

1 Title Page

2 Modeling vital rates and age-sex structure of Pacific arctic phocids: influence on aerial survey

3 correction factors

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16 Abstract

17 To estimate abundance, surveys of marine mammals often rely on samples of satellite-tagged
18 individuals to correct counts for the proportion of animals that are unavailable to be detected.
19 However, naïve application of this correction relies on the key assumption that availability of the
20 tagged sample resembles that of the population. Here, we show how matrix population models
21 can be used to estimate the stable stage structure of bearded seals (*Erignathus barbatus*),
22 ribbon seals (*Histiophoca fasciata*), ringed seals (*Pusa hispida*), and spotted seals (*Phoca*
23 *largha*) in the Bering and Chukchi Seas, and how these proportions can be used to adjust aerial
24 survey correction factors so that they represent population-level availability. We find that
25 correction factors ignoring age-sex composition can positively bias spotted seal abundance by
26 an average of 13% and negatively bias ribbon seal abundance by an average of 5%. Note that
27 we did not examine potential bias for bearded or ringed seals due to low sample sizes; as such,
28 we urge caution in interpretation of abundance estimates for these species.

29

30

31 KEYWORDS age and sex structure, availability, detection probability, *Erignathus barbatus*,
32 *Histiophoca fasciata*, matrix population model, *Pusa hispida*, *Phoca largha*, stable stage
33 distribution

34

35 **1. Introduction**

36 Analysis of animal survey counts of often include corrections for availability, the proportion of
37 animals that are detectable while surveys are being conducted (Marsh & Sinclair, 1989). For
38 marine mammals surveyed in water, availability consists of the proportion of animals that are at
39 the surface while the survey vessel passes (e.g. McLaren, 1961; Barlow et al., 1988); for aural
40 surveys of songbirds, it is the proportion of birds that sing while counts are conducted
41 (Diefenbach et al., 2007); and for aerial surveys of phocids on sea ice, it is the proportion of
42 seals that are hauled out (Bengtson et al., 2005; Simpkins et al., 2003). In all cases, availability
43 corrections are needed to prevent negative bias in abundance estimates (Nichols et al., 2009).

44
45 For ice-associated seals surveyed on sea ice, one possible avenue for estimating availability is
46 to use data from satellite-linked time-depth recorder tags (TDRs) to estimate the proportion of
47 time seals spend out of water (Bengtson et al., 2005). Indeed, availability estimates from TDRs
48 have been used to correct survey counts of seals in the Bering (Conn et al., 2014; Ver Hoef et
49 al. 2014) and Chukchi (Bengtson et al., 2005) seas. However, these previous efforts implicitly
50 assumed that availability computed from the sample of tagged seals was a good approximation
51 to that of the population – in other words, that the TDR data was not systematically biased in
52 some way.

53
54 Recently, London et al. (2022) examined the influence of environmental variables and age-sex
55 class on haul-out probabilities of bearded, ribbon, and spotted seals in the Bering and Chukchi
56 seas. For ribbon and spotted seals (sample sizes for bearded seals were insufficient), they
57 demonstrated that haul-out probabilities differed considerably by age- and sex-class. Age- and
58 sex-specific differences in availability are logical given biological constraints, with adult females
59 needing to spend substantial time on ice for whelping and lactation (12-18 days for bearded
60 seals; 21-28 days for ribbon seals; 14-35 days for spotted seals; reviewed in Oftedal et al.,

61 1987). Similarly, adult male phocids mate with females shortly after parturition, and will mate
62 with more than one female if possible (Stirling et al., 1981). Bearded seal males also exhibit
63 polygynous behavior and defend relatively stable territories that are advertised to females via
64 underwater vocalization (Van Parijs and Clark, 2006); we might, then, expect adult females to
65 spend considerably more time hauled out than adult males during pupping season, but for
66 adults to be concentrated near sea-ice haul-out locations. By contrast, subadults of all species
67 have no reproductive constraints, though all age classes use sea ice as a platform to undergo
68 an annual spring molt that ranges from ≈ 30 days in spotted and ringed seals to ≈ 120 days for
69 bearded seals (Thometz et al., 2021).

