Combining individual and close-kin mark-recapture to design an effective survey for Pacific walrus

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Abstract

The Pacific walrus *(Odobenus rosmarus divergens)* is an ice-associated marine mammal found in the Bering and Chukchi seas, where they are an important resource for indigenous peoples. In the late 20th century, the population declined, likely because it had overshot carrying capacity and was then subject to high subsistence harvests. Currently, Pacific walrus is species of conservation concern due to potential impacts of climate change, particularly related to loss of sea ice. To reduce uncertainty population size estimates, researchers undertook an individual genetic mark-recapture (IMR) sampling campaign from 2013-2017 and collected tissue samples from over 8,000 individuals. Another campaign of a similar scale is ongoing (2023-2027). While sample collection was designed for IMR, advances in close-kin mark-recapture (CKMR) methods and associated molecular techniques mean these samples could also be suitable for CKMR. The advantages of CKMR over IMR include increased effective sample size (since each individual tags not only itself, but also its parents, siblings, and offspring) and additional insights into demographic quantities of interest. Here, we combine individual and close-kin mark-recapture in a single modelling framework (ICKMR) and investigate whether different sampling strategies can increase precision in estimates of abundance and trend. Our modelling approach includes special considerations for walrus life-history, including a multi-year inter-birth interval. We implemented our model in R and used an individual-based simulation to test performance of the ICKMR model. We find that the expected precision of the ICKMR estimates of abundance are higher than those expected from IMR alone, and with ICKMR, 3 instead of 5 years of sampling can be conducted to obtain the same level of precision. These results suggest that ICKMR is a promising approach for assessing population size and trend of species which have been difficult to survey using more traditional methods. [285/350]

Keywords: close-kin mark-recapture, individual genetic mark-recapture, survey design, walrus

1 Introduction

Estimation of abundance and other demographic parameters such as survival is a key part of wildlife management and conservation. Traditional mark-recapture analysis (Williams et al., 2002) can deliver estimates with low bias and uncertainty, provided that enough individual animals i) are naturally, artificially, or genetically "marked" and identifiable and ii) can be recaptured over time. If genotypes are used as marks, as in genetic individual mark-recapture (IMR; Palsbøll et al., 1997), then kinship patterns amongst samples (parents, siblings, etc) contain additional demographic information (Skaug, 2001). Close-kin mark-recapture (CKMR; see Bravington et al., 2016) is a framework for using kinships, as inferred from genotypes, to estimate abundance and demographic parameters. CKMR provides additional flexibility and increased effective sample size compared with IMR since non-lethal and/or lethal samples (e.g., from sampling, hunting, or natural mortality) and/or non-lethal samples can be used. As of 2025, most CKMR projects have been for commercial fish (e.g., Davies et al., 2020) or sharks (e.g., Hillary et al., 2018), but there have been some for mammals, including Conn et al. (2020)'s modeling study of bearded seals and its implementation by Taras et al. (2024), and Lloyd-Jones et al. (2023) for flying foxes.

The principle behind CKMR is that every individual has (or had) one mother and one father; thus, for a given sample size, in a large population there will be few "recaptures" of parents or their other descendants, while in a small population there will be many. In practice, the data for CKMR comprise the outcome of pairwise kinship checks amongst samples, plus covariates associated with each sample such as its date of capture, age, size, sex, etc. The CKMR model has two components: a population-dynamics part driven by the demographic parameters; and formulae for expected frequencies of different kinship types in pairwise comparisons, conditional on sample covariates and population dynamics. By combining the kinship data with the population dynamics model, parameters can be estimated using maximum likelihood or Bayesian methods.

CKMR has mostly been used in situations where self-recaptures are unlikely or impossible (e.g., because sampling is lethal). Lloyd-Jones et al. (2023) did include IMR results in a CKMR study but did not integrate both datasets into a single model. Here, we focus on a population where IMR was the original project goal; therefore, we extend traditional CKMR to include IMR in the same model as an additional kinship type, whereby pairwise genetic comparisons can show that two samples are from the same animal.

The success of CKMR and/or IMR depends on whether the data collected contain sufficient recaptures. Sampling design (i.e., number of samples, sex and age composition of sampled individuals, study duration) is crucial to avoid predictable and expensive failure. The pairwise-comparison framework leads to analytical results for the expected number of kin pairs and expected variance given number of samples (and associated covariates), so that simulation is not essential. Nevertheless, simulation can be useful as a way to check kinship probabilities and design setup. In this study, we show how to perform and verify the CKMR calculations using a case study on the Pacific walrus (*Odobenus rosmarus divergens*; hereafter, walrus). We explore different demographic and design scenarios for walrus using IMR alone versus a combined CKMR and IMR (ICKMR) approach, and demonstrate how the latter can be used to substantially reduce the amount of survey effort required for adequate monitoring.

In the rest of this Introduction, we provide background on walrus biology and surveys. In Methods, we describe our walrus population dynamics model, derive walrus-appropriate kinship probability formulae, and show how to analytically calculate the expected variances that might come from different survey designs. We also outline the simulation we used to test our ICKMR model. The Results section shows how different survey designs are likely to perform (e.g., with/without CKMR). In the Discussion, we summarize our conclusions for walrus and also mention modeling simplifications made for design purposes that we may reconsider when working with real data.

1.1 Walrus biology and background

The walrus is a gregarious, ice-associated pinniped inhabiting continental shelf waters of the Bering and Chukchi seas. During winter (when sea ice forms south of the Bering Strait) virtually all walruses occupy the Bering Sea (Fay, 1982). In summer (when sea ice is absent from the Bering Sea) almost all juvenile and adult female walruses, and some adult male walruses, migrate north to the Chukchi Sea. When walruses rest offshore on sea-ice floes, their distribution is dynamic, because it generally follows the marginal ice zone (a moving, changing habitat which contains a mix of ice floes and water) but also concentrates in regions of high benthic productivity. This allows walruses to forage for benthic invertebrates while simultaneously having access to a nearby substrate for hauling out. Adult walruses are considered a single, panmictic genetic stock (Beatty et al. 2020), and satellite-tagged adult female walruses move between US and Russian waters of the Chukchi Sea over the course of a single season (Jay et al. 2012, Udevitz et al. 2017). We see this despite the preponderance of tagging having been conducted in US waters using remotely deployed tags that stay on for a matter of weeks, not months or years (Jay et al. 2012).

Sea ice has declined for decades (Perovich and Richter-Menge, 2009; Stroeve et al., 2012; Stroeve and Notz, 2018), and coupled global atmospheric-ocean general circulation models predict its continued decline (Årthun et al., 2021). When sea ice recedes from the continental shelf, walruses come on shore to rest in large herds at sites termed haulouts, from which they make long trips to foraging hotspots (Jay et al., 2012). This change in their activity budgets (Jay et al., 2017) may ultimately lead to a decline in body condition and an increase in mortality or a decrease in reproduction (Udevitz et al., 2017). Furthermore, disturbance at haulouts can cause stampedes, resulting in mass calf and juvenile mortality. Continued sea-ice loss and a concomitant increase in the intensity and expansion of industrial and shipping activities in Pacific Arctic waters (Silber and Adams, 2019) are expected to drive a substantial population decline (Garlich-Miller et al., 2011; MacCracken et al., 2017; Johnson et al., 2023; Johnson et al., 2024).

Range-wide abundance and demographic rate estimates are crucial for understanding population status, as well as for developing and implementing harvest management plans. In particular, subsistence walrus harvests in Alaska and Chukotka exceed 4,000 animals annually (USFWS, 2023); indigenous peoples and management agencies need information on the status of the walrus population in order to manage these harvests sustainably. Furthermore, in the United States, the Marine Mammal Protection Act (MMPA) requires a determination of potential biological removal for walrus, which, in turn, requires a precise abundance estimate (Gilbert, 1999; Wade and DeMaster, 1999).

Scientists have attempted to ascertain walrus population size since at least 1880 (Fay et al., 1989), and until very recently, unsuccessfully. The most concerted effort were the 1975-2006 range-wide airplane-based surveys conducted collaboratively by the U.S. and the Soviet Union and later Russian Federation. However, resulting estimates were biased and imprecise, and count-based methods were abandoned after the 2006 survey which, despite a rigorous design, innovative field methods, and sophisticated analyses, yielded a 95% confidence interval (CI) on the population size estimate of 55,000–507,000 animals (CV = 0.93). The extensive imprecision in the estimate resulted from the walrus population being widely dispersed with unpredictable local clumping (Speckman et al., 2011; Jay et al., 2012), which is, in turn, due to the large area of arctic and subarctic continental shelf over which they forage, their gregarious nature, and the dynamic nature of the marginal ice zone.

The first rigorous walrus survival rate estimates were obtained within the past decade via Bayesian integrated population models (IPMs), which combined multiple data sources to estimate demographic rates and population trend over multiple decades (Taylor and Udevitz, 2015; Taylor et al., 2018).

However, the original problems with the aerial survey data continued to preclude conclusions about population abundance in the IPMs (Taylor and Udevitz, 2015).

In 2013, the U.S. Fish and Wildlife Service (FWS) initiated a genetic IMR project to estimate walrus abundance and demographic rates. Under this approach, genetic "marking" via skin biopsy samples (Palsbøll et al., 1997) provided a major advantage over traditional marking techniques because walruses are extremely difficult to handle physically. Over five years of research cruises, biologists attempted to collect a representative sample of walruses in the accessible portion of the marginal ice zone in each year a cruise was conducted, although Russian waters were not accessible in all years. Sampling focused on groups of adult females and juveniles, as these classes are the demographically important population segments of this polygynous species (Fay, 1982). Further methods for the IMR study are detailed by Beatty et al. (2020) and Beatty et al. (2022).

Data analysis from the first generation of walrus research cruises (2013–2017) used a Cormack-Jolly-Seber multievent model to estimate survival rates, and a Horvitz-Thompson-like estimator to obtain population size. The total abundance of 257,000 had a 95% credible interval (CrI) of 171,000–366,000 (CV=0.19; Beatty et al. 2022). Although the precision of the abundance estimate from the IMR study was much improved over the final aerial survey, the IMR study required extensive investment of human and financial resources (i.e, USD $5,000,000). A more cost-effective approach is needed to assess the walrus population on a regular interval. As mentioned above, biopsy samples also contain information about kin relationships, which, through CKMR, can substantially augment the information content of genetic IMR without increasing sampling effort. [1608 words].

