Accounting for population growth, intermittent breeding, and aging error in close-kin mark-recapture assessments

John D. Swenson[1], Elizabeth N. Brooks[2], Dovi Kacev[3], Charlotte Boyd[4], Michael Kinney[5], Benjamin Marcy-Quay[6], Anthony Sévêque[7], Kevin Feldheim[8], Lisa M. Komoroske[1]

[1] Department of Environmental Conservation, The University of Massachusetts, Amherst, Massachusetts, USA

[2] Population Dynamics Branch, Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, Massachusetts, USA

[3] Marine Biology Research Division, Scripps Institute of Oceanography, San Diego, California, USA

[4] IUCN – Americas Office, 1630 Connecticut Ave NW, Washington DC ,USA

[5] Life History Program, Pacific Island Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii, USA

[6] Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, Vermont, USA

[7] Department of Wildlife, Fisheries and Aquaculture, Forest and Wildlife Research Center, Mississippi State University, Mississippi State, Mississippi, USA

[8] Pritzker Laboratory for Molecular Systematics and Evolution, The Field Museum, Chicago, Illinois, USA

Abstract: Obtaining robust estimates of population abundance is a central challenge hindering the conservation and management of many threatened and exploited species. Close-kin mark-recapture (CKMR) is a genetics-based approach that has strong potential to improve monitoring of data-limited species by enabling estimates of abundance, survival, and other parameters for populations that have been challenging to assess. However, CKMR models have received limited sensitivity testing under realistic population dynamics and sampling scenarios, impeding application of the method in population monitoring programs and stock assessments. Here, we use individual-based simulation to examine how unmodeled population dynamics and sampling strategy affect the accuracy and precision of CKMR parameter estimates, and present adapted models that correct the biases that arise from model misspecification. Our results demonstrate that a relatively simple CKMR model produces robust estimates of population abundance when key assumptions including annual breeding and stable population size are met; however, if strong population declines or non-annual breeding dynamics are present, a more complex CKMR model must be constructed to avoid biased parameter estimates. In addition, we show that CKMR can generate reliable abundance estimates for adults from a variety of sampling strategies, including juvenile-focused sampling where adults are never directly observed. Finally, we apply our adapted CKMR model to two decades of genetic data from juvenile lemon sharks (*Negaprion brevirostris*) in Bimini, Bahamas to demonstrate how juvenile-focused CKMR can be used to expand monitoring efforts for highly mobile populations. Overall, this study expands our understanding of the biological factors and sampling decisions that cause bias in CKMR models, and provides recommendations for sampling design and model construction that can aid biologists in planning and implementing an effective CKMR experiment, particularly for long-lived data-limited species.

Introduction

Population abundance plays important roles in both fundamental and applied biological research, and is associated with a wide range of ecological and evolutionary processes, including predator-prey dynamics (Carbone et al. 2011), competition (Robertson 1996), demographic rates (Herrando-Pérez et al. 2012), density-dependent population dynamics (Hassell 1975, Berryman 1989), and genetic drift (Ellegren and Galtier 2016). Abundance estimates and trends are also key metrics for conservation and management, and are commonly used to assess conservation status (Wilson et al. 2011), quantify the impacts of threats and/or recovery efforts (Jennings 2000, Ward-Paige et al. 2012, Magera et al. 2013), and scale regulated harvest quantities (e.g. allowable biological catch, annual catch limits) for managed populations of target and non-target species. Consequently, a wide range of methods have been developed for estimating population abundance (Schwarz and Seber 1999, Wilson and Delahay 2001, McCauley et al. 2012). Capture-mark-recapture (CMR) is one prominent and widely used method in which abundance is estimated by constructing capture histories for each sampled (or tagged) individual, estimating capture probabilities, and comparing the number of recaptured individuals to the total number of sampled individuals (Cormack 1964, Jolly 1965, Seber 1965). A number of variations of CMR methods have been developed over the years to account for varied population demographics and sampling schemes (Pollock 2000, Amstrup et al. 2010), but the approach remains largely intractable in situations where recapture rates are very low, as with many low density and highly mobile marine species (Kohler and Turner 2001, Webster et al. 2002, Boyd et al. 2018). Further, CMR can only directly inform about the sampled demographic, while many highly mobile marine species have spatially segregated life histories during which they are available for sampling as juveniles in nearshore habitats before transitioning to a less accessible pelagic habitat as adults. In such cases, CMR results are restricted to providing direct information about the juvenile portion of the population, while the population dynamics of adults can only be modeled effectively if additional data are available and if key assumptions are met (Kendall 1999, Pollock 2000). As alternatives to CMR, surveys or transect-based methods can be helpful tools to estimate regional abundance of species that are consistently available for observation. However, variability in survey length, uncertainty surrounding the proportion of habitat sampled, changes in behavior arising from the presence of human observers, and observation error are common pitfalls that can make such methods unreliable or incomparable across studies (McCauley et al. 2012, Davis et al. 2022).

While CMR, surveys, and transect-based methods can all be useful tools in certain contexts, applying them in an unbiased way can be prohibitively challenging in many systems. As such, when estimates of absolute abundance are infeasible, indices of relative abundance are commonly used to assess populations of exploited species (Campbell 2015). In fisheries, for example, abundance trends derived from catch and effort data (e.g., catch-per-unit-effort, CPUE), in concert with biological reference points, can inform management by providing critical information about whether a population is overfished or if overfishing is actively occurring (Cortés and Brooks 2018). However, it is extremely challenging to account for all the factors that could influence catchability (Maunder et al. 2006); hence, indices of relative abundance derived from CPUE are rarely linearly proportional to actual abundance (Harley et al. 2001, Maunder and Punt 2004, Lynch et al. 2012), which can result in fundamentally flawed conclusions if CPUE data are interpreted in isolation, or if linearity between catch rate and abundance is implicitly assumed (Maunder et al. 2006). Further, producing trends of relative abundance for highly mobile species frequently requires the integration of multiple independent surveys that suggest differing abundance trends, making it difficult to establish true abundance patterns (Peterson et al. 2021). All of these issues are amplified in taxa such as elasmobranchs (sharks, skates, and rays), which are often subject to high levels of illegal, unreported, and unregulated catch (Cortés and Brooks 2018). While CPUE can provide invaluable information regarding stock status and harvest pressure when analyzed in the right context (e.g., via an integrated model with substantial metadata), there is an urgent need for methods that can provide robust estimates of absolute population abundance and trends when catch data are unreliable or scarce.

Close-kin mark-recapture (CKMR) is a genetics-based approach for estimating absolute population abundance that overcomes many of the logistical challenges inherent to CMR and other conventional methods of abundance estimation, and it has the potential to greatly improve monitoring efforts for species that have been difficult to assess (Skaug 2001, Bravington et al. 2016b). In contrast to conventional CMR, the tags in CKMR are genotypes, and animals are considered "re-captured" when their kin are identified (Bravington et al. 2016b). This removes the need for individual recapture and allows for the estimation of adult abundance using samples collected solely from juveniles, as well as samples obtained lethally through fishing or hunting (Bravington et al. 2016b, Hillary et al. 2018). While CKMR can theoretically leverage any relationship, the most common applications so far have focused on parent-offspring pairs (POPs) (Bravington et al. 2016a, Ruzzante et al. 2019, Marcy-Quay et al. 2020) and/or half-sibling pairs (HSPs) (e.g., Hillary et al. 2018). In cases where sampling is limited to juveniles, CKMR can provide added value to conventional CMR by generating parameter estimates for the adult population while CMR estimates parameters for the sampled (in this case juvenile) portion of the population. Depending on the form of the model, CKMR can estimate additional quantities including survival (Hillary et al. 2018), fecundity (Bravington et al. 2016b), dispersal (Feutry et al. 2017, Conn et al. 2020, Patterson et al. 2022b), and population growth rate, if sufficient complementary data are available. These advantages and possibilities make CKMR an exciting tool to improve monitoring efforts and population assessments for data-limited species of management and conservation concern.

Despite CKMR's strong potential to provide key information for conservation and management, its implementation has been slowed due to a lack of clarity regarding the flexibility and limitations of the method. Several studies have discussed factors that are likely to cause bias if left unaccounted for in CKMR models (Bravington et al. 2016b, Conn et al. 2020, Waples and Feutry 2021, Trenkel et al. 2022), but there have been few quantitative assessments of the bias that arises from applying an overly simplistic CKMR model to a population with complex dynamics (but see Conn et al. 2020, Waples and Feutry 2021). For example, one key assumption of a simple base-case CKMR model (e.g., Equations 3.3 and 3.10 in Bravington et. al. 2016b) is stable population growth. However, real populations may exhibit significant interannual fluctuations in population size. If such changes are persistent, or if high levels of mortality are introduced (e.g., via environmental disaster or heavy fishing pressure), then it may be necessary to specify a more complex CKMR model that can accommodate a changing population. A second assumption of a simple base-case CKMR model is annual breeding, yet many long-lived species exhibit intermittent breeding whereby one or more years elapse between reproductive events (Shaw and Levin 2013). Systematic intermittent breeding dynamics are expected to cause bias in CKMR parameter estimates if unaccounted for in the model (Waples and Feutry 2021), but quantitative data regarding the degree of bias are scarce, as are concrete examples for how to mitigate the bias. Finally, a core component of CKMR is the use of age data, which is required to assign individuals to the correct cohort (Bravington et al. 2016b). Direct aging is very challenging for some taxa (Cailliet 2015), and length-based age assignment is prone to bias when growth curves are based on size-selective sampling, as they often are (Gwinn et al. 2010). While more advanced statistical methods can account for uncertainty in aging during the modeling process (Schwarz and Runge 2009), it may also be possible to alleviate bias by targeting sampling to age classes that can be reliably aged, such as young-of-the-year (YOY) which are often easily distinguished from other age classes by their small size and/or the presence of umbilical scars (Feldheim et al. 2002). A better understanding regarding the circumstances in which a simple base-case CKMR model is liable to produce biased parameter estimates, in combination with strategies to mitigate that bias, will help ensure robust application of the method and facilitate its integration into conservation and management frameworks.