70

71 Age- and sex-mediated differences in haul-out behavior suggest a potential for bias in
72 availability if the age-sex structure of satellite-tagged seals differs from that of the population.
73 For ice-associated seals in the Bering and Chukchi Seas, capture operations have largely been
74 opportunistic (Boveng et al., 2020). Adult bearded seals, for instance, are wary of humans and
75 are particularly hard to capture on ice. Most marking operations for bearded seals have thus
76 focused on young animals (e.g. Cameron et al., 2018; Olnes et al. 2021). Similarly, spotted
77 seals have sometimes been caught in coastal lagoons, a process that favors capture of young
78 individuals (e.g. Lowry et al., 1998). There is thus reason to expect that age-aggregated
79 availability estimates for these species will be biased towards younger age classes. If younger
80 age classes haul out less frequently than adults, naïve application of such estimates as aerial
81 survey correction factors will likely result in positively biased abundance estimates.

82

83 In this paper, we examine the potential for bias in ice seal availability estimates when the
84 sample of satellite-tagged seals is biased towards young individuals, and when age-sex class is
85 ignored during estimation. We compare age aggregation to an alternative approach that
86 attempts to estimate population-weighted availability, where age- and sex-specific availability

87 estimates are weighted by the proportion of animals thought to be in each age-sex class. To
88 derive these weights, we rely on stable stage distributions estimated from matrix population
89 models (Caswell, 2001). After using data from the literature to estimate stable stage proportions
90 for ice-associated seals, we illustrate our approach by applying both types of estimation
91 approaches to TDR records of spotted and ribbon seals in the Bering Sea.

92 **2. Methods**

93 2.1 Availability models

94 A number of authors have used generalized linear mixed models (GLMMs; Wolfinger and
95 O'connell, 1993) to investigate factors affecting haul-out probabilities of arctic and subarctic
96 seals (e.g., Bengtson et al., 2005; Crawford et al., 2019; London et al., 2022; Olnes et al., 2021;
97 Ver Hoef et al., 2010; Von Duyke et al., 2020). The GLMM framework is appealing because it
98 allows one to include individual-level random effects, as well as autocorrelated error structures
99 that are necessary to account for responses that are statistically dependent (as when seals
100 haul-out consecutively for many hours). We summarized haul-out records as Bernoulli
101 responses; for individual i and hour t , we set $Y_{it}=1$ if individual i has a dry tag for $\geq 50\%$ of hour t .
102 According to the GLMM framework, the expected value (i.e., prediction) for individual i at hour t
103 is a function of both fixed effects specified by the investigator (e.g., choice of explanatory
104 predictors) and random effects which are largely governed by the specific error structure
105 assumed and variability in the observed data. Specifically, the expected values of haul-out
106 observations given random effects can be given as

$$107 \quad E(\mathbf{Y}|\boldsymbol{\eta}) = g^{-1}(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\eta})$$

108 where predictive covariates are codified in a design matrix, \mathbf{X} (see McCullagh & Nelder, 2019),
109 $\boldsymbol{\beta}$ represents a vector of regression parameters, \mathbf{Z} gives a design matrix for random effects that
110 links random effects to particular observations, and $\boldsymbol{\eta}$ is a vector of random effects. The
111 function g^{-1} represents an inverse link function that will typically be used to convert the linear
112 predictor to the scale of the observations (in our application, this is the inverse logit function).

113

114 In specifying alternative models for haul-out distributions, we will focus on the fixed effects
115 structure, $\xi = \mathbf{X}\beta$, as it is here that researchers may specify different covariate effects (including
116 sex-age effects). In particular, we consider two types of models, one with sex-age effects, and
117 one without:

118 Model 1: $\xi_{as} = \mathbf{X}_1\beta_1 + \mathbf{X}_2\beta_2$

119 Model 1: $\xi_0 = \mathbf{X}_1\beta_1$.

120 Here, \mathbf{X}_2 and β_2 represent a design matrix and regression parameters for age- and sex-effects,
121 and \mathbf{X}_1 and β_1 represent a design matrix and regression coefficients for remaining covariates
122 (e.g., weather, time-of-day), including an intercept. For specific examples of how such models
123 can be formulated, see *Ribbon and Spotted Seal Analysis*.