2 Methods

To evaluate our proposed survey designs, we first constructed our ICKMR model for walrus. We encoded our knowledge about walrus biology and life history to (i) build a model of walrus population dynamics, including the breeding cycle, and (ii) formulate kinship probabilities between pairs of samples. The population dynamics model incorporates demographic parameters that need to be estimated: survival rates, adult abundance in some reference year, trend, etc. The kinship probabilities depend on population dynamics. Given a real dataset, we would estimate the parameters by maximizing the log-likelihood that combines the kinship probabilities with the actual outcomes of all pairwise comparisons. For design purposes, though, we instead use an analytical method to predict the precision of the estimates that would be expected under different sampling designs. Although it is not strictly necessary to simulate any data in this process, we did use simulations to check that our CKMR model was appropriately formulated. This section describes our population dynamics model, kinship probability formula, design calculations, and simulation setup.

2.1 Biological considerations

Adult males were not included in this study due to seasonal sex segregation and the geographical coverage of the sampling effort (see Section 1). Additionally, adult males form leks and compete for breeding access to females, which suggests the potential for persistent individual variability in breeding success. This variability could considerably complicate the interpretation of paternal half-sibling kinship data (see Discussion). Therefore, our analysis focuses exclusively on female-driven dynamics, considering three types of kinship: mother-offspring pair (MOP), cross-cohort maternal half-sibling pair (XmHSP), and self pair (SP), which represents individual recaptures. Our samples comprise juvenile and adult females, plus juvenile males. While there challenges with modelling males as parents, juvenile males can still be incorporated as potneital offsprning of females and as potential maternal half-siblings to other sampled individuals (female or male). We assume that individual variation in female fecundity is minimal.

We assume that age estimates will be available for all samples, based on epigenetic aging data (CITE). Our model is structured to allow for errors in estimated age (with standard deviation assumed known, i.e., after calibration of epigenetic against known-age samples), though the results here assume that there are no errors; see Discussion.

2.1.1 Stage-structured quasi-equilibrium dynamics

For our female-only population dynamics model, we adpoted a stage-structured (juvenile/adult), rather than fully-age-structured approach. This decision was based on two key considerations: (*i*) most female adults are expected to have similar reproductive capacity and chance of survival, regardless of age; and (*ii*) stage-structured models are simpler to implement for CKMR and require fewer parameters. Given these advantages, a stage-structured model should provide sufficient accuracy for study design purposes.

We used two stages: juveniles aged 1–5, and adults aged 6+ (the first age at which an accompanying calf is common) at sampling. We did not consider calves (age 0), to avoid complications around simultaneous mother-calf sampling. We assume constant survival within each stage (ϕ_{A} and ϕ_{J}), and that offspring survival from age 1 onwards is independent of its mother's survival, whether or not the offspring has fully weaned yet. We assume that adult female abundance was either stable, increasing exponentially, or decreasing exponentially over the period covered by the population dynamics (2000–2028; the lower limit of y_0 =2000 is set because there were large changes in the population prior to that; Taylor and Udevitz (2015) and Taylor et al. (2018)). We have

$$N_{y,\mathrm{A}} = N_{y_0,\mathrm{A}} e^{r(y-y_0)} \tag{1}$$

where $N_{y,\mathrm{A}}$ is the abundance of adult females in year y, and e^r is the rate of population increase.

Age composition within stage does not matter for MOP and XmHSP probabilities, but is relevant for SPs. For that purpose, we assume that age composition over the period is adequately described by the stable-age or "quasi-equilibrium" distribution consistent with survival ϕ_A and rate-of-increase e^r. As shown in e.g., Keyfitz and Caswell (2005) Chapter 5, this is $N_{y,a} \propto N_{y,\mathrm{A}} \phi_\mathrm{A}^a e^{-ra}$.

2.1.2 The breeding cycle

Walrus have a litter size of one, and due to a 14-15 month gestation, they cannot give birth in consecutive years Fay (1982) and Robeck et al. (2023). In addition, they are unlikely to give birth every second year (Taylor and Udevitz, 2015; Taylor et al., 2018; Robeck et al., 2023) except perhaps if the population is growing at a large exponential rate . We used a first order Markov model to describe the walrus breeding cycle (Fig. 1). We assume three breeding states: (S1) pregnant; (S2) with young-of-the-year (YOTY) calf; or (S3) non-breeding, i.e., neither of the above. From state S1 (pregnant), next year's state must be S2 (with YOTY calf). From state S2, a female may next year either return to state S1 (become pregnant again), with probability ψ_2, or move to state S3 (neither pregnant nor with calf) with probability $1 - \psi_2$. From state S3, she will either move to state S1 (become pregnant) with probability ψ_3, or remain in state S3 with probability $1 - \psi_3$.

Females enter state S3 (i.e., reach sexual maturity) at age 4, and therefore can become pregnant at age 5 and give birth at age 6 (Fay, 1982). Depending on the values of ψ_2 and ψ_3, this leads to an increase in effective fecundity (i.e., probability of being in state S2) over the first few years of adult life. Both ψ_2 and ψ_3 are estimated from the data. We do not use any data on whether females were with or without calf when sampled, so the estimates of ψ_2 and ψ_3 rely on the distribution of birth-gaps between maternal half-sibling pairs. In addition, our data are not able to distinguish between fine-scale aspects of the reproductive cycle, such as differences in fertilization/implantation rates versus

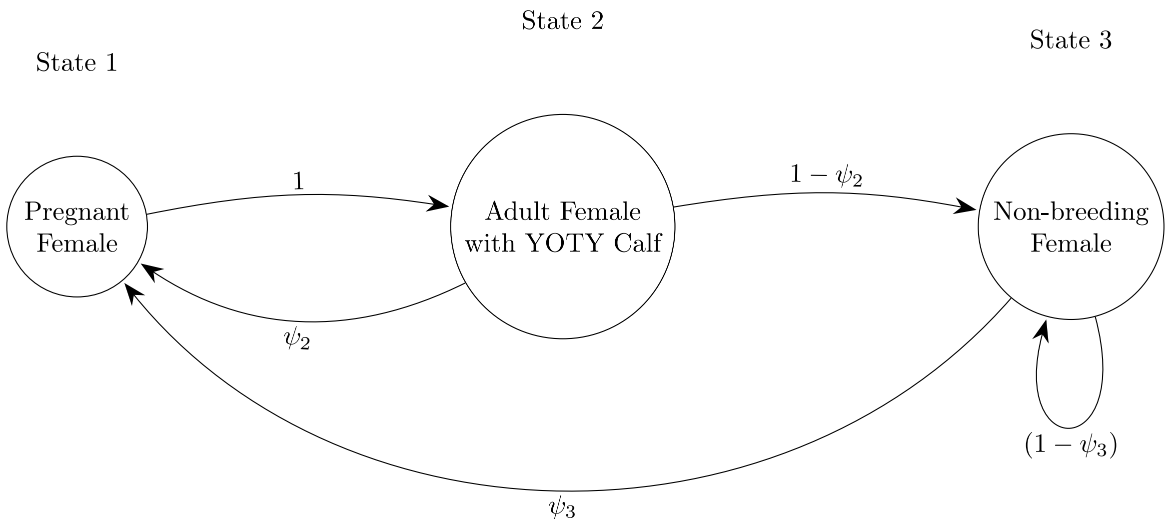


Figure 1: Directed cyclic graph showing the breeding cycle for walrus as represented in our Markov model. Nodes in the graph show the states (pregnant, with young-of-the-year (YOTY) calf, or non-breeding) and edges give the transition probabilities between those states. On average, walrus reach sexual maturity at age 4, so females enter the graph at node non-breeding.

pregnancy failures or neonatal deaths. Thus, reproductive failtures are subsumed by Eq. X and X, even though the transition from state S1 (pregnant) to S2 (with YOTY calf) is set to 1.

We later use two quantities, which are derived from the breeding cycle. First, we calculate the (average) proportion of adult females in S2 (with YOTY calf), $\bar{\beta}_2$. Let Ψ be the (3×3) transition matrix implied by Figure 1. Taking the eigendecomposition of Ψ, we can extract the second element of the eigenvector with the largest eigenvalue to obtain $\bar{\beta}_2$. Second, we define fecundity as a function of age

$$F\left(a\right) \triangleq \frac{\mathbb{P}\left[B\left(a\right)=2\right]}{\bar{\beta}_2}, \tag{2}$$

so that immature animals have fecundity 0, and an average adult has fecundity 1.

2.1.3 Formulating kinship probabilities

To establish the demographic probabilities of kinship between two sampled individuals, we apply the principle of effective relative reproductive output (ERRO). Specifically, the probability that a given adult sample is the parent of an independently sampled offspring is the ratio of that adult's expected fecundity to the total fecundity of all parents at the time the offspring was born. We denote the kinship for individuals i and j as K_{ij}, which in our case may be MOP, XmHSP, SP, or unrelated pair (UP). In the case of MOPs and XmHSPs, we ensure that only one sample from each individual is used (so "sample" and "individual" are interchangeable terms), whereas for SPs we need to consider multiple samples from one individual (in which case, "sample" and "individual" have different meanings).

Throughout, we use the following notation: individual i, sampled at age a_i in year y_i with birth year $b_i \triangleq y_i - a_i$. As noted above, we only consider female abundance, so throughout N refers to females only. When female abundance is considered for a given year (y) and development stage ($d = \mathrm{A}$ or J, for adult or juvenile, respectively), it is written with two arguments, $N_{y,d}$. We define the binary variable L to indicate lethality of sampling ($L_i = 1$ indicating lethal sampling for individual i). We use $\mathbb{I}()$ as an indicator function, returning 1 when the condition inside the brackets is true, else 0. Kinship probabilities are functions of demographic parameters such as $\phi_\mathrm{A}$and $N_{y_0,\mathrm{A}}$; we use $\boldsymbol{\theta}$ as shorthand for this set of parameters, which become explicit in later iterations of the formulae.

2.1.4 Mother-offspring pairs (MOPs)

Consider a comparison between a potential mother i, to a potential offspring j. We restrict our analysis to comparisons that satisfy the following:

- i is female (though j need not be);
- $a_j \geqslant 1$ (no calf samples are used);
- $b_j \geqslant 2000$ (population dynamics starts at year 2000).

We can now distinguish two cases: $y_i < b_j$ and $y_i \geqslant b_j$.

