlling the reproductive cycles of pinnipeds. Can J Zool 69:1135–1148

Boyd I, Lockyer C, Marsh H (1999) Reproduction in marine mammals. In: Reynolds J III, Twiss J Jr (eds) Biology of marine mammals. Smithsonian Institution Press, Washington, DC, p 218–286

Buckland ST, Newman KB, Thomas L, Koesters NB (2004) State-space models for the dynamics of wild animal populations. Ecol Model 171:157–175

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland, MA

Chapin FS III, Kofinas G, Folke C, Carpenter S and others (2009) Resilience-based stewardship: strategies for navigating sustainable pathways in a changing world. In: Principles of ecosystem stewardship: resilience-based natural resource management in a changing world. Springer, New York, NY, p 319–337

Crawford JA, Frost KJ, Quakenbush LT, Whiting A (2012) Different habitat use strategies by subadult and adult ringed seals (*Phoca hispida*) in the Bering and Chukchi seas. Polar Biol 35:241–255

Cronin M, Jessopp M, Houle J, Reid D (2014) Fishery-seal interactions in Irish waters: current perspectives and future research priorities. Mar Policy 44:120–130

Cummings C, Lea MA, Lyle J (2019) Fur seals and fisheries in Tasmania: an integrated case study of human-wildlife conflict and coexistence. Biol Conserv 236:532–542

de Koning K, Broekhuijsen J, Kühn I, Ovaskainen O and others (2023) Digital twins: dynamic model-data fusion for ecology. Trends Ecol Evol 38:916–926

DeMaster DP (1984) A review of density dependence in marine mammals. In: Proceedings of the workshop on biological interactions among marine mammals and commercial fisheries in the southeastern Bering Sea, Vol 84. Alaska Sea Grant Report. University of Alaska, Fairbanks, AK, p 139–148

Dietze MC, Fox A, Beck-Johnson LM, Betancourt JL and others (2018) Iterative near-term ecological forecasting: needs, opportunities, and challenges. Proc Natl Acad Sci USA 115:1424–1432

Durant S, Harwood J (1986) The effects of hunting on ringed seals (*Phoca hispida*) in the Baltic. C.M.1986/N:10. ICES committee meeting no. 10. Marine Mammal Committee. https://doi.org/10.17895/ices.pub.27302439.v1

Ellis S, Franks DW, Nattrass S, Cant MA and others (2018) Postreproductive lifespans are rare in mammals. Ecol Evol 8:2482–2494

Ersalman M (2024) A Bayesian state-space model for Baltic ringed seal demography. MSc thesis, University of Helsinki

Feltz ET, Fay FH (1966) Thermal requirements *in vitro* of epidermal cells from seals. Cryobiology 3:261–264

Ferguson SH, Stirling I, McLoughlin P (2005) Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. Mar Mamm Sci 21:121–135

Haapala JJ, Ronkainen I, Schmelzer N, Sztobryn M (2015) Recent change — sea ice. In: The BACC II Author Team (eds) Second assessment of climate change for the Baltic Sea basin. Springer, Cham, p 145–153

Halkka A, Tolvanen P (eds) (2017) The Baltic ringed seal — an Arctic seal in European water. WWF Finland Rep 36. https://wwf.fi/app/uploads/2/r/u/z4bm4bbejniod2hde4g2kce/wwf_norppa_2017_web_korj_d.pdf

Hamilton CD, Kovacs KM, Ims RA, Lydersen C (2018) Haul-out behaviour of Arctic ringed seals (*Pusa hispida*): inter-annual patterns and impacts of current environmental change. Polar Biol 41:1063–1082

Harding KC, Härkönen TJ (1999) Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. Ambio 28: 619–627

Härkönen T, Lunneryd SG (1992) Estimating abundance of ringed seals in the Bothnian Bay. Ambio 21:497–503

Härkönen T, Stenman O, Jüssi M, Jüssi I, Sagitov R, Verevkin M (1998) Population size and distribution of the Baltic ringed seal (*Phoca hispida botnica*). NAMMCO Sci Publ 1:167–180

Härkönen T, Jüssi M, Jüssi I, Verevkin M and others (2008) Seasonal activity budget of adult Baltic ringed seals. PLOS ONE 3:e2006

HELCOM (Baltic Marine Environment Protection Commission) (2023a) Population trends and abundance of seals. HELCOM core indicator report. https://indicators.helcom.fi/indicator/ringed-seal-abundance/ (accessed on 20 November 2024)

HELCOM (2023b) Reproductive status of seals. HELCOM core indicator report. https://indicators.helcom.fi/indicator/seal-reproduction/ (accessed on 29 November 2024)

Helle E (1979) Growth and size of the ringed seal *Phoca* (*Pusa*) *hispida* Schreber in the Bothnian Bay, Baltic. Z Säugetierkd 44:208–220

Helle E (1980a) Aerial census of ringed seals *Pusa hispida* basking on the ice of the Bothnian Bay, Baltic. Ecography 3:183–189

Helle E (1980b) Lowered reproductive capacity in female ringed seals (*Pusa hispida*) in the Bothnian Bay, northern Baltic Sea, with special reference to uterine occlusions. Ann Zool Fenn 17:147–158