124

125 The GLMM models can be fitted directly to TDR records to estimate β_1 and β_2 (we designate
126 such estimates as $\hat{\beta}_1$ and $\hat{\beta}_2$). However, for aerial survey corrections we need to make
127 predictions of the proportion of seals that were hauled out at the particular time when aerial
128 surveys were conducted. To make predictions, let \mathbf{X}_1^* denote a design matrix where relevant
129 entries correspond to the realized covariates at the time surveys were conducted. Availability
130 predictions at the time of the survey can then be made using the fixed-effects structure $\xi_0^* =$
131 $\mathbf{X}_1^* \hat{\beta}_1$ for the model without age- and sex-effects. If random effects have mean zero as is
132 standard, a vector of availability predictions (\mathbf{a}_0^*) can then be generated as $\mathbf{a}_0^* = g^{-1}(\xi_0^*)$;
133 variances of predictions are slightly more complicated; see Ver Hoef et al. (2014).

134

135 However, for models with age- and sex- effects, we can only make predictions for specific age-
136 and sex values. For instance, if we use a categorical fixed effect to represent age-sex class
137 (e.g., young-of-year, subadult, adult female, and adult male), we can only make predictions for

138 each of these groups separately. Without loss of generality, let us assume that we have these
139 four age-sex classes, and denote their predictions as \mathbf{a}_{yoy}^* , \mathbf{a}_s^* , \mathbf{a}_{af}^* , and \mathbf{a}_{am}^* , respectively. In the
140 usual case that aerial surveys are unable to discern age-sex class (possibly they would be able
141 to discern differences between young-of-year and other classes), it thus is necessary to average
142 among availability predictions somehow, e.g.,

$$143 \quad \tilde{\mathbf{a}} = \pi_{yoy}\mathbf{a}_{yoy}^* + \pi_{sub}\mathbf{a}_{sub}^* + \pi_{af}\mathbf{a}_{af}^* + \pi_{am}\mathbf{a}_{am}^*, \quad \text{Eq. 1}$$

144 where $\sum_i \pi_i = 1.0$. Ideally, the weights π_i should reflect the age-sex composition of the
145 population being surveyed. One possibility is to use stable stage proportions to help define
146 these weights.

147

148 2.2 Stable stage distributions

149 Our strategy for computing stable stage proportions (i.e., π_{yoy} , π_{sub} , π_{af} , π_{am}) was to (1) use
150 matrix population models (Caswell, 2001) for each species to calculate stable age proportions
151 (ages 0-39+), and (2) to use sexual maturity schedules reported in the literature to convert
152 stable age proportions to stable stage proportions.

153

154 In order to conduct these analyses, we first compiled data on survival, female reproduction, and
155 sexual maturity from the literature to help calculate stable stage proportions for bearded, ribbon,
156 ringed, and spotted seals. For survival, we used results from a hierarchical meta-analysis
157 previously fit to a variety of phocid mortality datasets (Trukhanova et al., 2018) to produce
158 annual survival estimates for the four species of interest. In particular, we used the same
159 methods and data reported in Trukhanova et al. (2018), using their ribbon seal example
160 template, to re-fit models and produce posterior predictions of survival for each of the four
161 species. These models specify a U-shaped mortality curve (Choquet et al., 2011), with typically
162 high mortality at the beginning of life, followed by a period of low mortality, and finally increasing

163 mortality at older ages corresponding to senescence. We conducted analysis with JAGS 4.2.0
164 (Plummer, 2003), using the highest-ranked DIC model from Trukhanova et al. (2018) which
165 included effects of subfamily, species, and dataset.