For $y_i < b_j$, individual i still has to survive several years in order to be individual j's mother (note that i may be immature when sampled, but mature by the time of j's birth). In this case i's sampling *must* be non-lethal ($L_i = 0$). The MOP probability is

$$\mathbb{P}\left[K_{ij} = \mathrm{MOP}|a_i, y_i, b_j, L_i = 0, \boldsymbol{\theta}\right] = \frac{R_i(b_j|y_i, a_i)}{R^+(b_j)}$$

where $R_i(b_j|y_i, a_i)$ is the expected reproductive output (ERO) of individual i in year b_j given i is age a_i in year y_i. $R^+(b_j)$ is the total reproductive output (TRO) of the whole population in year b_j. ERO and TRO are in units of "number of calves" here (though generally their units are arbitrary but matching). TRO is the total number of adult females in the population when j is born, $N_{b_j\mathrm{A}}$, multiplied by the proportion of females with calves (breeding state S2), $\bar{\beta}_2$: $R^+(b_j) = \bar{\beta}_2 N_{b_j,\mathrm{A}}$.

There are two components to i's ERO: first, she has to survive; second, she has to be calving (breeding state 2) in b_j:

$$R_i\left(b_j|y_i,a_i\right)=\Phi\left(y_i-b_j,a_i\right)\mathbb{P}\left[B\left(a_i+b_j-y_i\right)=2\right],$$

where $\Phi\left(\Delta t,a\right)$ gives the probability of survival for Δt years, starting from age a (product of annual juvenile and adult survival probabilities). $B\left(a\right)$ is an individual's breeding state at age a, which here is individual i's age at b_j ($a_i+b_j-y_i$, assuming she survives).

Then, using our definition of fecundity at age, (2), we have

$$\mathbb{P}\left[K_{ij}=\mathrm{MOP}|a_i,y_i,b_j,L_i=0,y_i<b_j,\boldsymbol{\theta}\right]=\frac{\Phi\left(y_i-b_j,a_i\right)F\left(a_i+b_j-y_i\right)}{N_{b_j,\mathrm{A}}}. \tag{3}$$

If i is sampled after the birth of j ($b_j<y_i$), then we can infer that i was alive at that time (or not yet been born), eliminating the need to account for survival or lethality terms. However, i may not have reach reproductive maturity by b_j. Letting $F\left(a\leqslant 0\right)=0$,

$$\mathbb{P}\left[K_{ij}=\mathrm{MOP}|a_i,y_i,b_j,b_j<y_i,\boldsymbol{\theta}\right]=\frac{F\left(a_i-y_i-b_j\right)}{N_{b_j,\mathrm{A}}}. \tag{4}$$

2.1.5 Maternal half-sibling pairs (XmHSPs)

To find probabilities of cross-cohort maternal half-sibling pairs (XmHSPs), we check whether individual k and individual l have the same mother. We impose the following criteria:

- $b_l>b_k$ (avoiding double-counting);
- $b_k\neq b_l$ (walrus give birth to a single offspring at a time);
- $b_k\geqslant 2000$ (population dynamics starts at 2000).

If we call m the mother of k, what is the probability that l's mother was m? We know that m was alive, mature, and in breeding state S2 at k's birth, and that m survived at least one more year after k's birth, otherwise k would not have lived long enough to be sampled. In order for m to also be l's mother, three more things have to happen:

1. m survives until b_l;
2. m is in breeding state S2 in b_l;

3. amongst all the females that are alive and in breeding state S2 in year b_l, m is the mother.

Let $\Phi(\Delta t)$ be the adult probability of survival for Δt years from "now" and recall Ψ is the breeding cycle transition matrix. The probability 3-vector of an animal being in each state (S1, S2, S3) at time t is $p^{[t]}$. The probability vector at time $t+1$ is then $p^{[t+1]} = \Psi p^{[t]}$. Now define $p^{[0]} = (0,1,0)^\top$ which is the probability vector of m's breeding state at k's birth (certain state 2), and recall $\bar{\beta}_2$ is the proportion of adult females in breeding state S2. Then

$$
\begin{aligned}
&\mathbb{P}\left[K_{k\ell} = \text{XmHSP} | b_k, b_\ell, \theta\right] \\
&= \mathbb{P}\left[K_{km} = \text{MOP} | B_m(b_k) = \text{S2}, m \text{ alive at } b_k + 1, b_\ell, \theta\right] \\
&= \frac{\Phi(b_l - b_k - 1)\left[\Psi^{b_l - b_k} p^{[0]}\right]_2}{N_{b_l,\text{A}} \bar{\beta}_2}
\end{aligned} \tag{5}
$$

where $[]_2$ gives the second element of the vector, i.e., the probability that m (given she was alive) was again in breeding state S2 at l's birth.

HSPs are just one of several “second-order” kin-pairs that are practically indistinguishable genetically, hence cannot be identified directly and unambiguously. Fortunately, HSPs are demographically by far the most common when the birth-gap is short. When the birth-gap approaches twice the age-of-maturity, though, grandparent-grandchild pairs (GGPs) bcome more prevalent [Citation?]. To mitigate this issue, we restrict the range of birth gaps considered in the model to those where GGPs are very rare (e.g., below twice the age at maturity).

2.1.6 Self-recaptures (SPs)

Our stage-structured model keeps the population dynamics simple, but we do have to make extra assumptions about sampling selectivity to include IMR data. Here, we assume that selectivity varies only by stage (adult/juvenile), not by age within stage. We only consider female samples for self-recapture, since males are prone to "permanent emigration" when they mature (Beatty et al., 2022), so do not yield readily-interpretable inferences.

To compute stage-structured self-recapture probabilities, we condition on the age of the first sample but *not* explicitly on the age of the second sample; instead, we condition on the second sample's developmental stage at sampling (d_2). If the first sample would have reached the right developmental stage (i.e., the two could be the same animal), then we assume it is equally likely to be *any* of the females in that developmental stage in the given year. This implies that sampling is non-selective within each developmental stage. Therefore, the probability that the first sample is the same individual as the second sample is the reciprocal of the developmental stage abundance. Additionally, we account for survival over the intervening years. The self-recapture kinship probability between samples 1 and 2 is (where $y_1 < y_2$):

$$\mathbb{P}\left[K_{12} = \mathrm{SP}|a_1, y_1, d_2, y_2, L_1 = 0, \boldsymbol{\theta}\right] = \frac{\mathbb{I}\left[d\left(a_1 + \left(y_2 - y_1\right)\right) = d_2\right] \Phi\left(y_2 - y_1, a_1\right)}{N_{y_2,d_2}}, \tag{6}$$

where $d(a)$ is the function that maps age to developmental stage, with $d(a < 6) =$ "juvenile" and $d(a \geqslant 6) =$ "adult". We also condition on the first sample being non-lethal (since we have a second sample). To obtain N_{y_2,d_2}, we need either adult or juvenile abundance. Adult abundance is included in the population dynamics model, however, additional steps are required to deduce juvenile abundance. Assuming stable age composition, we show in Appendix C that for walrus:

$$N_{y,\mathrm{J}} = N_{y,\mathrm{A}} \frac{\rho - \phi_\mathrm{A}}{\rho - \phi_\mathrm{J}} \left(\left(\frac{\rho}{\phi_\mathrm{J}} \right)^5 - 1 \right),$$

where $\rho = e^r$ is the relative annual population increase/decrease.

2.2 Simulations

We developed an individual-based simulation with the life history and population dynamics of Pacific walrus to test our ICKMR model. The simulation was modified from the R package `fishSim` by Shane Baylis (`https://github.com/SMBaylis/fishSim`). The simulation is stochastic and operates on an annual basis. Individuals are tracked using unique identifiers allowing for the identification of kinship pairs in simulated samples. We initialized the simulation in 1950 with a population of 250,000 animals. These individuals are considered “founders” and do not have mothers or fathers. The age and sex structure of the initial population is determined by the survival rates used in the simulation (Table 1), which were based on rates reported in Taylor et al. (2018). Individuals that are at or beyond the age of first reproduction mate randomly and males can potentially father more than one calf. Female reproduction follows Section 2.1.2. Females that are in state 2 of the breeding cycle give birth to a single offspring with 1:1 sex ratio (Fay, 1982). There is no systematic age-effect on female reproductive dynamics, except that they are guaranteed not-pregnant in the year immediately prior to

Table 1: Demographic parameters for simulation under four scenarios (D0, D1, D2, and D3)

Parameter	D0 NULL	D1 Stable	D2 Decreasing	D3 Increasing
	Demographic Scenario			
Maximum age (AMAX)	37	37	37	37
Age at first reproduction for females (AFR)	6	6	6	6
Age of last reproduction for females (ALR)	37	29	29	29
Age of first reproduction for males	15	15	15	15
Young-of-the-year (Age 0 calf) survival	0.7	0.7	0.66	0.7
Juvenile survival (Ages 1 to 5)	0.9	0.9	0.85	0.9
Reproductive adult female survival (Ages 6 to ALR)	0.9622	0.99	0.985	0.99
Non-reproductive adult female survival (Ages ALR to AMAX)	NA	0.55	0.5	0.55
Probability of breeding at 2-yr interval (ψ_2)	0.1	0.1	0.1	0.1
Probability of breeding at 3-yr+ interval (ψ_3)	0.5	0.5	0.5	0.5
Resulting rate of increase (r)	0	0	-0.02	+0.01

maturity (Section 2.1.2), which slightly lowers effective fecundity for the first few years of adulthood until the Markov chain reaches equilibrium. We did not include senescence in our CKMR model, but we do include it in our simulations. Parameters in Table 1 were adjusted to maintain the desired population rate of increase (r).

In sampling years, captures are simulated according to either historical or planned future sample sizes. Females are available to be sampled at any age, while only calf and juvenile males are available for sampling. For simulated captures between 2014 and 2017, we used the realized sample sizes by age or age class as the basis for simulation. For simulated captures between 2023 and 2027, we used the target number of samples per age class as the basis for simulation. After sampling, some individuals die (according to age and/or sex specific mortality rates, Table 1). If a female with a young-of-the-year calf dies, her calf also dies. Individuals automatically die if they reach the maximum age. Living individuals then have their age incremented.

The female breeding cycle is as described in Section 2.1.2. Although we assume in the simulation that all pregnancies result in live births, this rate is aliased with the nominal calf-survival probability, since only samples from age 1 onwards are considered; only the product (nominal pregnancy success rate $\times$ nominal calf survival) affects the simulated samples, not the two constituent parameters. Males and females less than 4 years old (or older than the age of last reproduction; ALR) are exempt from this cycle. The simulation then proceeds to the following year.

All simulations had a starting population size of 250,000 and were run from 1950 to 2030.