Elasmobranchs (sharks, skates, and rays) are a group of highly vulnerable marine species that play key ecological roles as apex- and meso-predators in ecosystems around the world (Vaudo and Heithaus 2011, Ferretti et al. 2018), and are likely to benefit from future application of CKMR. Around one-third of the 1200+ elasmobranch species are threatened with extinction, due primarily to overfishing (Dulvy et al. 2021), while nearly half of elasmobranch species (46%) are classified by the IUCN as Data Deficient and only a small fraction of exploited populations are managed sustainably (Kindsvater et al. 2018). Conventional methods for estimating abundance and mortality are intractable for many elasmobranch populations because individual recapture rates for highly mobile elasmobranch species can be very low (Kohler and Turner 2001), and it can be logistically challenging to physically capture and mark larger species (Guttridge et al. 2017). In contrast to conventional methods, CKMR requires only small tissue samples that can be obtained from adults via biopsy or from juveniles that are easier to handle than their adult counterparts - without need for individual recapture - making this a more tractable approach for many elasmobranch populations. CKMR has added potential for elasmobranchs because the life histories of many species allow for the use of juvenile-only CKMR models (e.g., half-sibling (HS) CKMR) that can estimate adult abundance without sampling a single adult (Bravington et al. 2016b), and many migratory elasmobranchs utilize nursery areas where juveniles are readily available for sampling (Heupel et al. 2007). Accordingly, CKMR has been applied to several elasmobranch populations to date (Bradford et al. 2018, Hillary et al. 2018, Bravington et al. 2019, Delaval et al. 2022, Trenkel et al. 2022, Patterson et al. 2022b) and is likely to be an important tool to inform elasmobranch conservation and management in the future. However, elasmobranchs are susceptible to steep population declines (Ferretti et al. 2018), commonly exhibit multiennial breeding cycles (Nosal et al. 2021), and are exceptionally challenging to age (Cailliet 2015), and we do not know how much bias can accrue when such factors are unaccounted for in CKMR models. As such, there is a risk that biased parameter estimates from CKMR will unwittingly be incorporated into management frameworks for elasmobranchs, leading to incorrect management actions that ultimately threaten their populations.

To facilitate the robust application of CKMR to elasmobranchs and other taxa facing similar challenges with abundance estimation, we investigated the sensitivity of CKMR to unmodeled dynamics related to population growth and breeding schedule, as well as uncertainty in age assignment. We used stochastic individual-based simulation to generate distinct populations of lemon sharks (*Negaprion brevirostris*) under different population dynamics scenarios and sampled each population using sampling schemes that targeted different age classes. Two different CKMR models were fit to each dataset: one that was naïve to at least one component of the data-generating model (naïve model) and one that was adapted to account for all relevant population dynamics (adapted model). We compared the bias in parameter estimates from both models (naïve vs adapted) and across all sampling schemes, including one in which age data were unreliable. Finally, we applied a model that was adapted for population growth and multiennial breeding to two decades of real genetic data from lemon sharks in Bimini, Bahamas to generate a time-series of abundance estimates for the breeding population of females. Collectively, these results provide important insights into the ways in which unmodeled population dynamics, sampling selectivity, and aging error affect CKMR model performance, while also offering guidance regarding sampling design and model construction.

2. Methods

Our simulation framework comprised four primary components: 1) an individual-based population simulation that stochastically generated distinct populations with known parameters, 2) selective sampling of age classes from those populations, 3) construction of a pairwise comparison matrix from the samples, and 4) a CKMR model that was fit to the pairwise comparison matrix to estimate the known population parameters. The first two components comprised our data-generating model (DGM) while the latter two formed our estimation model (Figure 1).

We then tested the interplay of population dynamics and model complexity by iteratively varying a subset of population parameters (Table 1) and fitting two CKMR models to the data: one that was naïve to the added dynamics, and one that was adapted to account for them. Each scenario was repeated 500 times, with each iteration producing a population with a distinct pedigree and parameter estimates.

2.1 Data generating model

Parameters governing our individual-based population simulations were designed to replicate the life history traits of lemon sharks, beginning with an adult population size of 1000 in year 1 (Appendix S1: Table S1). We allowed females to breed with up to three males each breeding cycle, which is typical for this species (Feldheim et al. 2004), and set no limit on the number of females a male could breed with. Survival was assumed constant within each of three life stages, which we designated as young-of-year (age 0), juvenile (age 1-11) and adult (age 12-50). We assigned knife-edged maturity, so every individual age 12 and over was available for breeding, while no individuals younger than age 12 were allowed to breed. After maturity, fecundity was age-invariant, with the mean offspring produced per female per breeding event varying with the breeding cycle to keep population growth approximately stable except for simulations where we explicitly tested population change (Table 1: Scenarios 2.1-2.3).

2.1.1 Population growth

We varied population growth in our DGM in two ways depending on our desired magnitude of change in population growth rate. First, to examine whether CKMR parameter estimates were affected by population trends, we reduced or increased annual female fecundity by 0.5 for the last 50 years of the 90-year simulation (Scenarios 2.1 and 2.2), which resulted in a population that declined or grew by an average of 1% per year over this time period. To achieve more substantial declines in population size (~7%; Scenario 2.3), we stochastically imposed 5-10% additional mortality into the simulation for juvenile and adult age classes over the last 10 years of the simulation.

2.1.2 Intermittent breeding

Many elasmobranchs systematically breed on multiennial cycles (Feldheim et al. 2002, 2017, Nosal et al. 2021), which violates the assumption of annual breeding in a simple base-case CKMR model. To examine the bias that accrues when this trait is unaccounted for in a CKMR model, we ran simulations where 50%, 75%, 90% or 100% of females bred on a two-year cycle, and the rest bred on an annual cycle, analogous to the mixed mating periodicity observed in the finetooth shark (*Carcharhinus isodon*) in the Northern Gulf of Mexico (Higgs et al. 2020). Each female in our simulation was assigned an annual or biennial breeding cycle at birth; the biennial breeders were then randomly assigned to breed on odd or even years once they reached maturity. This resulted in a population where half of the biennially breeding females reproduced for the first time in the year they matured (age 12) and the other half reproduced for the first time the following year (age 13). Mature males were assumed available to breed every year once they reached maturity. Because some elasmobranchs breed on tri-ennial cycles, we also ran a simulation where 100% of females bred on a three year cycle, while males, again, were assumed available to breed each year. Finally, we added a degree of stochasticity and examined a scenario where females generally bred on a biennial schedule, but 10% of off-cycle breeders gave birth each year while 10% of on-cycle breeders failed to breed each year.

2.2 Sampling

All simulated populations were sampled using three different schemes that selected for different age classes: the first drew samples exclusively from young-of-year (age 0) individuals; the second made juveniles of all ages except young-of-year (ages 1-11) available to sample; and the third allowed sampling of all age classes (ages 0-50). These scenarios were chosen to replicate potential sampling scenarios for elasmobranchs such as in nursery areas (Feldheim et al.

2002, Heupel et al. 2007), juvenile aggregation sites (Rowat et al. 2007, Jacoby et al. 2012), and resident populations (Snelson and Williams 1981), respectively.

In each case, the population was initially sampled at four different intensities representing 0.5%, 1%, 1.5%, and 2% of the population. Samples were drawn annually for four years at the end of the population simulation (i.e. years 87 – 90), following reproduction but before mortality each year. Sampling 1.5% of the population resulted in an average of 615 total samples and 100-200 half-sibling pairs (HSPs), which is expected to produce a reasonable CV for all sampling schemes (Bravington et al. 2016b). Therefore, following model validation, we focused on sampling 1.5% of the population for the remainder of our simulations.

2.2.1 Aging uncertainty

A crucial component of CKMR is accurate aging, yet some taxa, including elasmobranchs, are notoriously difficult to age, with most efforts relying on length-at-age growth curves to assign age to sampled individuals (Cailliet 2015). To examine how imprecision in growth curves affects CKMR parameter estimates, we first constructed an age-length key for lemon sharks using data from a long-term study of the population in Bimini, Bahamas (Feldheim et al., 2014), and calculated the standard deviation of lengths for individuals with known ages, the majority of which (>95%) spanned ages 0-3. We then simulated lengths for each sampled individual (which were assigned ages in our DGM) using a Von Bertalanffy growth curve for the species (Brown and Gruber 1988). Each individual was assigned a length by drawing a value from a normal distribution with the mean length-at-age specified by the Von Bertalanffy curve, and the standard deviation derived empirically from our age-length key for individuals aged 0-2, and arbitrarily from a CV of 5%, 10%, or 20% for individuals aged 3+. After assigning lengths to each individual, we used a reverse Von Bertalanffy growth curve with the same values for t_0 (-

2.302), L_{inf} (317.65), and K (0.057) to re-assign ages to sampled individuals based on their lengths, rounding to the nearest integer, thus giving plausible, yet sometimes incorrect, ages (similar to age-slicing; see Ailloud et al. 2015, e.g.). These re-assigned ages were then used to construct the pairwise comparison matrix that was input to the CKMR model.

2.3 Pairwise comparison matrix

CKMR produces estimates of abundance and other population parameters by defining kinship probabilities for every pair of sampled individuals given relevant covariates (e.g., age, sex). We constructed two standard pairwise comparison matrices for each set of samples. The first matrix contained positive and negative kinship assignments for half-siblings. To satisfy the assumption of independent sampling, whenever full siblings or self-recaptures were present, all but one individual/instance was removed prior to construction of the matrix. Once the matrix was created, same-cohort comparisons were removed, as these can complicate analyses considerably (Bravington et al. 2016b, Førland 2019). Kinship assignment in our simulations was known without error, so each comparison was assigned as a positive if the two individuals being compared were a half-sibling pair, and negative if not.