Helle E, Olsson M, Jensen S (1976) DDT and PCB levels and reproduction in ringed seal from the Bothnian Bay. Ambio 5:188–189

Heppell SS, Caswell H, Crowder LB (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665

Hiby L, Lundberg T, Karlsson O, Watkins J, Jüssi M, Jüssi I, Helander B (2007) Estimates of the size of the Baltic grey seal population based on photo-identification data. NAMMCO Sci Publ 6:163–175

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Entomol 91:385–398

Holling CS (1978) Adaptive environmental assessment and management. John Wiley & Sons, Chichester

Janssen J, Manca R (2006) Applied semi-Markov processes. Springer, New York, NY

Jounela P, Sipilä T, Koskela J, Tiilikainen R, Auttila M, Niemi M, Kunnasranta M (2019) Incidental bycatch mortality and fishing restrictions: impacts on juvenile survival in the Endangered Saimaa ringed seal *Pusa hispida saimensis.* Endang Species Res 38:91–99

Jounela P, Auttila M, Alakoski R, Niemi M, Kunnasranta M (2024) Effects of fishing restrictions on the recovery of the endangered Saimaa ringed seal (*Pusa hispida saimensis*) population. PLOS ONE 19:e0311255

Kauhala K, Bergenius M, Isomursu M, Raitaniemi J (2019) Reproductive rate and nutritional status of Baltic ringed seals. Mammal Res 64:109–120

Kelly B (1988) Ringed seal, *Phoca hispida*. In: Lentfer JW (ed) Selected marine mammals of Alaska: species accounts with research and management recommendations. Marine Mammal Commission, Washington, DC, p 57–75

Kelly BP, Badajos OH, Kunnasranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P (2010) Seasonal home ranges and fidelity to breeding sites among ringed seals. Polar Biol 33:1095–1109

Kingsley MC, Byers TJ (1998) Failure of reproduction in ringed seals (*Phoca hispida*) in Amundsen Gulf, Northwest Territories in 1984–1987. NAMMCO Sci Publ 1: 197–210

Koivuniemi M, Kurkilahti M, Niemi M, Auttila M, Kunnasranta M (2019) A mark–recapture approach for estimating population size of the endangered ringed seal (*Phoca hispida saimensis*). PLOS ONE 14:e0214269

Kokko H, Lindström J, Ranta E, Sipilä T, Koskela J (1998) Estimating the demographic effective population size of the Saimaa ringed seal (*Phoca hispida saimensis* Nordq.). Anim Conserv 1:47–54

Kokko H, Helle E, Lindström J, Ranta E, Sipilä T, Courchamp F (1999) Backcasting population sizes of ringed and grey seals in the Baltic and Lake Saimaa during the 20th century. Ann Zool Fenn 36:65–73

Königson S, Fjälling A, Berglind M, Lunneryd SG (2013) Male gray seals specialize in raiding salmon traps. Fish Res 148:117–123

Lahoz-Monfort JJ, Guillera-Arroita G, Hauser CE (2014) From planning to implementation: explaining connections between adaptive management and population models. Front Ecol Evol 2:60

Lecarpentier D, Biro T, Endresen D, Golivets M and others (2024) Developing prototype digital twins for biodiversity conservation and management: achievements, challenges and perspectives. Res Ideas Outcomes 10:e133474

Lindén A, Mäntyniemi S (2011) Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92:1414–1421

London JM, Conn PB, Koslovsky SM, Richmond EL and others (2024) Spring haul-out behavior of seals in the Bering and Chukchi Seas: implications for abundance estimation. PeerJ 12:e18160

Lydersen C, Gjertz I (1987) Population parameters of ringed seals (*Phoca hispida* Schreber, 1775) in the Svalbard area. Can J Zool 65:1021–1027

Lydersen C, Hammill MO (1993) Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Can J Zool 71:991–996

Maris V, Huneman P, Coreau A, Kéfi S, Pradel R, Devictor V (2018) Prediction in ecology: promises, obstacles and clarifications. Oikos 127:171–183

Marolla F, Henden JA, Fuglei E, Pedersen ÅØ, Itkin M, Ims RA (2021) Iterative model predictions for wildlife populations impacted by rapid climate change. Glob Change Biol 27:1547–1559

McKenzie J, Parry LJ, Page B, Goldsworthy SD (2005) Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). J Mammal 86:1237–1246

McLaren IA (1958) The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. Bull Fish Res Board Can 118

Meier HEM, Döscher R, Halkka A (2004) Simulated distributions of Baltic Sea-ice in warming climate and consequences for the winter habitat of the Baltic ringed seal. Ambio 33:249–256

Ministry of Agriculture and Forestry (2007) Management plan for the Finnish seal populations in the Baltic Sea. Tech Rep 4b/2007. Ministry of Agriculture and Forestry of Finland, Helsinki

Mouquet N, Lagadeuc Y, Devictor V, Doyen L and others (2015) Predictive ecology in a changing world. J Appl Ecol 52:1293–1310