Table 2: Sampling scenarios

Sampling Scenario	Description	Effort per Year					
		2023	2024	2025	2026	2027	2028
S0	NULL: 100% effort 2023-2027	1	1	1	1	1	0
S1	Reality + 100% effort 2025-2026	1	0	1	1	0	0
S2	Reality + 100% effort 2025-2027	1	0	1	1	1	0
S3	Reality + 100% effort 2025-2028	1	0	1	1	1	1
S4	Reality + 75% effort 2025-2026	1	0	0.75	0.75	0	0
S5	Reality + 75% effort through 2027	1	0	0.75	0.75	0.75	0
S6	Reality + 75% effort through 2028	1	0	0.75	0.75	0.75	0.75
S7	100% effort 2023-2025	1	1	1	0	0	0

2.3 Model checking

To evaluate agreement between the simulation and CKMR model, we generated 50 replicate simulated datasets with demographic parameters under a null scenario as in Table 1 demographic scenario D0 and simulated historical and future sampling according to realized or target sample sizes by age class, with effort per year from 2023 as in sampling scenario S0 in Table 2). We checked each of the simulated datasets against the CKMR model for observed and expected numbers of kin pairs in different categories (MOPs, XmHSPs, and SPs), observed versus expected gaps between half-sibling pairs, and the log-likelihood derivatives at the true parameter values. See Section Ffor details.

2.4 Survey design

We were interested in evaluating the performance of CKMR under different demographic and sampling scenarios. The demographic scenarios were a stable population (D1), a slightly decreasing population (D2) and a slightly increasing population (D3). Demographic parameters for these simulated scenarios are shown in Table 1. For these simulations, we simulated historical sampling according to realized sample sizes by age and sex, and future sampling by target sample sizes by age class. We simulated scenarios with (L2) and without (L1) the collection of 100 lethal samples per year in sampling years.This is where we-all might wanna consider investigatin wotif a LOT more lethal ones; 100 is too small to help. We also simulated various reductions in sampling effort, either by reducing the number of sampling years or by reducing the amount of sampling effort within years (S1-S7; Table 2). With three demographic scenarios, two lethality scenarios, and seven sampling scenarios, this resulted in a total of 42 simulated datasets from which to evaluate survey design.

2.5 Design calculations

CKMR sampling designs can often be evaluated by calculation alone. These calculations are based on adapting standard methods used to find the statistical information from the (pseudo-)likelihood (i.e., its derivatives) and enumerating the pairwise comparisons that would be required based on covariate combinations (which are few, given we have a relatively small range of covariates; e.g., age, year of sample, etc).

Let w_{ijk} be the kinship outcome for samples i and j and target kinship k: $w_{ijk} = 1$ if their actual kinship $K_{ij} = k$, or 0 if $K_{ij} \neq k$; and let $w = \{w_{ijk}; \forall i, j, k\}$ (in practice, some "impossible" comparisons are excluded; e.g., second-order kin born a long time apart). Define $p_{ijk}(\boldsymbol{\theta}) = \mathbb{P}[K_{ij} = k | z_i, z_j, \boldsymbol{\theta}]$ to be the kinship probability for samples i and j, parameter values $\boldsymbol{\theta}$ and covariates z_i and z_j (computed from, e.g., (3)). In each case, the probability that $w_{ijk} = 1$ is on the order of the reciprocal of adult abundance (very small), and is well approximated by a Poisson distribution with mean $p_{ijk}(\boldsymbol{\theta})$. The pseudo-log-likelihood is:

$$\Lambda(\boldsymbol{\theta}; \mathbf{w}) = C + \sum_{i<j; k \in \mathcal{K}} \left\{ -p_{ijk}(\boldsymbol{\theta}) + w_{ijk} \log_e p_{ijk}(\boldsymbol{\theta}) \right\},$$

where C is a constant and $\mathcal{K}$ are the kinship relationships being considered.

We use $H(\boldsymbol{\theta}_0) = d^2 \Lambda(\boldsymbol{\theta}_0; \mathbf{W}) / d\boldsymbol{\theta}^2$ (the expected Hessian) over datasets $\mathbf{W}$ at true parameter values $\boldsymbol{\theta}_0$. As Λ is a sum of individual comparison terms, so is $H(\boldsymbol{\theta}_0) = \sum_{i<j; k \in \mathcal{K}} h_{ijk}(\boldsymbol{\theta}_0)$, where

$$h_{ijk}(\boldsymbol{\theta}_0) = 4 \boldsymbol{\Delta}_{ijk}(\boldsymbol{\theta}_0) \boldsymbol{\Delta}_{ijk}(\boldsymbol{\theta}_0)^\top \qquad \text{where } \boldsymbol{\Delta}_{ijk}(\boldsymbol{\theta}) = \frac{d\sqrt{p_{ijk}(\boldsymbol{\theta})}}{d\boldsymbol{\theta}}.$$

$\boldsymbol{\Delta}_{ijk}(\boldsymbol{\theta})$ can be obtained efficiently for all (i, j, k) by numerical differentiation of the probabilities calculated by the ICKMR model, using some reasonable guess about $\boldsymbol{\theta}_0$. using squared 1st derivatives is the Fisher information? Can we call this the pseudo-Fisher information? Oh, sorry, I always get confused by which one is the formal definition (2nd D, or 1st D ^2). The thing is that under "sparse sampling", the two will be the same here anyway... let's wing it ;)

We can now exploit the small range of possible covariates and group across all pairs with identical covariate values. Let $m(\mathbf{z})$ denote the number of samples with covariate combination $\mathbf{z}$; the number of comparisons between two samples is $m(\mathbf{z}_1)\, m(\mathbf{z}_2)$. The grouped version of the expected Hessian can be written as

$$H\left(m_{\mathcal{Z}};\boldsymbol{\theta}_0\right)=\sum_{\mathbf{z}_1<\mathbf{z}_2\in\mathcal{Z};k\in\mathcal{K}} m\left(\mathbf{z}_1\right)m\left(\mathbf{z}_2\right)h\left(\mathbf{z}_1,\mathbf{z}_2,k\right), \tag{7}$$

where $h\left(\mathbf{z}_1,\mathbf{z}_2,k\right)$ is the single-comparison expected Hessian for two samples with covariates $\mathbf{z}_1$ and $\mathbf{z}_2$ respectively[1]. The set $\mathcal{Z}$ comprises all possible combinations of covariates, and $m_{\mathcal{Z}}$ is the corresponding breakdown of total sample size by covariate combinations (e.g., year, age, sex). We can then invert (7) to give the average predicted variance $V\left(m_{\mathcal{Z}};\theta_0\right)$ of a parameter estimate. Uncertainty from any function of the parameters, $g\left(\boldsymbol{\theta}\right)$, can then be approximated by the delta method:

$$\mathbb{V}\left[g\left(\boldsymbol{\theta}\right);m_{\mathcal{Z}},\boldsymbol{\theta}_0\right]\approx\left[\left.\frac{dg\left(\boldsymbol{\theta}\right)}{d\boldsymbol{\theta}}\right|_{\boldsymbol{\theta}_0}\right]V\left(m_{\mathcal{Z}},\boldsymbol{\theta}_0\right)\left[\left.\frac{dg\left(\boldsymbol{\theta}\right)}{d\boldsymbol{\theta}}\right|_{\boldsymbol{\theta}_0}\right]^{\top}.$$

While a "design" must, by definition, include some specification of sample sizes, it may not specify the full breakdown of samples into specific $\mathbf{z}$-categories. For example, the plan might be to sample 1000 adult walruses per year, but the age composition cannot be controlled directly. However, we still need to know $m_{\mathcal{Z}}$, so some extra assumptions and calculations might be required. For example, our population-dynamics model does not explicitly represent the adult age composition within the population, let alone within the samples; probabilities like (4) are *conditioned* on sample age, but make no prediction about how many samples of each age there will be. It would be possible to calculate expected sample sizes based on quasi-stable age compositions and non-selective sampling assumptions (assumptions that are implicit for the self-recapture probability (6)), but somewhat laborious. Since we are simulating sampled datasets in any case, the simulated sample composition can be used directly for $m_{\mathcal{Z}}$.

The proposed walrus sample size (about 15,000 in total) is large relative to adult female abundance (~70,000; effectively more because of turnover during the years modelled), so ~10% of samples are self/kin-recaptures. This means that a comparable proportion of pairwise comparisons have predictable outcomes based on the results of other comparisons, breaking independence. The "sparse sampling" assumption of Bravington et al. (2016) is therefore not strictly justified, so the variance might be slightly over- or under-estimated relative to our calculations here; the direction is not obvious. I am changing my thinking about this; it's highly not obvious... (there is no effect on point estimates).

[1]The ordering "$z_1 < z_2$" is arbitrary, included just to avoid double-counting. Sometimes it makes sense to also do comparisons with $z_1 = z_2$, in which case an extra factor of $1/2$ is required.

Appendix E details some effective sample size adjustments to our calculations in order to account for the non-independence of the pairwise comparisons. [~3950 words excluding big notes].

3 Results

3.1 Demographic parameters

The simulated values of adult female survival and post-senescent adult female survival (Table 1) resulted in effective survival of 0.96, 0.95, 0.96 for stable, decreasing, and increasing populations respectively. The expected CVs on adult female survival were always lower when ICKMR was used than when IMR alone was applied (mean decrease in CV = 0.02). The mean expected CVs were 0.02 (range 0.01-0.04), 0.01 (range 0.01-0.02), and 0.03 (0.01-0.06) for stable, decreasing, and increasing populations respectively. Expected CVs were less than 0.2 for all scenarios where CKMR was applied, but as high as 0.06 when it was not.