The second matrix was composed of parent-offspring (PO) comparisons. Our simulations included sampling over four years only, so the PO matrix was only relevant to the scenario that included sampling of adults. For each birth year represented in the data (a.k.a. reference year), individuals that were alive in that year were split into potential offspring or parents based on whether they were born in that year (potential offspring), reproductively mature at the time (potential parent), or neither, in which case they were left out of the matrix corresponding to that year. A separate pairwise comparison matrix was constructed for each reference year that compared all potential parents to all potential offspring in that year, and each comparison was assigned as a positive or negative.

Once the appropriate half-sibling and parent-offspring comparisons were defined for each reference year, all matrices were collated and grouped by 1) type of relationship (half-sibling or parent-offspring), 2) reference year (a.k.a. birth year of younger individual for half-sibling comparisons, or birth year of the offspring for parent-offspring comparisons), 3) reference year gap (difference between the reference year and the estimation year when specifying a population growth model; see Section 2.4.2 below), and 4) mortality year gap (difference between the birth years of the individuals being compared; see Eq. 1), as applicable. Each row was treated as a binomially distributed random variable in the CKMR model, with the probability of success defined by Equations 1-4 below, and *n* equal to the total number of comparisons in each group (see Appendix S1: S1.1 and Table S2 for more details).

2.4 Estimation models

Kinship probabilities for each pairwise comparison in CKMR are derived from the expected reproductive output of individual animals (defined by covariates such as age and sex) relative to the total reproductive output of the population in the specified reference year (Bravington et al. 2016b). The specific equations we used to define kinship probabilities in our CKMR models varied with the scenarios we tested, with each scenario comparing a “naïve” model to an “adapted” model, where the naïve model ignored one key dynamic of the simulated population and the adapted model accounted for it. All of our equations are based on the general equations defined in Bravington et. al. (2016b).

2.4.1 Base-case CKMR model

Let $Y\{K_{i,j} = MHSP\}$ be the probability that individuals *i* and *j* are a maternal half-sibling pair (i.e. they share a mother but not a father). Probabilities for *Y* depend on the likelihood that the same individual that birthed the older offspring (*i*) survived and gave birth to the younger offspring (*j*). If we assume that all animals of reproductive age in the population during *i* and *j*'s birth years are equally likely to have birthed each of them, and if we only include as potential parents the animals that were of reproductive age during the birth years of *i* and *j*, then the probability of kinship (*K*) can be defined as

$$Y\left\{K_{i,j} = MHSP\right\} \sim Binomial\left(\frac{\phi^{\delta}}{N_{♀(yj)}},\ R_{(y_i,y_j)}\right) \quad (1),$$

where,

ϕ is the annual survival probability for adults,

y_{j} is the birth year of individual *j* (the younger sibling),

δ is the number of years between the birth years of individuals *i* and *j* (i.e. $y_j - y_i$) during which any potential parent of *i* may have died a.k.a. the "mortality year gap",

$R_{(y_i,y_j)}$ reflects the total number of pairwise comparisons between individuals born in years y_i and y_j, and

$N_{♀(yj)}$ is the total number of mature females in year y_j.

Notably, *K* can be generalized to refer to either half-sibling (HS) or parent-offspring (PO) relationships by re-interpreting the parameter δ, which for HS relationships refers to the difference between cohort birth years, but for PO kinship refers to the difference between the birth year of the offspring and the capture year of the adult. In the latter scenario, if the parent was captured in or after the offspring's birth year, whether sampling was lethal or non-lethal, then we know that the parent was alive in the year the offspring was born. Thus, any value for δ which is <= 0 (which would reflect a parent that is captured in or after the year the offspring was born) is assigned a value of 0 and ϕ^{δ} reduces to 1. Thus,

$$Y\{K_{i,j} = MHSP\ or\ MPOP\} \sim Binomial\begin{pmatrix} \frac{1}{N_{♀(yj)}}\phi^{\delta}, R_{(y_i,y_j)} & \delta > 0 \\ \frac{1}{N_{♀(yj)}}, R_{(y_i,y_j)} & \delta \leq 0 \end{pmatrix} \quad (2).$$

Equation 2 defines our simple base-case CKMR model. Though the model focuses on maternal kinship, the same probabilities also apply to males. POPs were only included in the likelihood for the sampling scheme in which adults were sampled with all other age classes; otherwise, the likelihood included HS probabilities only.

2.4.2 Population growth model

To account for population growth/decline in our CKMR model, we chose a simple exponential growth model to describe the population dynamics and added the parameter λ to our model. As such, our adapted model that accounts for population growth is:

$$Y\{K_{i,j} = MHSP\ or\ MPOP\} \sim Binomial\begin{pmatrix} \frac{1}{N_{♀(yj)}\lambda^{(yj-\gamma)}}\phi^{\delta}, R_{(y_i,y_j)} & \delta > 0 \\ \frac{1}{N_{♀(yj)}\lambda^{(yj-\gamma)}}, R_{(y_i,y_j)} & \delta \leq 0 \end{pmatrix} \quad (3),$$

where λ defines the annual population growth rate, γ represents the estimation year (a.k.a. the year to which the abundance estimate is targeted), and *(yj-γ)* is the reference year gap (see Appendix S1: S1.2). To assess the degree to which the choice of estimation year affects model performance, our simulations included an evaluation of model performance for three different estimation years (γ): 10 years in the past, 5 years in the past, and the present year (i.e. the last year of the simulation), while all other dimensions were held constant.

2.4.3 Intermittent breeding model

If a population – or subset of a population – systematically breeds on a non-annual schedule, then CKMR estimates will be biased unless this behavior is accounted for in the model (Waples and Feutry 2021). We accounted for intermittent breeding dynamics in our CKMR model via the inclusion of parameters *a* and Ψ , where *a* refers to the number of years between breeding (e.g., 2 for biennial breeders), and Ψ is the proportion of individuals that breed every *a* years (similar to Patterson et al. 2022a). This implies that (*1* - Ψ) individuals breed annually. Of the non-annual breeders, we assume that *1/a* breed in a given year. Thus, the effective number of female breeders in a given year is given by $(1-\ \psi)N_{♀}+\frac{\psi}{a}N_{♀}$, and the probability of maternal half-sibling kinship is

$$Y\{K_{i,j}=MHSP\}\sim Binomial\left(\frac{a\phi^{\delta}}{(a+\psi-a\psi)N_{♀(yj)}\lambda^{(j-\gamma)}},R_{i,j}\right) \qquad (4).$$

As part of Objective 3 of our simulations, we fixed the parameter *a* to 2 to reflect biennial breeding, and explored the ability of our model to estimate Ψ. If 100% of females breed on a biennial cycle (i.e. *a* = 2 and Ψ = 1), then the probability of finding half-siblings that are separated by an odd number of birth years is 0. It is the presence of δ intervals that are not divisible by *a* that provide information on the parameter Ψ (see Appendix S1: S1.3).

In our simulations we assumed that intermittent breeding dynamics were only present for females, and that all males in the population were available for breeding each year; as such, Equation 4 only applied to maternal comparisons, while Equation 3 was still used for the males. Finally, because the parent is directly sampled in PO CKMR, there is no need to explicitly account for breeding periodicity in the likelihood; therefore, we continued to use Equation 3 for maternal PO comparisons when applicable.

2.4.4 Estimation framework

We adopted a Bayesian approach to CKMR parameter estimation, which allows for the incorporation of auxiliary data and/or expert knowledge as priors on model parameters (Kéry and Schaub, 2012b). For model validation, survival (Φ) was given an informed beta prior which was derived by solving for α and β using the equations: $\mu = \frac{\alpha}{\alpha + \beta}$ and $\sigma^2 = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}$, where μ was set to the mean adult survival in the DGM (0.825) and σ^2 was calculated from a CV of 5%. For the rest of the scenarios, survival and other parameters were assigned diffuse priors to reflect data-limited situations (Table 2).

The posterior distributions for parameter estimates were approximated using Markov Chain Monte Carlo (MCMC) sampling, implemented using the software JAGS (Plummer, 2003) and applied in the *R* environment (Denwood, 2016; *R* Core Team, 2021). We ran two Markov chains with a thinning rate of 20, drawing 40,000 samples from the posterior distribution following a burn-in of 50,000 samples. These settings were empirically derived by assessing autocorrelation among successive draws and convergence among the chains. We assessed convergence of the final Markov chains with trace plots and the Gelman-Rubin statistic (Gelman and Rubin, 1992), and removed from further analysis any iteration with an Rhat value > 1.01, although these instances were rare.

2.5 Application to Lemon sharks

A long-term genetic dataset from lemon sharks in Bimini, Bahamas was used to illustrate application of our multiennial CKMR model (Eq. 4) to a dataset derived entirely from juvenile tissue samples (Feldheim et al. 2014). Lemon sharks are large viviparous (live-bearing) elasmobranchs that reach sexual maturity at approximately 12 years of age (Brown and Gruber 1988) with a lifespan exceeding 30 years (Brooks et al. 2016). Female lemon sharks at Bimini are regionally philopatric and return to Bimini to pup on a biennial schedule, while the males with which they mate likely reproduce over a much larger area (Feldheim et al. 2002). Juveniles use the shallow waters surrounding Bimini as a nursery and remain in the area until 2-3 years of age or until they reach 90 cm in length (Morrissey and Gruber 1993) and generally do not move between the North and South Islands (Gruber et al 2001). The Bimini nursery contributes to a larger Western Atlantic population that is classified as Vulnerable by the IUCN (Hansell et al. 2018, 2021, Carlson et al. 2021). The Bimini nursery has been intensively studied since 1995, with an estimated 99% of newborn sharks sampled at the Bimini North Island each year (Dibattista et. al. 2007) and maternal kinship assigned for the majority of sampled individuals (Feldheim et al. 2002, 2004, 2014).