Niemi M, Auttila M, Viljanen M, Kunnasranta M (2013) Home range, survival, and dispersal of endangered Saimaa ringed seal pups: implications for conservation. Mar Mamm Sci 29:1–13

Nyman M, Bergknut M, Fant ML, Raunio H and others (2003) Contaminant exposure and effects in Baltic ringed and grey seals as assessed by biomarkers. Mar Environ Res 55:73–99

Oksanen SM, Ahola MP, Lehtonen E, Kunnasranta M (2014) Using movement data of Baltic grey seals to examine foraging-site fidelity: implications for seal–fishery conflict mitigation. Mar Ecol Prog Ser 507:297–308

Oksanen SM, Ahola MP, Oikarinen J, Kunnasranta M (2015a) A novel tool to mitigate by-catch mortality of Baltic seals in coastal fyke net fishery. PLOS ONE 10: e0127510

Oksanen SM, Niemi M, Ahola MP, Kunnasranta M (2015b) Identifying foraging habitats of Baltic ringed seals using movement data. Mov Ecol 3:33

Palo JU, Mäkinen HS, Helle E, Stenman O, Väinölä R (2001) Microsatellite variation in ringed seals (*Phoca hispida*): genetic structure and history of the Baltic sea population. Heredity 86:609–617

Pitcher KW, Calkins DG, Pendleton GW (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? Can J Zool 76:2075–2083

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reimer JR, Caswell H, Derocher AE, Lewis MA (2019) Ringed seal demography in a changing climate. Ecol Appl 29:e01855

Rice C (1998) Marine mammals of the world, systematics and distribution. Society for Marine Mammalogy Special Publication 4. Allen Press, Lawrence, KS

Routti H, Letcher RJ, Chu S, Van Bavel B, Gabrielsen GW (2009) Polybrominated diphenyl ethers and their hydroxylated analogues in ringed seals (*Phoca hispida*) from Svalbard and the Baltic Sea. Environ Sci Technol 43: 3494–3499

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. J Ornithol 152:227–237

Sipilä T, Helle E, Hyvärinen H (1990) Distribution, population size and reproductivity of the Saimaa ringed seal (*Phoca hispida saimensis* Nordq.) in Finland, 1980–84. Finn Game Res 47:3–10

Sjöberg M, Ball JP (2000) Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic sea: bathymetry or central-place foraging? Can J Zool 78: 1661–1667

Smith TG (1973) Population dynamics of the ringed seal in the Canadian Eastern Arctic. Bull Fish Res Board Can 181. Fisheries Research Board of Canada, Ottawa

Smith TG, Stirling I (1975) The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Can J Zool 53:1297–1305

Smith TG, Hammill MO, Taugbøl G (1991) A review of the developmental, behavioural and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. Arctic 44:124–131

Stan Development Team (2023) RStan: the R interface to Stan. R package version 2.26.23. https://mc-stan.org/

Stenson GB, Buren AD, Koen-Alonso M (2016) The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal, *Pagophilus groenlandicus*. ICES J Mar Sci 73: 250–262

Stewart RE, Stewart BE, Stirling I, Street E (1996) Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). Mar Mamm Sci 12:383–401

Stirling I (1983) The evolution of mating systems in pinnipeds. In: Eisenberg JF, Kleiman DG (eds) Advances in the study of mammalian behavior. Spec Publ 7. American Society of Mammalogists, Shippensburg, PA, p 489–527

Stirling I, Smith TG (2004) Implications of warm temperatures and an unusual rain event for the survival of ringed seals on the coast of southeastern Baffin Island. Arctic 57: 59–67

Sundqvist L, Härkönen T, Svensson CJ, Harding KC (2012) Linking climate trends to population dynamics in the Baltic ringed seal: impacts of historical and future winter temperatures. Ambio 41:865–872

Thomas L, Russell DJF, Duck CD, Morris CD and others (2019) Modelling the population size and dynamics of the British grey seal. Aquat Conserv 29:6–23

Thometz NM, Hermann-Sorensen H, Russell B, Rosen DA, Reichmuth C (2021) Molting strategies of Arctic seals drive annual patterns in metabolism. Conserv Physiol 9: coaa112

Trantas A, Plug R, Pileggi P, Lazovik E (2023) Digital twin challenges in biodiversity modelling. Ecol Inform 78:102357

Tubbs S, Berggren P (2024) Questionnaire surveys to investigate marine mammal fisheries bycatch: systematic review and best practice. Front Mar Sci 11:1481840

Vanhatalo J, Vetemaa M, Herrero A, Aho T, Tiilikainen R (2014) By-catch of grey seals (*Halichoerus grypus*) in Baltic fisheries—a Bayesian analysis of interview survey. PLOS ONE 9:e113836

Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 27:1413–1432

Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner PC, Paananen T, Gelman A (2022) loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.5.1. https://mc-stan.org/loo/

Waltner-Toews D, Kay JJ, Lister NME (2008) The ecosystem approach: complexity, uncertainty, and managing for sustainability. Columbia University Press, New York, NY

Zipkin EF, Saunders SP (2018) Synthesizing multiple data types for biological conservation using integrated population models. Biol Conserv 217:240–250

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