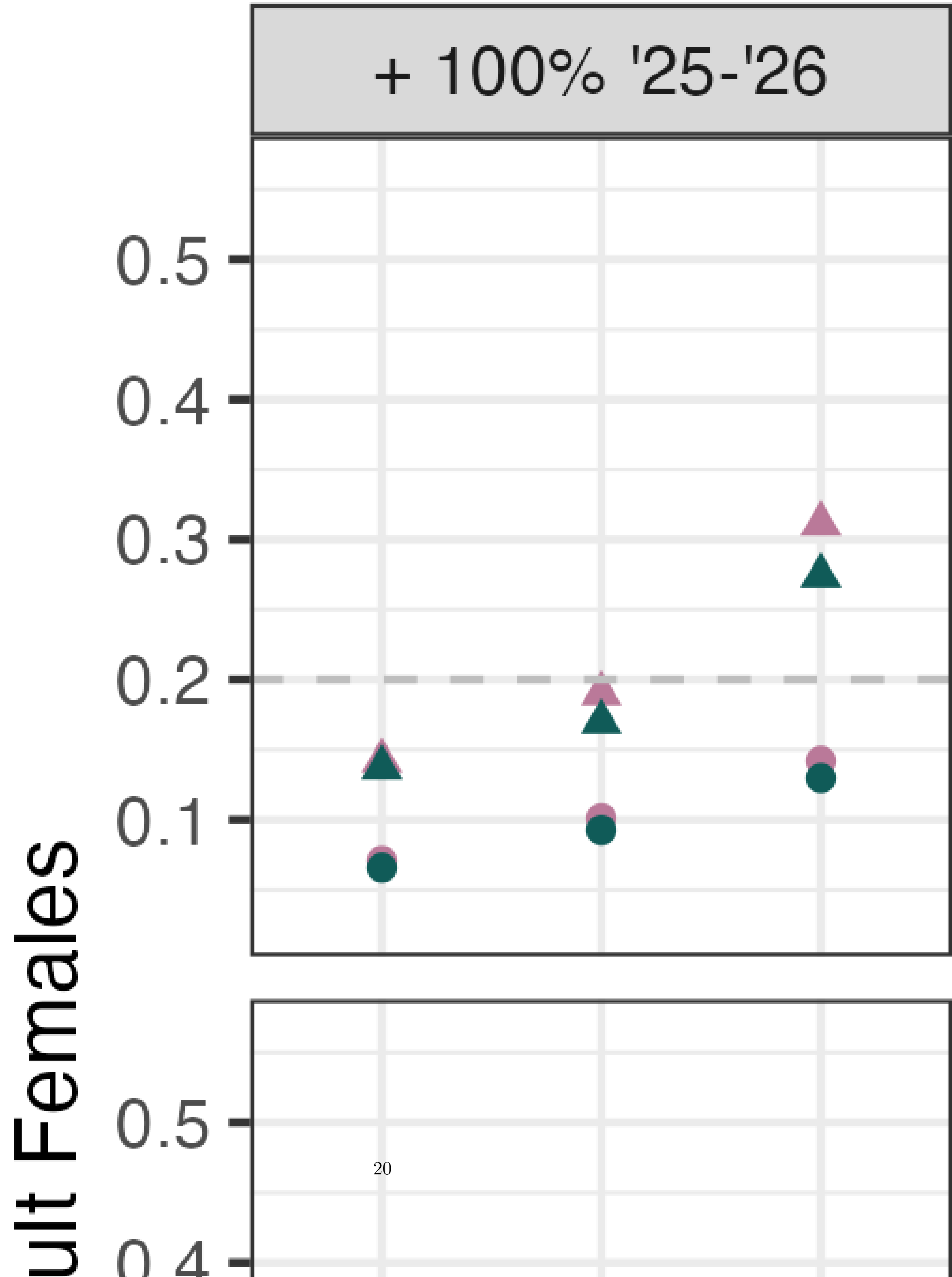
The simulated values of juvenile female survival were 0.9, 0.85, and 0.925 (Table 1). Again, the expected CVs on juvenile survival were always lower when ICKMR was used than when IMR alone was applied (mean decrease in CV = 0.02). The mean expected CVs on juvenile female survival were 0.06 (range 0.04-0.09), 0.03 (range 0.02-0.05), and 0.07 (range 0.05-0.07) for stable, decreasing, and increasing populations respectively.

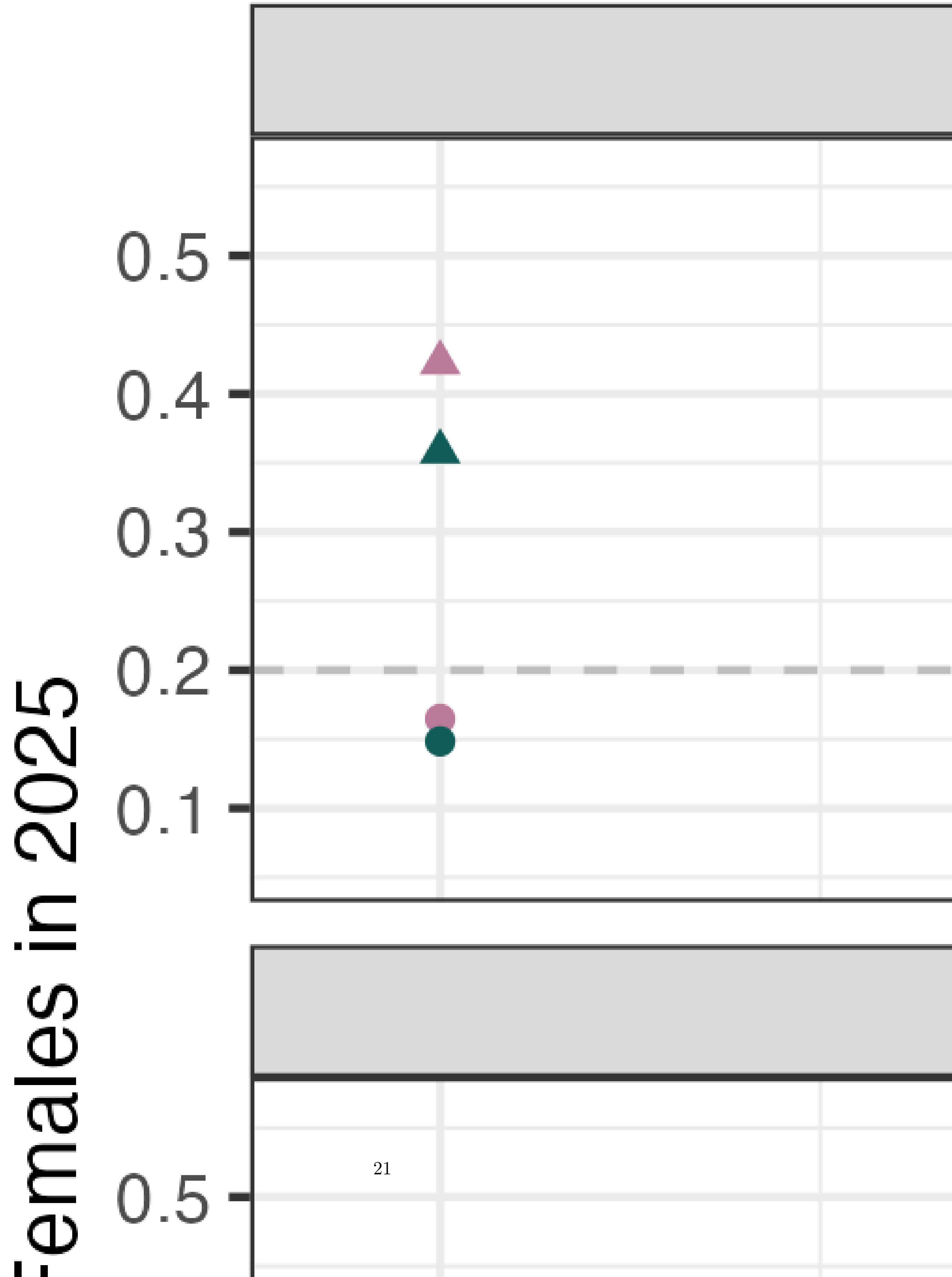
Across all demographic and sampling scenarios, the simulated proportion of adult females in breeding state 2 was 0.26. The expected CVs varied greatly depending on both demographic and sampling scenario, but were notably lower when ICKMR was used compared to IMR (mean decrease in CV = 0.82). The mean expected CVs on the proportion of adult females in breeding state 2 were 0.54, 0.31, and 0.66 for stable, decreasing, and increasing populations respectively.

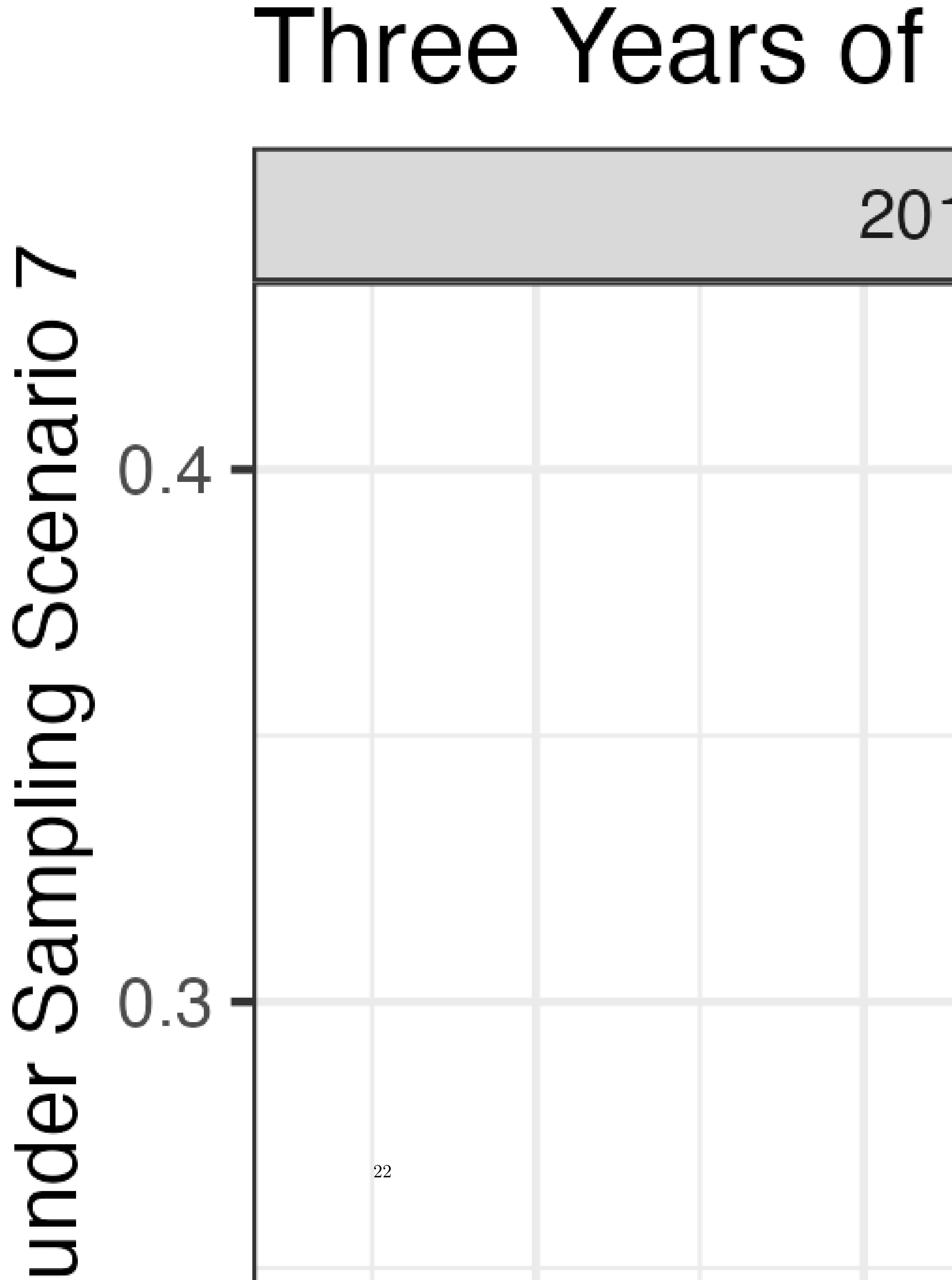
See Table 3 for expected CVs of life history parameters across all demographic and sampling scenarios with and without the use of lethal samples and ICKMR.