For CKMR abundance estimation, we focused on samples collected from the North Island, which represents a small isolated nursery for lemon sharks aged 0-3 years old (Chapman et al. 2009), collected from 1993-2015. Most individuals in our dataset were sampled as YOY and easily identified by the presence of umbilical scars, so their ages were known. Maternal kinship was assigned with high confidence, but paternal kinship was not, so we focused our efforts on maternal comparisons only. We estimated abundance as a derived quantity in our CKMR model by dividing $N_{♀(yj)}$ by a, which we fixed to 2 for this population that primarily breeds biennially. Thus, our scope of inference for parameter estimation encompassed the adult females that visited the North Island nursery to give birth during each year of estimation, a number which is likely very small (White et al. 2014). We excluded from analysis sampled individuals without a known birth year as well as same-cohort comparisons (Bravington et al. 2016b), and any individuals for which maternal kinship assignment was uncertain. Since 92% of individuals were sampled as YOY, our likelihood utilized HSPs only (Eq. 4).

To replicate the type of outcome that could be produced by integrating CKMR into long-term monitoring efforts, we subset the dataset to generate a separate abundance estimate for each year from 1997 – 2015. Though our dataset includes samples from as far back as 1993, intensive sampling of the population began in 1995 (Dibattista et al. 2007) and lemon sharks breed biennially; therefore, we used 1997 as our first estimation year (i.e. one full breeding cycle after exhaustive sampling began). To generate an abundance estimate for 1997, we included samples collected from 1993-1997 only, and specified 1997 as our estimation year in the model. For 1998, we added samples collected from 1998 to those collected from the years prior, specified 1998 as the estimation year, and fit another CKMR model, repeating this process through 2015. We used our simulation results from the targeted sampling of YOY with no aging error to guide our expectations for the first few years of application when relatively few cohorts were included, but we expected our results to better align with the sampling scheme that included all juveniles (again with no aging error) as we increased the number of cohorts included in the dataset.

Recognizing that the Bimini lemon shark dataset is unique in how thoroughly the population was sampled, we also examined whether the model performed similarly with sparser datasets. First, we applied the same iterative process as with the full dataset and generated a time-series of abundance estimates, but this time the number of samples collected each year was randomly cut to 30% of the full dataset. Finally, we generated a third time-series of abundance estimates wherein we subsampled the full dataset for five-year intervals to examine whether we recovered similar estimates and trends with datasets that span smaller time series.

3. Results

3.1 Model validation

When the assumptions of the model were met, a simple base-case CKMR model (Eq. 2) generally produced unbiased estimates of abundance under all sampling schemes and intensities (Figure 2a), with increasing precision as sampling intensity increased (Figure 2b). The model produced unbiased estimates of abundance whether the likelihood included HSPs only (as in the sample all juveniles and target YOY scenarios) or jointly considered HSPs and POPs (as in the sample all ages scenario), though we note improved precision for the latter. At very low sampling intensities (0.5% of the target population sampled), fewer than 25 HSPs were identified for all sampling schemes (Figure 2c) and fewer than 5 parent-offspring pairs (POPs) were identified for the sampling scheme that included all ages (Figure 2d). In contrast, when 2% of the population was sampled, over 200 HSPs were identified on average for all sampling schemes, while 10-40 POPs were identified for the scenario in which all age classes were sampled. These results demonstrate that a simple base-case CKMR model can produce unbiased abundance estimates across a range of potential sampling scenarios when population dynamics align with the model's assumptions.

3.2 Population growth

3.2.1 Naïve vs adapted model

When the simulated population had a trend of consistent growth or decline (+/- 1% per year), our simple base-case CKMR model that was naïve to annual population fluctuations performed almost identically to an adapted model with a narrow prior on λ (Eq. 3; Figure 3a-c). However, when we added mortality to the last ten years of the DGM to simulate a period of severe population decline, we observed considerable differences in performance depending on whether the naïve or adapted model was used, and whether the prior on λ was wide enough to encompass the true value (Figure 3d). These results indicate that a naive CKMR model is robust to minimal increasing or decreasing population trends, but must be adapted if the data span a period of substantial population change.

Using the adapted model (Eq. 3), we also tested the impact of prior specification on λ. When the simulated population exhibited a trend that was stable, slightly increasing, or slightly declining (+/-1% per year), abundance estimates were mostly unbiased whether λ was given a narrow (yellow) or diffuse (blue) prior, as long as a range of age classes were sampled (Figure 3a-c, left two columns). When the population experienced a 10-year period of severe decline, a diffuse prior that encompassed the realized range of λ values (mean population $\lambda = 0.93$) was necessary to produce unbiased estimates on average (Figure 3d, left two columns). If sampling included YOY only, then giving a diffuse prior to λ resulted in poor model performance even when the population was stable, while the naïve model and the adapted model with the narrow prior on λ performed similarly to one another, giving reasonable abundance estimates when population change was minimal but producing biased abundance estiamtes when population decline was severe (Figure 3a-d, right column). Taken together, these results suggest that specification of a prior for λ can improve model performance considerably, especially under scenarios of severe population decline or when limited age classes are sampled.

3.2.2 Estimation of λ and survival

Estimates of λ exhibited slight bias that varied with the estimation year. The bias was generally small as long as sampling included multiple age classes, with targeted sampling of YOY producing less consistent results (Appendix S1: Figure S1). Estimates of survival were accurate regardless of estimation year; however, there were differences in bias correlated with sampling scheme, with targeted sampling of YOY again performing worse than when a greater array of cohorts were represented in the data (Appendix S1: Figure S1).

For cases where λ was given a diffuse prior, we tallied how often the model correctly identified a positive or negative population trend, regardless of the amount of bias surrounding the estimate of λ. When population change was slight in either the positive or negative direction, the model was able to correctly identify the trend (positive or negative) 57% - 66% of the time, depending on sampling scheme and estimation year (Appendix S1: Figure S2a,). When population decline was severe, the model was able to accurately determine the direction of population change in nearly all cases regardless of sampling scheme (Appendix S1: Figure S2b), though we noted a slight decline in this capacity as the estimation year was projected closer to the present.

3.2.3 Impact of estimation year

All combinations of sampling scheme and CKMR model performed progressively worse as the year of estimation was projected farther into the past, a trend that was reflected in estimates of abundance (Figure 3) and λ (Appendix S1: Figure S1, left), but not survival (Appendix S1: Figure S1, right). These results suggest that when population size cannot be assumed constant, the choice of estimation year can have a strong effect on CKMR parameter estimates.

3.3 Intermittent breeding

3.3.1 Naïve vs adapted model

When a CKMR model that is naïve to intermittent breeding (Eq. 3) was applied to data from a population with females that bred biennially, the resulting parameter estimates were substantially more biased than those generated by a model that was adapted to account for intermittent breeding (Eq. 4). In particular, estimates of abundance (Figure 4a) and survival (Appendix S1: Figure S3a) were strongly influenced by the choice of model, while estimates of λ were less affected (Appendix S1: Figure S3b). These results confirm the importance of accounting for multiennial breeding dynamics in a CKMR model.

3.3.2 Variations in breeding schedule

When we included a proportion of biennial breeders that stochastically bred off-cycle (Table 1; Scenario 3.6), or when the population comprised a mix of annual and biennial breeders (i.e. Ψ <1), estimates of abundance from the multiennial model remained unbiased for both females and males, though we note a slight tendency for the model to underestimate female abundance when there is a high percentage of annual breeders (Figure 4a, Table 3). For the scenarios that sampled across a broad range of cohorts, survival estimates from the multiennial model were unbiased on average regardless of the proportion of annual breeders included in the simulation (Appendix S1: Figure S3a). As the ratio of biennial to annual breeders was shifted towards annual breeders (i.e. as Ψ was made smaller in the DGM), the performance gap between the naïve (annual) and adapted (multiennial) model diminished for all parameters and sampling schemes.

Estimates of Ψ were unbiased when the population comprised a high proportion of intermittent breeders that reliably bred on-cycle, but became more biased as the relative proportion of annual breeders in the population increased, or when some proportion of biennial breeders stochastically bred off-cycle (Appendix S1: Figure S3c). When we simulated a population of females that bred on a triennial cycle and fit both an annual and multiennial model, results were similar to the case where all females bred on a biennial cycle, though the performance gap between the annual and multiennial model was greater with a population that breeds triennially (Appendix S1: Figure S4).

3.4 Aging uncertainty

The frequency with which samples were assigned to the incorrect cohort varied by age, with older individuals being more likely to be assigned to the wrong cohort (Appendix S1: Figure S5). The probability of age misassignment roughly corresponded to the slope of the von Bertalanffy growth curve, with the probability of age misassignment being greatest as the curve approached its asymptote (Appendix S1: Figure S5a). Consequently, the effects of aging error were minimal in the scenario in which sampling was targeted to YOY, as these individuals were far more likely to be assigned to the correct cohort (Appendix S1: Figure S5b).

When multiple age classes were represented in the data, bias accrued in estimates of female abundance and survival as the CV surrounding age assignment widened regardless of whether we simulated a population that bred annually or biennially (Figure 4b). Estimates of λ had a tendency towards downward bias (Appendix S1: Figure S6a) while estimates of male abundance showed the same pattern as females (Appendix S1: Figure S6b). Targeted sampling of YOY showed a different trend, where increasing the CV on age assignment did not affect the bias of parameter estimates (Figure 4b) because the probability of misassigning an age-0 individual to the wrong cohort was very low (Appendix S1: Figure S5, right column). These results confirm that reliable aging is a key component of CKMR and suggest that targeted sampling of age classes that can be reliably aged can improve model performance when accurate aging for some age classes is challenging.

3.5 Application to lemon shark data

When we applied our multiennial CKMR model (Eq. 4) to different subsets of data from lemon sharks in Bimini, Bahamas, the abundance trend showed a rise and fall in abundance from 1997 – 2015, with peak abundance occurring between 2006 – 2010 depending on which subset of data was used (Figure 5a). The overall parabolic trend was the same whether we used the full dataset, the downsampled dataset, or five year intervals of data. Absolute estimates of abundance for breeding females were very low in all three cases (max = 41, Table 4), suggesting that a small number of mature females visit the North Island in Bimini to breed each year.