3.2 Adult female abundance

Across all demographic and sampling scenarios, the application of ICKMR resulted in lower expected precision in estimates of abundance compared to the application of IMR alone (Fig. 2). The mean gain in CV on adult female abundance in paired scenarios with and without ICKMR was 11% for a stable population, 5% for a decreasing population, and 15% for an increasing population. See Table 4


+ 100% '25-'26
0.5
0.4
0.3
0.2
0.1
0.5
Females


0.5
0.4
0.3
0.2
0.1
0.5
Females in 2025


Three Years of
201
under Sampling Scenario 7
0.4
0.3

for expected CVs of adult female abundance across all demographic and sampling scenarios with and without the use of ICKMR.

The demographic scenarios (see Table 1) affected expected precision of simulated survey designs in that a decreasing population resulted in a smaller population size in the years of desired inference (2015-2025) and therefore the number of kin pairs was higher (and expected precision was lower) given a set number of samples (Fig. 2, second row). Conversely, with an increasing population size, the number of kin pairs resulting from a set number of samples was lower, and therefore expected precision was higher (Fig. 2, third row). With an arbitrary target CV of 0.2 on estimates of adult female abundance in 2015, 2020, and 2025, all demographic and sampling scenarios resulted in sufficient precision when the population was decreasing, while scenarios including ICKMR would be required to achieve sufficient precision when the population was increasing.

Lethal samples provided greater gains in precision on abundance estimates when only IMR was used; the mean gain in precision was 2% when only IMR was used but 1% when ICKMR was applied. Note that when lethal samples were included, we simulated the collection of 100 lethal samples per year. We would expect the gain in precision for both IMR and ICKMR to increase with an increased number of lethal samples.

The simulated sampling scenarios resulted in between 2.5 and 5 years of survey effort, where 5 years of survey effort was the original plan for IMR (Fig. 3). When the population was simulated to be stable or decreasing, sufficient precision in abundance estimates could be achieved with as few as 2.5 years of survey effort when ICKMR was applied and lethal samples were used. However, in scenarios when the population was increasing, 4-5 years of survey effort would be required even with the application of ICKMR and use of lethal samples.

Some scenarios resulted in the same total number of years of sampling but in different configurations (i.e., some had more calendar years with less effort each year whereas others had fewer calendar years with more effort each year). Scenarios 1 and 7 both resulted in 3 years of survey effort, while sampling scenarios 2 and 6 both resulted in four years of sampling effort (Fig. 4). Scenario 1 included sampling effort in 2023, 2025, and 2026, while scenario 7 included sampling in 2023, 2024, and 2025 (see Table 2). The expected CVs on estimates of adult female abundance in 2025, 2020, and 2025 were comparable between these sampling scenarios (Fig. 4, top panel). Scenario 2 included sampling in 2023, 2025, 2026, and 2027, while scenario 6 included sampling in 2023 and a lower level of sampling (75% effort) in 2025, 2026, 2027, and 2028. Expected precision of abundance estimates was greater for scenario 6 than for scenario 2 in all years of desired inference, with the greatest gains in the 2025 estimate (Fig. 4, bottom panel). This suggests that more years of effort with fewer samples collected per year could improve overall precision in estimates of adult female abundance. [1204 words].

4 Discussion

- We show how sample collection plans could be modified to achieve desired monitoring goals with less sampling effort.
- We didn't bother doing X coz IJAD[2]. For real data analysis, we might do Y instead.
- Ways to extend the model... impact of DNAge
- Future utility of lethal samples (although my guess is: there won't be enough. Glass-half-full, or glass-half-empty, if you're a walrus?)
- The full ramifications of opting for a stage-structured quasi-equilibrium model, which avoids having to model age composition but does entail an *assumption* about selectivity, are not at all obvious, but the model seems to us fairly reasonable; it might be worth revisiting when large numbers of DNAge samples become available. At that point it would be possible to compare the actual age compositions with the predicted compositions assuming partly-unselective sampling and quasi-equilibrium.
- As should be evident from the preceding text and number of authors on this paper, building a close-kin model involves a high level of collaboration between statisticians, biologists and geneticists. CKMR is very much a multidisciplinary methodology and each discipline has a great deal to input into the process of model building.
- Would be great to mention that CKMR was motivated by fisheries and is an example of a shared tool between fisheries scientists and ecologists, maybe cite Schaub et al 2024
- on stage-structured dynamics: That assumption may turn out to be unreasonable for juveniles especially; but it will only be possible to check once enough sample-age-composition data become available. However, if it does turn out to be the case that (say) 2yo are disproportionately likely to be sampled (given their estimated abundance from the fitted model), then it would not be

[2] It's Just A Design

hard to adjust the stage-structured IMR equations to incorporate sample-composition-data and (estimated) selectivity. Sample sizes in this project are large enough that selectivity (i.e., the ratio of age-specific sample compositions to model-estimated population age compositions) should be estimated with respectable precision and without "propagating" a lot of uncertainty into other parameter estimates. We therefore think that our current somewhat crude IMR sub-model should give a reasonable guide to ultimate precision, even if it gets adjusted somewhat in the cold light of real data. Note that similar assumptions appear to be made in Beatty et al. 202 (to be confirmed).

- A purely-age-structured version of \eqref{eq:self-staged} would need to explicitly keep track of numbers-at-age, not just adult abundance (as would the other kin types). The quasi-equilibrium assumption might allow us to do this, but that assumption directly constrains relative abundances-at-age. In practice, a fully age-structured CKMR formulation for walrus will need something more sophisticated and time-varying than a quasi-equilibrium age distribution, and therefore additional parameters to estimate. We therefore opted for a stage- rather than age-structured SP model in the hope that the overall statistical information content about total abundance is reasonably realistic compared to what we might get from a more complicated population dynamics model.

- appendix (**??**) discusses skip-breeding

- While a stable-age-composition between 2000–2027 is probably not valid for the entire range of adult ages—since older adults would have experienced long periods of increased mortality from hunting—it is perhaps a reasonable assumption for younger adults, and it is only younger adults that matter here because they indirectly determine the number of juveniles. A stable age composition for juveniles seems fairly reasonable, since "recruitment variability" cannot be high for an animal with a litter size of 1, and it only requires a few years for the juvenile distribution to settle down.

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Appendices here...

A Derivation of self-recapture “the other way round”

As discussed in Section 2.1.6, (6) can also be formulated "the other way round", i.e., considering whether the second sample is the same as the first. The answer turns out the same, but the derivation is slightly different and *appears* to involve an explicit survival term. Again, suppose two female samples (y_1, a_1 and y_2, a_2 , where $y_1 < y_2$), then

$$\begin{gathered}\mathbb{P}\left[K_{21} = \mathrm{SP} | y_1, a_1, y_2, a_2\right] \\ = \frac{\mathbb{P}\left[\text{Sample 1 survived until Sample 2 was taken}\right] \mathbb{I}\left(y_2 - a_2 = y_1 - a_1\right)}{N\left(y_2, a_2\right)} \\ = \frac{\Phi\left(y_2 - y_1, a_1\right) \mathbb{I}\left(y_2 - a_2 = y_1 - a_1\right)}{N\left(y_2, a_2\right)}.\end{gathered}$$

However, the results are readily seen to be identical because, by definition of "survival", we have

$$N\left(y + t, a + t\right) \equiv N\left(y, a\right) \Phi\left(t, a\right). \tag{A.1}$$

B Self-recapture when exact age is known

we don't reference this subsection anywhere, do we need it?

Beatty et al. (2022) used a fairly complex IMR formulation to cope with historically-very-imprecise estimates of age (or, more realistically, of "stage") estimates. However, when accurate age data are available, the pairwise comparison probabilities for self-recapture are remarkably simple. Suppose two female samples (y_1, a_1 and y_2, a_2 , where $y_1 < y_2$). Then the probability that the first one is the same as the second is just

$$\mathbb{P}\left[K_{12} = \text{SP} | y_1, a_1, y_2, a_2\right] = \frac{\mathbb{I}\left(y_2 - a_2 = y_1 - a_1\right)}{N_{y_1,a_1}}. \tag{B.1}$$

The indicator $\mathbb{I}(\cdot)$ is 1 if the two samples were born in the same year, or 0 if not, The samples can only be from the same animal if they were both born in the same year and if they were, we then need to know how many females of age a_1 were alive at y_1, N_{y_1,a_1}. This implicitly assumes that all females of the same age have the same survival and sampling probabilities. (See appendix for the equivalent derivation of $\mathbb{P}\left[K_{21} = \text{SP} | y_1, a_1, y_2, a_2\right]$).

In principle, given unlimited data, we could separately apply (B.1) to each combination of (y, a)-consistent pairs, to empirically estimate from all numbers-at-age-and-year from the reciprocal of the observed rates. Then we could apply (A.1) to estimate year-and-age-specific survivals. In practice, that would be ridiculous, since it would require an enormous number of recaptures and would lead to noisy abundance estimates, estimated survivals greater than one, and so on. However, the principle does illustrate the great power of *known-age* mark-recapture data. Note also that there are no assumptions about equiprobable sampling across ages, etc; all probabilities are simply conditioned on observed ages, and it does not particularly matter *why* there are more samples of one age than another.

The big problem with applying (B.1) in an ICKMR setting, i.e., with conditioning on age explicitly, is that it requires explicit calculation of all N_{y_1,a_1} within the model. This is normally unnecessary with CKMR for mammal-like species, where the main information is *only* connected with aggregate adult abundance (via TRO). It is extremely convenient to work just with a "homogenous block" of adults, and there is in any case no direct information on population age composition unless extra data are used. One option is "just" to work with a fully-age-structured population dynamics framework— but that is a lot of work to develop (from experience in fisheries work) and requires modelling extra data.

C Derivation of juvenile abundance

The key point here is that we don't need to decompose the adult stage into separate age classes.

Following notation from the rest of the paper, let the number of adults in year y be $N_{\mathrm{A},t}$ where adulthood means being aged α or older. The number next year will be $\rho N_{\mathrm{A},y+1}$ where $\rho = e^r$ and r is the rate of increase as in (1). That will be made up of survivors from adults at t, plus survivors from the incoming cohort of oldest juveniles, aged $\alpha - 1$. Thus

$$N_{y+1,\mathrm{A}} = \rho N_{y,\mathrm{A}} = \phi_{\mathrm{A}} N_{y,\mathrm{A}} + \phi_{\mathrm{J}} N_{y,\alpha-1}. \tag{C.1}$$

Rearranging, we have

$$N_{y,\alpha-1} = \frac{\rho - \phi_{\mathrm{A}}}{\phi_{\mathrm{J}}} N_{y,\mathrm{A}}. \tag{C.2}$$

We now need to infer the numbers in the other juvenile age-classes (not just $\alpha - 1$). Starting with the penultimate juvenile age-class, we have:

$$\begin{aligned}
& N_{y,\alpha-1} = \phi_{\mathrm{J}} N_{y-1,\alpha-2} && \text{(survival)} \\
& N_{y,\alpha-1} = \rho N_{y-1,\alpha-1} && \text{(population growth)} \\
\implies & N_{y,\alpha-2} = \frac{\rho}{\phi_{\mathrm{J}}} N_{y,\alpha-1}.
\end{aligned}$$

Similar relationships apply to each preceding juvenile age class, down to age 1. The total number of juveniles in year y, $N_{y,\mathrm{J}}$, is given by a sum from age $x = \alpha - 1$ down to age 1:

$$\begin{aligned}
N_{y,\mathrm{J}} = \sum_{x=1}^{\alpha-1} N_{y,\alpha-x} &= \sum_{x=1}^{\alpha-1} N_{y,\alpha-1} \left(\frac{\rho}{\phi_{\mathrm{J}}}\right)^{x-1} \\
&= N_{y,\alpha-1} \sum_{x'=0}^{\alpha-2} \left(\frac{\rho}{\phi_{\mathrm{J}}}\right)^{x'} \\
&= N_{y,\alpha-1} \frac{1 - (\rho/\phi_{\mathrm{J}})^{\alpha-1}}{1 - \rho/\phi_{\mathrm{J}}},
\end{aligned} \tag{C.3}$$

using the standard result for a geometric series: $\sum_{i=1}^{n} ar^i = a\frac{1-r^n}{1-r}$. Substituting for $N_{t,\alpha-1}$ from

(C.2), we have

$$
\begin{aligned}
N_{y,\mathrm{J}} &= N_{y,\mathrm{A}} \frac{\rho - \phi_{\mathrm{A}}}{\phi_{\mathrm{J}}} \frac{1 - \left(\frac{\rho}{\phi_{\mathrm{J}}}\right)^{\alpha-1}}{1 - \frac{\rho}{\phi_{\mathrm{J}}}} \\
&= N_{y,\mathrm{A}} \frac{\rho - \phi_{\mathrm{A}}}{\rho - \phi_{\mathrm{J}}} \left(\left(\frac{\rho}{\phi_{\mathrm{J}}} \right)^{\alpha-1} - 1 \right).
\end{aligned}
$$

Now, for the case of walrus, we know that $\alpha = 6$, so:

$$
N_{y,\mathrm{J}} = N_{y,\mathrm{A}} \frac{\rho - \phi_{\mathrm{A}}}{\rho - \phi_{\mathrm{J}}} \left(\left(\frac{\rho}{\phi_{\mathrm{J}}} \right)^{5} - 1 \right).
$$

D Further HSP complications

The second issue with all second-order kin, is that pairwise-kinship statistics are not currently powerful enough to completely distinguish them all from a few "lucky" third-order kin such as Great-Gandparent-Grandchild. To handle this without bias, the best approach is set a threshold for the statistic that should almost completely exclude false-positives from third-order kin, then to estimate empirically the proportion of true second-order kin that will be lost below the threshold (i.e., the false-negative rate) based on the observed distribution of kin-pair statistics. Only kin-pairs that are above the threshold will be treated as HSPs, but the probability formula can be multiplied by the complement of the false-negative probability to compensate. See Bravington et al. (2016) or Hillary et al. (2018) for more details. The false-negative rate depends both on the species and the genotyping method (in particular, the number of loci) and cannot be predicted in advance, but experience suggests that 15% is usually a safe upper limit.

Determining that a pair is HSP does not differentiate between mHSPs (maternal; shared mother) and pHSPs (paternal; shared father). This can be determined by genotyping the mitochondrial DNA (mtDNA; always inherited from the mother only) of known HSPs. If the genotypes are different, the descent must be paternal; if the same, descent is probably maternal, but could arise by chance in a few paternal-HSP cases. However, in our experience, except for very small populations (hundreds of adults), mtDNA diversity has always been high enough that shared-mtDNA HSPs might as well be treated as definite mHSPs. We assume as much here.

E Adjustments for non-sparse sampling

Use of the pseudo-log-likelihood Hessian to approximate the inverse variance is not strictly justified in a mathematical sense, because the pairwise comparisons are not fully mutually independent. The "sparse sampling" assumption of Bravington et al. (2016), which underlies the use of the Hessian, is therefore not strictly justified; this does not lead to bias in point estimates, but the Hessian-based approximation is likely to underestimate the true variance somewhat. Accordingly, we have made some simple adjustments to "effective sample size" based on summaries of the simulated datasets. This should be quite adequate for design purposes— since, in any case, all our variance estimates have to be based on uncertain assumptions about true parameter values— but a more detailed treatment may be worthwhile when it comes to analysing the real data.

A general and comprehensive treatment of non-independence in CKMR is beyond the scope of this paper. We restrict attention to some obvious aspects for walrus that are easy to address. We consider the comparisons in stages: SPs, then MOPs, then XmHSPs. We adjust set the effective sample size for each stage based on recaptures from the preceding stages in one simulated dataset, as follows:

- Sample sizes are initially taken from the simulated dataset (thus allowing detailed breakdown of sample size by age, year, etc). All available samples are used for SP comparisons.
- If an individual is self-recaptured, only its final capture will be used in MOP and XmHSP comparisons (i.e. duly adjusting the sample sizes sample sizes for MOPs and XmHSPs, as well as the number of MOPs etc found if that individual is involved).
- Any Offspring o identified in a MOP, will be excluded from XmHSP comparisons (since o's sibship with any other sample i can be deduced from the MOP results, based on whether i is also an offspring of o's Mother).

This deals with the implications of one type of kinship for the others, but does not deal with multiple recaptures within a kinship class (e.g. an individual who is sampled 3 times; given that sample A matches sample B, and B matches C, it is redundant to compare A with C). There are simple ways to handle that with real datasets, as long as age is known fairly accurately.

F Model checking

model checking

I have an open mind about how much of this should go in the main MS (first para only?), how much in an Apx, and how much not at all— but it'd be kind-of a shame to miss this chance to showcase a practical benefit of CKMR simulations, especially since I have frequently maintained that simulations are *not* necessary in CKMR (true, but as we see here they can still be very *useful*). The other Q is how much to mix in the results of the checks (once everything worked...) with the description of them; it doesn't make sense to me to have this as a Methods section, then a huge gap with a tonne of other results, then return to this with a small set of results pertaining to an aspect of methods that all readers will by that point have forgotten. So again an Apx could be the place for much of it.

Close-kin pairwise probability formulae are usually quite simple, at least with hindsight, but they still can be awkard to get right in the first place. One way to reduce the risk of mistakes is to generate simulated datasets, and check that the CKMR code is giving the expected results when known parameter values are inserted. CKMR simulation code looks utterly different from kinship-probability code, and the chance of "making the same mistake twice" is therefore much less than with many statistical simulations. Robustness is improved even further if two different people are involved, one to simulate and one to write kinship-probability code. Even though simulation is not strictly necessary for most CKMR design exercises, simulation may be worth the additional effort in order to help the whole process, and that is the approach we took for walrus. We did find and fix several mistakes this way, both in the CKMR code and in the simulation code, so the exercise was certainly worthwhile.

The obvious question is how to approach CKMR model-checking when simulated datasets are available. There are various options and no . One thing to avoid, if possible, is the naive and laborious approach of actually *fitting* a CKMR to each simulated dataset, which can be painfully slow. (Note, perhaps for discussion: We started this project before RTMB became available, expecting that the actual model-fitting code for real data would eventually have to be written in TMB itself, but keen to avoid the complexity of TMB at the design stage. In contrast, design calculations are quick because it is only necessary to calculate probability arrays once, and R alone is adequately fast, without TMB or RTMB. However, it would not be practical to fit even our simple model to multiple datasets without RTMB; and even with RTMB, repeated fitting of a more complicted model, e.g. with copious random effects, might be a challenge.) We used several checks. All are aimed at detecting gross errors (and we did find some); power to detect subtle mistakes is lower, but in our experience subtle mistakes are actually less likely than big ones. The first two checks are based on single realizations of simulated data, and so are also suitable as diagnostics when fitting to real data; the last two require multiple simulated datasets.

- Observed and expected totals of sampled kin-pairs of each type. Clearly, unless these match reasonably well, there must be a major inconsistency between model and simulationg. The definition of "reasonably well" can be guided by the inherent Poisson variability. If an expected total is 227, say, then we would not expect to see observed total much outside, say, the 95% confidence limits for a Poisson distribution with mean (and therefore variance) 227. This can be roughly approximated by $227 \pm 2\sqrt{227}$ or about [195,255]. Clearly, the expected total needs to be fairly large for this to have much power, so it might be useful to increase the simulated sample size for checking purposes.
  OPTIONlist the totals here (for first test dataset, chosen so that sim matches CK code as closely as possible)

- Breakdown of observed and expected kin-pair totals across some covariate of interest. If the totals from the previous step are not matching well, then the breakdown may shed light on where to look for problems. For example: the distribution of birth-gaps between XmHSPs is driven in the longer term by the adult rate mortality rate, so if observed and expected do not correspond, then the treatment of mortality is likely inconsistent. Also, the number of mothers by age-at-birth should fluctuate over the first few years of adulthood because of the typically-three-year breeding cycle (most 6yo have just given birth; most 7yo are still nursing last year's offspring, etc), until it settles down because of the averaging effects of irregularities. If the observed and expected patterns do not match, then the breeding cycle treatment is inconsistent.
  OPTION show the 2 graphs here.