Estimates of adult survival generally agreed with the proposed range of possible values from other studies (see White et. al. 2014 for an overview), although the year-to-year consistency of survival estimates varied with the number of years sampled and richness of the dataset (Figure 5b). When we used the full or downsampled dataset, estimates of survival converged as more years of data were included in the analysis, while the five-year interval dataset showed more variable estimates, consistent with our simulations that utilized fewer cohorts. All three datasets generally showed very high survival rates for mature female lemon sharks (>0.85).

4. Discussion

Obtaining unbiased estimates of abundance is a central challenge for effective conservation and management of many threatened and exploited populations, and is especially pertinent for populations of low density and highly mobile species where sampling of adults is largely intractable. Our simulation results broadly concur with recent work supporting CKMR as a promising approach to estimate abundance and survival in data-limited circumstances, but emphasize the critical need to adapt CKMR models adequately to accommodate population dynamics and life history traits that violate the assumptions of a simple base-case model. Additionally, although we also confirm sensitivity of CKMR to aging error, our finding that bias in parameter estimates can be mitigated by focused sampling of as few as four cohorts that can be reliably aged provides options for applying the method in species where accurate aging is difficult. Finally, our application to lemon sharks in Bimini, Bahamas demonstrates that CKMR is a flexible framework that can be used to estimate abundance and survival of breeding adults when only juveniles are available for sampling. Taken together, our simulation results and application to lemon sharks demonstrate that CKMR is a robust tool for estimation of adult abundance and survival even when adults are not directly observed, making this framework a potentially powerful tool in monitoring programs for populations of low density and highly mobile species, including in data-limited circumstances.

4.1 Accounting for population growth/decline

A simple base-case CKMR model (e.g., Eqs. 1 and 2) assumes that population abundance is stable over time, such that the quantities estimated by CKMR could equally apply to every reference year in the pairwise comparison matrix. If the assumption of a stable population size is inappropriate, or if estimates of underlying population parameters are desired, population dynamics can be modeled with CKMR using latent variables. By specifying a population growth model, data can be shared among cohorts to produce a single estimate of abundance for a specified estimation year, whereas without a growth model, estimates would be wholly independent for each cohort. Other studies have referred to the designation of an estimation year as “arbitrary” (Bradford et al. 2018). While this may be true in cases where sampling is extensive and perfectly represents the age class distribution of the population, our simulation results suggest that parameter estimates become more biased as the year of estimation is projected outside the bounds of reference years in the dataset. Importantly, the reference years do not necessarily relate to the years of sampling, but rather to the cohorts (i.e. birth years) represented in the dataset (see Appendix S1, Table S2). If sampling includes a high proportion of older age classes, then the best estimation year for the dataset may extend farther into the past than the first year of sampling. Regardless, when specifying a population growth model in conjunction with CKMR, the specified estimation year should be calibrated to the distribution of reference years in the dataset, and not necessarily the years of sampling.

In our simulations, we chose to specify an exponential growth model where inter-annual population dynamics were broadly captured in the parameter λ. While inclusion of this parameter generally improved CKMR parameter estimation in scenarios of consistent population growth or decline, giving too much flexibility to the prior on λ impeded estimation of other parameters, particularly when few cohorts were represented in the data. In practical applications of CKMR, knowledge of a species' life history in combination with Leslie matrix simulations can help set realistic bounds on λ (e.g. Hillary et al. 2018); alternatively, ancillary data sources (e.g. CPUE) could be integrated into the model via specification of the prior on λ.

4.2 Intermittent breeding dynamics

Intermittent breeding is a commonly observed reproductive strategy in long-lived species where reproduction bears additional “accessory” costs in terms of time, energy and/or survival (Shaw and Levin 2013), such as when reproduction includes migration to reproductive grounds and/or live-birth (Bull and Shine 1979). This strategy can be observed across a range of taxa such as reptiles (Bauwens and Claus 2019), mammals (Desprez et al. 2018), birds (Cubaynes et al. 2011, Öst et al. 2018), teleosts (Morbey and Shuter 2013, Skjæraasen et al. 2020), and elasmobranchs (Feldheim et al. 2002, Nosal et al. 2021), including species of conservation concern like leatherback sea turtles (*Dermochelys coriacea*; Rivalan et al. 2005) and smalltooth sawfish (*Pristis pectinata*; Feldheim et al. 2017). When intermittent breeding coincides with a population that is most easily sampled during the juvenile life stage (e.g., when adults are not directly observed), our results indicate that abundance estimates derived from a CKMR model that relies on samples of juveniles and assumes annual breeding will be positively biased. However, the multiennial CKMR model presented here accommodates intermittent breeding via inclusion of the parameters Ψ and a (see Appendix S1, S1.3). While our model can accurately estimate Ψ in some highly controlled cases, in real populations, some proportion of individuals are likely to stochastically breed off-cycle, which can hinder the model's ability to estimate Ψ even while it retains the ability to accurately estimate abundance and survival. The juxtaposition of biased estimates of Ψ with unbiased estimates of abundance and survival suggests that Ψ provides needed flexibility for the model to accurately estimate other parameters, even though the parameter itself likely cannot be estimated under realistic conditions. Similarly, the parameter a must be fixed to the expected breeding cycle. If the breeding cycle for a population is unknown, and if adults are not available for sampling, then it may be possible to estimate a from the dataset apart from the CKMR model (Waples and Feutry 2021). As a cursory example, if 50 HSPs are found and nearly all were born in year gaps that are divisible by 2, then fixing a to 2 would be a logical approach. If a can be fixed to a reasonable value, then the multiennial model presented here can produce reliable estimates of abundance and survival, opening the door for application of CKMR to populations that breed intermittently. Future work that adapts CKMR to estimate Ψ and a across a range of scenarios would further expand the potential of CKMR to illuminate aspects of population breeding dynamics.

4.3 Aging error

CKMR depends heavily on accurate cohort assignment, which can be very challenging for many species, including elasmobranchs. Our results confirm that age misassignment can substantially bias CKMR parameter estimates. A hierarchical model that accounts for aging error may help alleviate this issue, but such a model would require some estimate of the probability of age misassignment (Hirst et al. 2004, Schwarz and Runge 2009), which may not be available in data-limited situations. It is preferable, therefore, to treat ages as fixed if sufficient data are available to assign age with confidence. In cases where only YOY can be reliably aged, our results show that CKMR can generate reliable abundance estimates from as few as four cohorts, even for a population that breeds bi- or triennially. If mature individuals are also available to sample – e.g., when visiting a nursery site to breed – then sampling potential parents as well as YOY can enable the use of POPs in the likelihood and improve precision of parameter estimates. Aging error in this case would be less critical for adults as long as maturity can be confirmed in the year of sampling, though care must be taken to ensure that potential parents and offspring are sampled independently, as parameter estimates will be biased if the probability of sampling a parent is correlated with the probability of sampling its offspring (Bravington et al. 2016b).

4.4 Population dynamics and abundance of lemon sharks in Bimini

Our application of CKMR to Bimini lemon sharks highlights the flexibility and potential of CKMR for long-term monitoring of populations of low density highly mobile species with geographically distinct life histories. Estimates of abundance from CKMR suggest that a very small number of female lemon sharks give birth at the North Bimini Lagoon during each biennial breeding cycle (Table 4). These results align with a previous study that reconstructed a pedigree for the population and identified the number of adults that successfully bred at the North Island each year between 1995-2007 (DiBattista et al. 2011). In both cases, the number of females that gave birth at the North Island during this time period was estimated to be very small (<~40 per year), with an increasing abundance trend through 2006. At some point after 2006, however, our results suggest that the number of females using Bimini for breeding began to decline. Intense dredging and mangrove deforestation took place around the North Bimini Island in March 2001 in preparation for development of a mega-resort (Jennings et al. 2008). Although the number of breeding females at the North Island counterintuitively increased immediately after the disturbance (DiBattista et al. 2011), there was a transient, but statistically significant, drop in the survival rates of age 0 and age 1 individuals (Jennings et al. 2008). These cohorts would have reached maturity and begun returning to Bimini for reproduction around 2013. Indeed, in our application of CKMR, we observed a declining abundance trend for adult females in 2013 in the full dataset as well as the two subsets of data (Figure 5), although the year in which the decline began varies depending on if/how the data were subsetted.

Although our results closely resemble those reported in DiBattista et. al. (2011), we note that our abundance estimates from CKMR were slightly higher. CKMR with small populations is an active area of research, as there is a known tendency to underestimate variance when the method is applied to populations with fewer than 100 individuals (M. Bravington, Pers. Comm.). When dealing with abundance estimates that are small enough to cause such issues, the practical implications of this known bias are likely minimal. For example, our model estimated a maximum of 41 females visited the North Island across all 18 years of abundance estimation, regardless of if/how we subsetted the dataset (Table 4). This value is small enough that any amount of added fishing pressure would likely threaten the sustainability of this portion of the population, especially if the true abundance is lower than what CKMR estimates.

Recognizing that the dataset for lemon sharks is uniquely rich in terms of the proportion of the population sampled and the decades over which sampling occurred, we applied CKMR to two different subsets of data: one that reduced sampling intensity each year and one that reduced the number of years over which sampling occurred. In both cases, the abundance estimates and trend were similar to the results we obtained using the full dataset, demonstrating the robustness of CKMR to less exhaustive and extensive sampling efforts. Indeed, one of the more exciting aspects of CKMR is its potential to generate rapid estimates of adult abundance without sampling a single adult (see Patterson et al. 2022b for an applied example). Once a reliable genotyping panel, workflow for assigning kinship, and appropriate CKMR model are developed for a population (see Appendix S1, Figure S7), contemporary abundance estimates could conceivably be obtained within weeks of sampling. As such, CKMR can offer a rapid and cost-effective method for population monitoring in real time following an initial investment in the laboratory and analytical workflows.