- P-values of observed kin-totals by type, based on the Poisson distribution as above. Given a reasonable number of simulated datasets (say 20 or more), these should be roughly uniform across the interval [0,1]. Clearly, it would require a large number of simulations to get a precise check here, but precision is not necessary: the goal is to pick up fairly coarse errors.
  OPTION show 4 histos here (instead of box'n'whiska)

- Looking at the mean and variance of the derivative of the pseudo-log-likelihood at the true parameter values θ_0 (something which can be calculated fairly quickly by numerical differentiation). The mean should be close to 0 and the variance determines what "close" might mean, given the number of simulations available. This checks the crucial "unbiased estimating equation" (UEE) assumption required by most statistical estimation frameworks, including maximum-likelihood. If UEE does not hold, then by definition there is a mismatch between simulation and model. **OPTION** there's some numbers printeed at the end of compare2sims.R, I thnk.

The description so far implicitly assumes that the CKMR model (if working right) corresponds exactly to the data-generation mechanism in the simulations. However, it might be desirable to make the CKMR model simpler, especially for design purposes where the goal is just to make sure that sampling plans are sensible; developing a more complicated and realistic model can often be left until the real data appears. For example, we wanted to avoid reproductive senescence in the CKMR equations, so that all adults could be treated as a single block without requiring age-structured dynamics inside the model. Nevertheless, senescence is likely a reality of the walrus world, and there is such a thing as "too simple to be useful", so it is worth checking whether the simpler formulation is going to run into serious trouble. Simulated datasets can be used to estimate approximate bias in a slightly-mis-specified CKMR model, again without needing to do any estimation. The idea is to approximate the MLE for each dataset, based only on calculations using the true parameter value for the simulations. The MLE $\hat{\theta}$ will by definition satisfy the equation $d\Lambda/d\theta|_{\hat{\theta}} = 0$, and we can take a first-order Taylor expansion around the true value θ_0 to give

$$
\begin{aligned}
0 = \left.\frac{d\Lambda}{d\theta}\right|_{\hat{\theta}} &\approx \left.\frac{d\Lambda}{d\theta}\right|_{\theta_0} + \left(\hat{\theta} - \theta_0\right) \left.\frac{d^2\Lambda}{d\theta^2}\right|_{\theta_0} \\
\implies \hat{\theta} - \theta_0 &\approx - \left[\left.\frac{d\Lambda^2}{d\theta^2}\right|_{\theta_0} \right]^{-1} \left.\frac{d\Lambda}{d\theta}\right|_{\theta_0}
\end{aligned}
\tag{F.1}
$$

The square-bracketed term can be replaced (to the same order of accuracy as the rest of the approxmation) by the *expected* Hessian which is the crux of our design calculations anyway, and which of course does not vary from one simulation to the next. Thus, the only quantity that has to be calculated per simulated dataset is $d\Lambda/d\theta|_{\theta_0}$, already required for the unbiased-estimating-equation check above. The estimated bias is the average across simulations of (F.1). This is quite similar to the UEE check above, but with a change in focus: this time, we may be prepared to tolerate some small violation of UEE, provided that it does not imply substantial bias on the parameter scale. In particular, if the estimated bias for the r^{th} parameter (i.e. r^{th} component of θ) is below its sampling variability—say, if bias is less than 1 standard deviation, computed from the square-root of the diagonal of the inverse Hessian or $\sqrt{H^{-1}(r,r)}$— then there is little reason to worry about bias for that particular parameter.

OPTION stuff from the end of compare2sims.R

DISCUSSION?

In the end, based on the checks above, our estimation and simulation codes did indeed appear consistent, and any bias induced by (among other minor things) ignoring senescence did not seem problematic. Of course, we only reached that position *after* going thru the checking process several times, to find and fix inconsistencies.

G Additional results

Would these not be better as graphs and the tabular versions as, say, csv files?

Table 3: Expected CVs on adult female survival, juvenile female survival, and the proportion of adult females in breeding state 2 under different demographic and sampling scenarios with and without the use of lethal samples and CKMR.

Demographic Scenario	Lethal Samples	Sampling Scenario	CKMR	Adult Female Survival	Juvenile Female Survival	P. Adult Female in State 2
1	No	1	Yes	0.01	0.05	0.1
1	No	2	Yes	0.01	0.04	0.09
1	No	3	Yes	0.01	0.04	0.09
1	No	4	Yes	0.02	0.05	0.11
1	No	5	Yes	0.01	0.05	0.1
1	No	6	Yes	0.01	0.05	0.1
1	No	7	Yes	0.01	0.05	0.1
1	Yes	1	Yes	0.01	0.04	0.1
1	Yes	2	Yes	0.01	0.04	0.09
1	Yes	3	Yes	0.01	0.04	0.09
1	Yes	4	Yes	0.01	0.05	0.1
1	Yes	5	Yes	0.01	0.04	0.1
1	Yes	6	Yes	0.01	0.04	0.1
1	Yes	7	Yes	0.01	0.05	0.09
2	No	1	Yes	0.01	0.03	0.06
2	No	2	Yes	0.01	0.02	0.05
2	No	3	Yes	0.01	0.02	0.05
2	No	4	Yes	0.01	0.03	0.07
2	No	5	Yes	0.01	0.03	0.06
2	No	6	Yes	0.01	0.03	0.06
2	No	7	Yes	0.01	0.03	0.06
2	Yes	1	Yes	0.01	0.03	0.06
2	Yes	2	Yes	0.01	0.02	0.05
2	Yes	3	Yes	0.01	0.02	0.05
2	Yes	4	Yes	0.01	0.03	0.06
2	Yes	5	Yes	0.01	0.03	0.06
2	Yes	6	Yes	0.01	0.03	0.06
2	Yes	7	Yes	0.01	0.03	0.06
3	No	1	Yes	0.02	0.06	0.13
3	No	2	Yes	0.02	0.05	0.11
3	No	3	Yes	0.02	0.05	0.11
3	No	4	Yes	0.02	0.07	0.14
3	No	5	Yes	0.02	0.06	0.13
3	No	6	Yes	0.02	0.06	0.13
3	No	7	Yes	0.02	0.06	0.12
3	Yes	1	Yes	0.02	0.06	0.12
3	Yes	2	Yes	0.01	0.05	0.11
3	Yes	3	Yes	0.01	0.05	0.11
3	Yes	4	Yes	0.02	0.06	0.13
3	Yes	5	Yes	0.02	0.06	0.12
3	Yes	6	Yes	0.02	0.06	0.12
3	Yes	7	Yes	0.02	0.06	0.12
1	No	1	No	0.03	0.07	1.01
1	No	2	No	0.03	0.06	0.92
1	No	3	No	0.03	0.06	0.92
1	No	4	No	0.04	0.08	1.1
1	No	5	No	0.04	0.08	1.04
1	No	6	No	0.04	0.08	1.04
1	No	7	No	0.03	0.07	1
1	Yes	1	No	0.03	0.06	0.94
1	Yes	2	No	0.02	0.06	0.86
1	Yes	3	No	0.02	0.06	0.86

Table 4: Expected CV on adult female population size in 2015, 2020, and 2025 with different demographic and sampling scenarios and with and without the use of lethal samples and CKMR.

Demographic Scenario	Lethal Samples	Sampling Scenario	CKMR	2015 Adult Females	2020 Adult Females	2025 Adult Females
1	No	1	Yes	0.07	0.1	0.14
1	No	2	Yes	0.06	0.08	0.12
1	No	3	Yes	0.06	0.08	0.12
1	No	4	Yes	0.08	0.12	0.16
1	No	5	Yes	0.07	0.1	0.14
1	No	6	Yes	0.07	0.1	0.14
1	No	7	Yes	0.07	0.1	0.14
1	Yes	1	Yes	0.07	0.09	0.13
1	Yes	2	Yes	0.06	0.08	0.11
1	Yes	3	Yes	0.06	0.08	0.11
1	Yes	4	Yes	0.07	0.11	0.15
1	Yes	5	Yes	0.07	0.09	0.13
1	Yes	6	Yes	0.07	0.09	0.13
1	Yes	7	Yes	0.07	0.09	0.13
2	No	1	Yes	0.04	0.05	0.08
2	No	2	Yes	0.03	0.04	0.06
2	No	3	Yes	0.03	0.04	0.06
2	No	4	Yes	0.04	0.06	0.09
2	No	5	Yes	0.04	0.05	0.08
2	No	6	Yes	0.04	0.05	0.08
2	No	7	Yes	0.04	0.05	0.08
2	Yes	1	Yes	0.03	0.05	0.07
2	Yes	2	Yes	0.03	0.04	0.06
2	Yes	3	Yes	0.03	0.04	0.06
2	Yes	4	Yes	0.04	0.05	0.08
2	Yes	5	Yes	0.03	0.05	0.07
2	Yes	6	Yes	0.03	0.05	0.07
2	Yes	7	Yes	0.03	0.05	0.07
3	No	1	Yes	0.09	0.13	0.18
3	No	2	Yes	0.08	0.11	0.15
3	No	3	Yes	0.08	0.11	0.15
3	No	4	Yes	0.1	0.15	0.21
3	No	5	Yes	0.09	0.13	0.18
3	No	6	Yes	0.09	0.13	0.18
3	No	7	Yes	0.09	0.13	0.18
3	Yes	1	Yes	0.08	0.12	0.17
3	Yes	2	Yes	0.08	0.1	0.14
3	Yes	3	Yes	0.08	0.1	0.14
3	Yes	4	Yes	0.09	0.14	0.19
3	Yes	5	Yes	0.09	0.12	0.17
3	Yes	6	Yes	0.09	0.12	0.17
3	Yes	7	Yes	0.08	0.12	0.17
1	No	1	No	0.14	0.19	0.31
1	No	2	No	0.14	0.15	0.23
1	No	3	No	0.14	0.15	0.23
1	No	4	No	0.15	0.25	0.42
1	No	5	No	0.15	0.21	0.34
1	No	6	No	0.15	0.21	0.34
1	No	7	No	0.14	0.19	0.31
1	Yes	1	No	0.14	0.17	0.27
1	Yes	2	No	0.13	0.14	0.21
1	Yes	3	No	0.13	0.14	0.21
1	Yes	4	No	0.14	0.21	0.36