4.5 Implications for sampling design

We have shown that application of CKMR to long-lived species can generate reliable estimates of abundance from a limited number of cohorts as long as aging is reliable; however, estimates of all parameters – especially non-abundance parameters – are more reliable when more cohorts are included in the dataset. We observed this in our simulations as well as the lemon shark dataset, where estimates of survival converged as more cohorts were added to the dataset. A dataset that spans enough cohorts to reliably estimate parameters beyond abundance can be obtained via intense sampling of multiple age classes over a small number of years, but this strategy would require reliable aging of all sampled age classes to avoid biased parameter estimates. Alternatively, long-term non-lethal sampling of nursery areas represents another way that CKMR can be used to monitor low density highly mobile populations in circumstances where aging error is likely for older age classes. We are not the first to suggest that CKMR benefits from focusing sampling efforts on individuals that can be reliably aged (Trenkel et al. 2022), but our results are the first to demonstrate empirically that this approach can mitigate the bias that accrues when aging is less certain. In cases where sampling of juveniles is focused on nursery areas, sufficient biological knowledge to determine the scope of inference for CKMR will be required.

Conclusion and Future Directions

CKMR is a powerful tool for estimating population abundance of species that have been historically difficult to assess. However, CKMR is not a panacea, and reliable application of the method requires careful consideration of the relevant population dynamics matched to an appropriate sampling scheme. Here, we have shown that abundance estimates derived from CKMR are robust to a variety of sampling schemes, provided substantial population growth/decline and intermittent breeding dynamics are accounted for, while estimates of survival and population growth/decline rate are more sensitive to sampling constraints. When ages are prone to misassignment, focusing sampling efforts on individuals with known ages (e.g., YOY), or subsampling for these individuals if the dataset is sufficiently rich, can alleviate bias in parameter estimates, particularly abundance. Long-term monitoring of highly mobile species can be enhanced by CKMR via sampling of nursery areas when one or both sexes are philopatric, and can provide estimates of present-day abundance and abundance trends for adults that visit the nursery area without directly sampling a single adult. Overall, this study highlights the sensitivity of simple base-case CKMR models to assumptions about population dynamics and sampling, while also demonstrating that the CKMR framework is easily adaptable to accommodate these factors, making it a promising tool for integration into long-term monitoring programs.

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Table 1: Simulation scenarios for data-generating model and estimation model.

Scenario	**Test**	**10 year mean λ**	**10 year sd λ**	**Model equation(s) used**	**Aging**	**CV on aging error**
1	Model validation	1	0.003	Eq. 2	Precise	NA
2.1	Slight population decline	0.99	0.003	Eq. 2, Eq. 3	Precise	NA
2.2	Slight population growth	1.01	0.002	Eq. 2, Eq. 3	Precise	NA
2.3	Severe population decline	0.93	0.01	Eq. 2, Eq. 3	Precise	NA
3.1	100% biennial breeders	1	0.003	Eq. 3, Eq. 4	Precise	NA
3.2	90% biennial breeders	1	0.003	Eq. 3, Eq. 4	Precise	NA
3.3	75% biennial breeders	1	0.003	Eq. 3, Eq. 4	Precise	NA
3.4	50% biennial breeders	1	0.003	Eq. 3, Eq. 4	Precise	NA
3.5	100% triennial breeders	1	0.003	Eq. 3, Eq. 4	Precise	NA
3.6	100% biennial breeders w/ stochastic off-cycle breeding	1	0.003	Eq. 3, Eq. 4	Precise	NA
4.1	Minimal age-length uncertainty	1	0.003	Eq. 3, Eq. 4	Imprecise	5%
4.2	Moderate age-length uncertainty	1	0.003	Eq. 3, Eq. 4	Imprecise	10%
4.3	Substantial age-length uncertainty	1	0.003	Eq. 3, Eq. 4	Imprecise	20%

Note: λ is the annual population growth/decline rate.

Table 2: Priors used in CKMR model for results highlighted in text and figures.

Objective	N_s	Φ	**λ prior**	ψ
1: Model validation	$N_S \sim$ Normal(μ, σ) $\mu \sim$ Uniform(1, 10000) $\sigma \sim$ Uniform(1, 10000)	Beta(69.175, 14.673)	None	NA
2: Population change	Same as 1	Uniform(0.5, 0.95)	None Uniform(0.95, 1.05) Uniform(0.80, 1.20)	NA
3: Intermittent breeding	Same as 1	Uniform(0.5, 0.95)	Uniform(0.95, 1.05)	Uniform(0, 1)
4. Aging uncertainty	Same as 1	Uniform(0.5, 0.95)	Uniform(0.95, 1.05)	Uniform(0, 1)
5: Bimini lemon shark data	Same as 1	Uniform(0.5, 0.99)	Uniform(0.95, 1.05)	Uniform(0, 1)

Note: λ is the annual population growth/decline rate; *Ns* is sex specific adult abundance; Φ is annual adult survival (not sex-specific); ψ is the proportion of individuals that breed every *a* years.

Table 3: Relative bias, HSPs, and percent in the 95% HPDI for female abundance (N♀) under different scenarios using the model that was adapted for each scenario.

		Target YOY				Sample all juveniles				Sample all ages				
Equation	**Scenario**	**HSPs**	**CV**	**% in HPDI**	**Rel. bias**	**HSPs**	**CV**	**% in HPDI**	**Rel. bias**	**POPs**	**HSPs**	**CV**	**% in HPDI**	**Rel. bias**
Eq. 2	**1**: model validation	149	**10**	**99**	2.47	136	11	96	3.01	15	144	10	94	**2.39**
Eq. 3	**2.1**: slight decline	74	21	**98**	**1.57**	65	18	92	6.08	5	67	**17**	96	5.43
Eq. 3	**2.2**: slight growth	272	14	**98**	6.35	263	9	94	2.39	17	270	**9**	95	**2.32**
Eq. 3	**2.3**: severe decline	85	33	**98**	18.4	59	20	95	9.77	8	66	**18**	96	**5.22**
Eq. 4	**3.1**: 100% biennial breeders	101	22	**97**	6.13	130	14	93	6.61	15	111	**13**	91	**5.66**
Eq. 4	**3.2**: 90% biennial breeders	132	20	**98**	-0.84	152	13	91	-1.93	15	130	**12**	93	**-0.75**
Eq. 4	**3.3**: 75% biennial breeders	161	18	**94**	**-3.79**	170	12	83	-6.26	15	145	**12**	88	-4.1
Eq. 4	**3.4**: 50% biennial breeders	185	17	**97**	**-4.44**	179	**11**	85	-6.06	15	153	**11**	86	-4.45
Eq. 4	**3.5**: 100% triennial breeders	53	29	**99**	18.7	98	17	92	7.55	14	84	**15**	94	**7.47**
Eq. 4	**3.6:** 100% biennial breeders + stochasticity	121	20	**98**	5.98	140	13	90	5.97	16	121	**12**	93	**3.95**
Eq. 3 (annual)	**4.1**: 5% CV	179	16	**98**	**5.2**	164	**11**	90	8.61	9	141	12	89	8.97
Eq. 4 (multiennial)		102	22	**97**	**6.3**	148	**12**	83	15.4	9	125	13	85	14.5
Eq. 3 (annual)	**4.2**: 10% CV	179	16	**98**	**5.2**	162	**11**	84	13	8	140	12	84	13.2
Eq. 4 (multiennial)		102	22	**97**	**6.3**	149	**12**	77	17.9	8	125	13	74	20.2
Eq. 3 (annual)	**4.3**: 20% CV	179	16	**98**	**5.2**	158	**11**	57	24.4	7	138	12	61	25.2
Eq. 4 (multiennial)		102	22	**97**	**6.3**	145	**12**	48	28.8	7	123	13	43	34

Table 4: Abundance estimates and sampling metrics for Bimini lemon sharks when a CKMR model adapted for intermittent breeding was fit to the full dataset, a downsampled dataset in which 30% of samples were retained for each year, and a subset of the full dataset in which five-years of data were used to estimate abundance in each year.

	Full dataset				**Downsampled dataset**				**Five year intervals**			
Estimation year	**Median**	**95% HPDI**	**Total samples**	**MHSPs**	**Median**	**95% HPDI**	**Total samples**	**MHSPs**	**Median**	**95% HPDI**	**Total samples**	**MHSPs**
1997	15	(10 - 19)	104	105	14	(5 - 28)	33	11	15	(10 - 19)	104	105
1998	15	(11 - 18)	121	141	12	(4 - 23)	39	15	15	(10 - 19)	115	113
1999	18	(14 - 22)	157	239	23	(7 - 49)	50	13	18	(12 - 23)	143	180
2000	19	(15 - 22)	180	306	16	(10 - 24)	57	33	18	(13 - 23)	134	130
2001	20	(15 - 25)	214	357	26	(13 - 41)	68	30	13	(7 - 22)	146	111
2002	26	(22 - 31)	251	462	24	(14 - 35)	80	45	32	(24 - 40)	147	100
2003	29	(24 - 33)	283	564	27	(18 - 38)	90	57	38	(30 - 47)	162	113
2004	32	(28 - 35)	316	678	27	(19 - 36)	100	74	34	(24 - 43)	159	107
2005	31	(27 - 35)	374	822	31	(23 - 40)	118	95	36	(26 - 44)	194	158
2006	36	(32 - 40)	424	1029	29	(19 - 41)	133	99	37	(29 - 44)	210	175
2007	34	(30 - 38)	470	1248	27	(19 - 37)	147	135	34	(28 - 40)	219	214
2008	38	(34 - 42)	493	1349	41	(29 - 52)	154	122	35	(25 - 44)	210	165
2009	36	(33 - 40)	539	1556	33	(23 - 44)	168	158	30	(21 - 39)	223	227
2010	38	(34 - 42)	559	1665	37	(28 - 48)	174	175	31	(21 - 40)	185	138
2011	35	(31 - 39)	611	1977	30	(20 - 40)	190	208	31	(25 - 37)	187	210
2012	37	(32 - 41)	619	1995	23	(16 - 33)	193	159	33	(25 - 42)	149	96
2013	33	(30 - 37)	657	2240	24	(16 - 32)	205	255	29	(19 - 40)	164	160
2014	31	(27 - 34)	678	2374	32	(24 - 40)	212	273	23	(19 - 28)	139	113
2015	27	(24 - 30)	718	2708	31	(21 - 44)	224	239	24	(18 - 29)	159	202

Note: MHSPs refers to the number of maternal half-sibling pairs identified.

Figure 1: Schematic of CKMR sensitivity tests, examined via individual-based simulation (see also Tables 1 and 2; Scenario 1 was model validation, and Scenario 5 involved real genetic data, so are not included here). Populations with distinct pedigrees were produced and sampled via an individual-based data-generating model (purple). Population parameters were individually varied for each of three scenarios. Each population was sampled in three ways, and each set of samples was used as input to two estimation models (green): one model was naïve to the added population dynamics of the DGM, and one model was adapted to account for them. The prior on λ and the year of estimation was varied for Scenario 2; otherwise, simulation results that are highlighted in the text used the model settings highlighted in bold (narrow prior on λ, estimating abundance five years in the past).

Figure 2: Base CKMR model performance and kin pairs detected for three different sampling schemes at four different sampling intensities over 500 iterations. **a)** Relative bias of abundance estimates of adult females and males as a percentage of the truth (i.e. relative bias x 100). Bias was calculated from the median of each of 500 posterior distributions. **b)** CV on abundance estimates with log-scaled Y axis for visualization. **c)** Number of sex-specific half-sibling pairs detected by sampling scheme and sampling intensity. For each iteration, the number of half sibling pairs for each sex was calculated and averaged. **d)** Number of sex-specific parent-offspring pairs detected for the “sample all ages” sampling scheme.

Figure 3: Relative bias of CKMR abundance estimates for mature females (N♀) when applied to populations experiencing variable degrees of population growth or decline. Plots are split by sampling scheme (column), population growth pattern (row facet) and the year of estimation (rows within population growth facet). Scenarios assessed had population growth as **a)** stable (+/-0% per year), **b)** slightly increasing (+1% per year), **c)** slightly declining (-1% per year), or **d)** severely declining (-5-10% per year over the final 10 years). Three different models were fit to 500 simulated populations for each scenario: a naïve model without a parameter for population growth (red), an adapted model with population growth constrained to +/-5% per year (yellow), and an adapted model with population growth more loosely constrained to +/- 20% per year (blue). Plots were truncated at +/-100% for visualization because there were long tails of positive bias for the 10 year past scenarios.

Figure 4: Relative bias of CKMR parameter estimates with intermittent breeding and aging error. **a)** Relative bias of abundance estimates for females (Nf, top facet) and males (Nm, bottom facet) in a simulated population with different ratios of biennial vs. annual female breeders. An annual CKMR model that was naïve to intermittent breeding dynamics was examined (Eq. 3, orange) as was a multiennial model that was adapted to account for these dynamics (Eq. 4, blue). On the x-axis, 1* is the case with 10% of biennial breeders that breed off-cycle and 10% of on-cycle females that fail to breed. **b)** Relative bias of abundance estimates for females (top facet) and survival (bottom facet) when uncertainty was introduced to length-based age assignments. In contrast to a, there was no intentional model misspecification in these simulations; rather, annual models were fit to populations that bred annually (light blue), while multiennial models were fit

to populations that bred biennially (dark blue), thereby isolating the effects of aging error on the resulting bias.

Figure 5: Time series of CKMR parameter estimates for mature female lemon sharks at Bimini, Bahamas using the full dataset (green; solid trendline), a dataset that was downsampled to 30% of the sampling effort for each year of sampling (orange; dotted trendline), and a dataset that included five years of samples for each instance of abundance estimation (purple; dashed trendline). Points represent the median of the posterior distribution, and error bars reflect the 95% highest posterior density interval (HPDI). **a)** Estimates of annual female abundance. **b)** Estimates of survival.

Figure 1

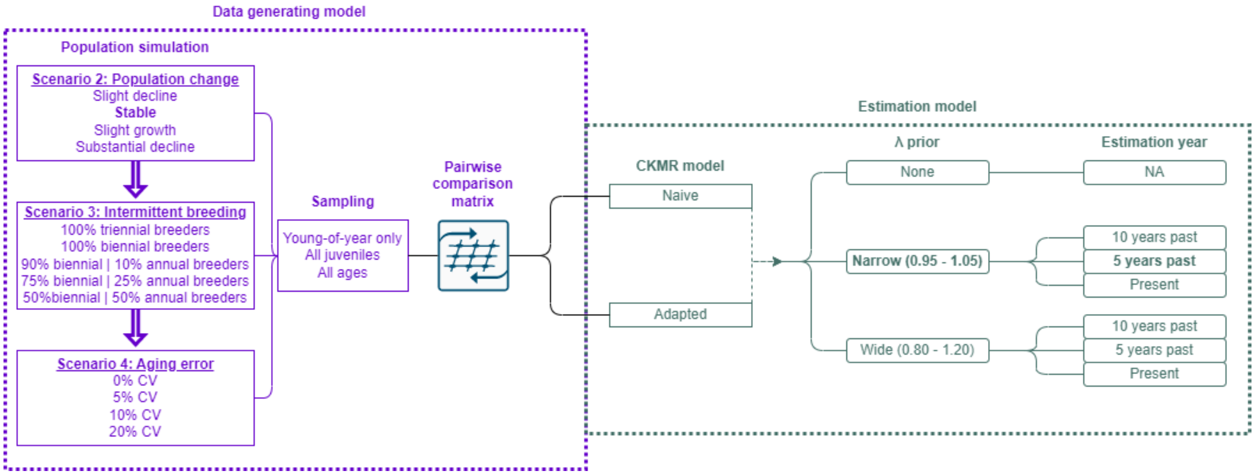
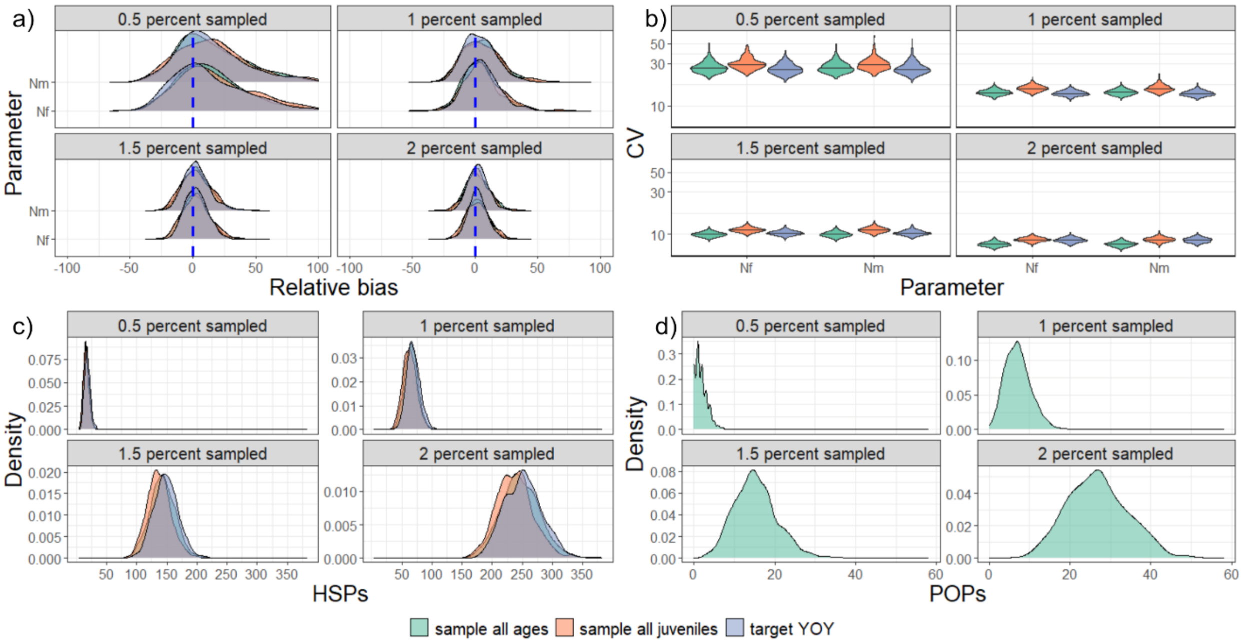
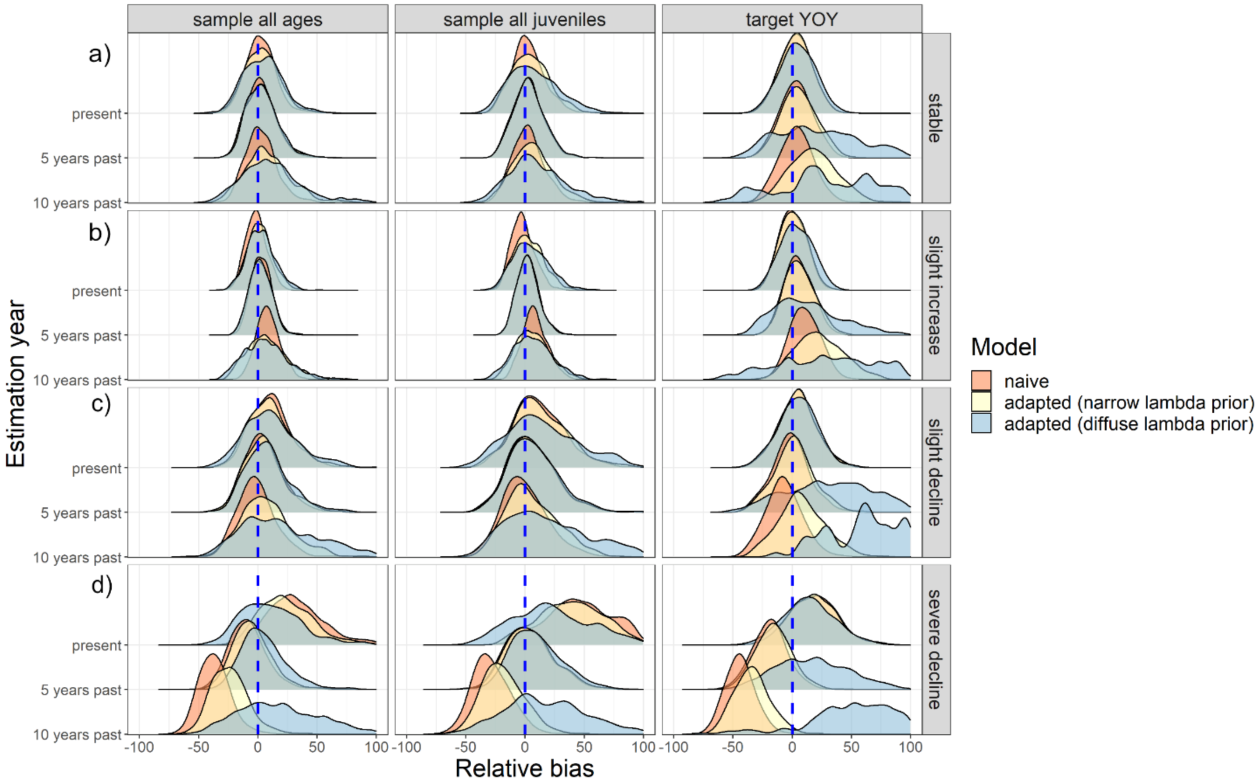

Data generating model
Population simulation
Scenario 2: Population change
Slight decline
Stable
Slight growth
Substantial decline
Scenario 3: Intermittent breeding
100% triennial breeders
100% biennial breeders
90% biennial | 10% annual breeders
75% biennial | 25% annual breeders
50%biennial | 50% annual breeders
Scenario 4: Aging error
0% CV
5% CV
10% CV
20% CV
Sampling
Young-of-year only
All juveniles
All ages
Pairwise comparison matrix
Estimation model
CKMR model
Naive
Adapted
λ prior
None
Narrow (0.95 - 1.05)
Wide (0.80 - 1.20)
Estimation year
NA
10 years past
5 years past
Present
10 years past
5 years past
Present

Figure 2


a)
0.5 percent sampled
1 percent sampled
1.5 percent sampled
2 percent sampled
Parameter
Nm
Nf
-100
-50
0
50
100
Relative bias
b)
CV
50
30
10
Nf
Nm
Parameter
c)
Density
0.075
0.050
0.025
0.000
0.03
0.02
0.01
0.00
0.020
0.015
0.010
0.005
0.010
50 100 150 200 250 300 350
HSPs
d)
0.3
0.2
0.1
0.0
0.10
0.05
0.08
0.06
0.04
0.02
0 20 40 60
POPs
sample all ages
sample all juveniles
target YOY

1033 **Figure 3**



1034

1035

Figure 4

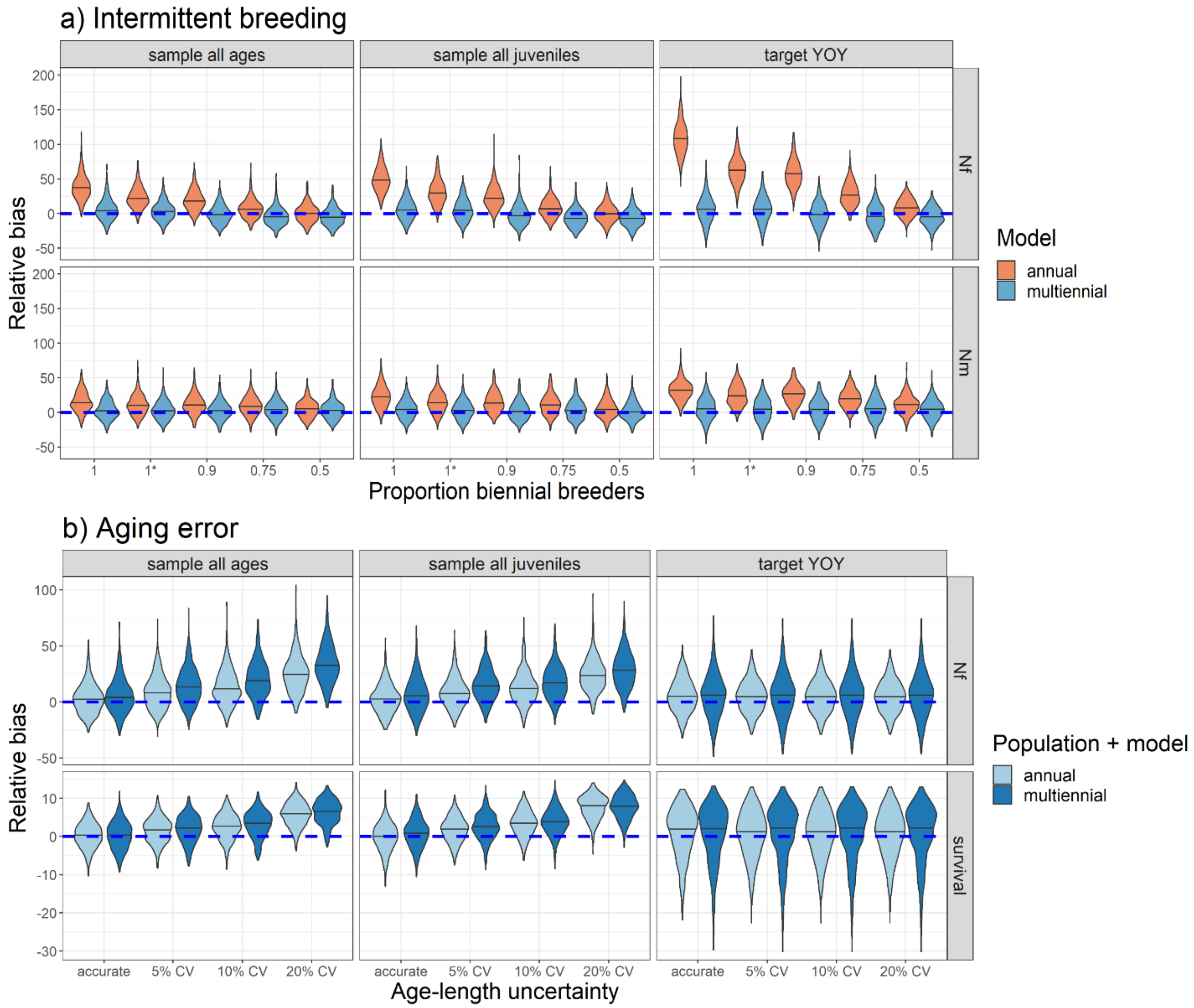
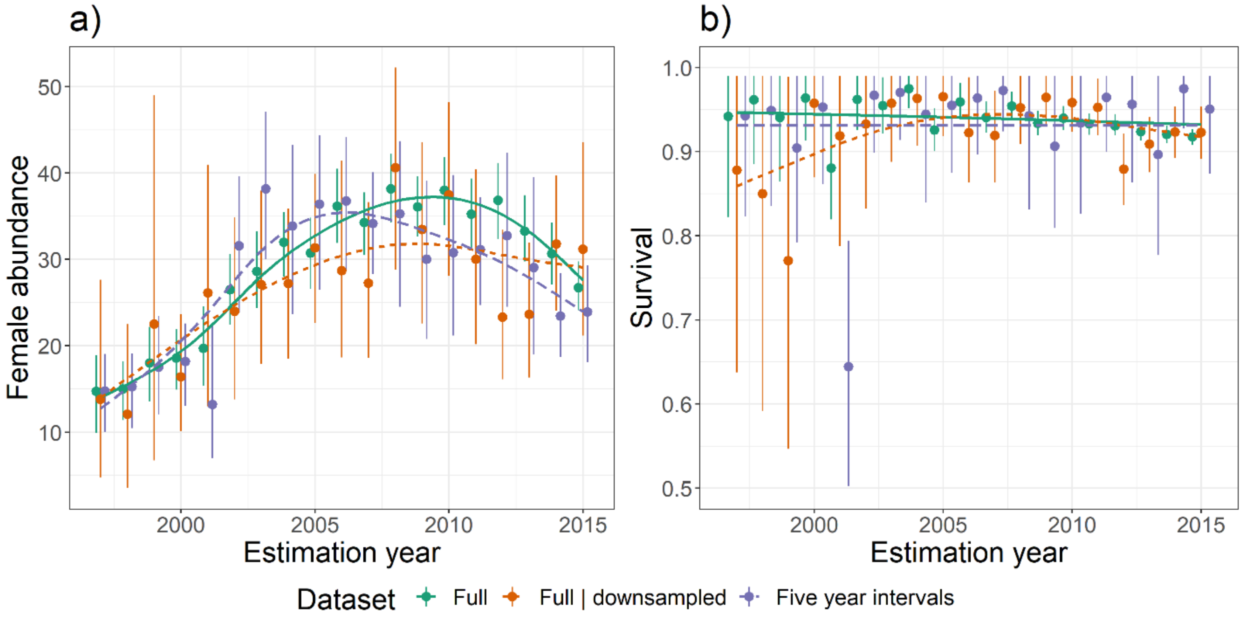

a) Intermittent breeding
sample all ages
sample all juveniles
target YOY
Nf
Nm
Relative bias
200
150
100
50
0
-50
1
1*
0.9
0.75
0.5
Proportion biennial breeders
Model
annual
multiennial
b) Aging error
sample all ages
sample all juveniles
target YOY
Nf
survival
Relative bias
100
50
0
-50
10
0
-10
-20
-30
accurate
5% CV
10% CV
20% CV
Age-length uncertainty
Population + model
annual
multiennial

Figure 5


a)
Female abundance
50
40
30
20
10
2000
2005
2010
2015
Estimation year
b)
Survival
1.0
0.9
0.8
0.7
0.6
0.5
2000
2005
2010
2015
Estimation year
Dataset
Full
Full | downsampled
Five year intervals