166
167 For female fecundity, we used a combination of different data sources depending on species
168 and the amount of data available, with preference towards data collected in the Bering and
169 Chukchi Seas (where we collect aerial survey and satellite telemetry data) and to data that were
170 recently collected. We favored recent data since there is some indication that pregnancy rates
171 have increased and age at sexual maturity have decreased in recent decades (Alaska Dept. of
172 Fish & Game, 2020; Krafft et al., 2006, Quakenbush, 2020). For ringed and spotted seals, we
173 based female reproductive and maturity on data that the Alaska Department of Fish and Game
174 (ADFG) gathered from Alaska subsistence hunters between 2010 and 2019 (Quakenbush et al.,
175 2020 and Alaska Dept. of Fish and Game, 2020, respectively). Reproductive assessments
176 were limited to specimens gathered in winter and spring, when seals were reliability pregnant or
177 had just given birth. For bearded seals, ADFG data were quite limited, so we widened the years
178 considered to 1964-2020 and combined them with Russian data from the Bering Sea gathered
179 in the 1980s (Fedoseev, 2000, Table 47). For ribbon seals, we based female fecundity entirely
180 on Russian records from the Bering Sea gathered in the 1980s (Fedoseev, 2000, Table 24).

181 From these data, we summarized the number of specimens (n_{ia}) for each species (i) and
182 age class (a), and the number of these which were pregnant or had given birth in the year they
183 were examined (y_{ia}), as well as the number that were sexually mature (z_{ia}). We truncated ages
184 9 and greater into a single 9+ group to reduce the likelihood of aging errors. Raw proportions by
185 age did not necessarily increase in a smooth, monotonic fashion (particularly for ADFG data
186 where sample sizes were small), a feature of the data that we ascribed to low sample size. In
187 these cases, we used generalized additive models (GAMs) to smooth proportions of
188 reproducing or mature females as a function of age. This was accomplished using the mgcv

189 package (Wood, 2017) in the R programming environment (R Core Team 2017), using a
190 binomial error structure:

$$191 \quad y_{ia} \sim \text{Binomial}(n_{ia}, p_{i,a}),$$

192 where $p_{i,a}$, gives the proportion of females of species i and age class a that give birth in any
193 particular year. Note that these species almost never give birth to more than a single pup per
194 year, so p_{ia} is roughly synonymous with per capita fecundity. The GAM models incorporated
195 smooth effects of age, and predictions from these models were incorporated into stable stage
196 calculations (see below).

197
198 We used the notation $m_{i,s,a}$ to denote the proportion of species i , sex s , and age a that are
199 reproductively mature. For females, we used the same data sets and analysis procedures
200 described above to estimate $m_{i,s,a}$ from n_{ia} and z_{ia} . For Russian data, sample sizes were large
201 enough that we simply used raw data proportions (i.e., $m_{i,s,a} = z_{ia}/n_{ia}$). Data for the proportion
202 of mature bearded, ribbon, and spotted seal males were taken from Tikhamorov (1966) from
203 collections in the Bering Sea and Sea of Okhotsk. For male ringed seal maturity, we averaged
204 proportions reported in Fedoseev (1965) and Tikhamorov (1966), weighting by sample size
205 when they were available for both studies, and weighting each study equally when sample sizes
206 were missing.

207
208 We used survival and reproductive values to parameterize a Leslie matrix model (Caswell,
209 2001). Our matrix model was structured with a post-breeding census (so that fecundity
210 represents the product of adult survival and reproduction); it was also parameterized entirely in
211 terms of females:

$$212 \quad \mathbf{A}_i = \begin{bmatrix} F_{i,0} & F_{i,1} & F_{i,2} & \cdots & F_{i,38} & F_{i,39} & 0 \\ S_{i,0} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{i,1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{i,2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{i,38} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{i,39} & 0 \end{bmatrix}.$$

213 Here, $S_{i,a}$ gives survival probability for an age a seal, and $F_{i,a} = 0.5p_{i,a}S_{i,a}$ gives per capita births
 214 of female offspring for age a female alive at the start of the year (this assumes a sex ratio at
 215 birth of 0.5). Using this framework, we computed stable age distributions for each species as
 216 the dominant eigenvector of that species' Leslie matrix (Caswell, 2001). All calculations were
 217 done in the R programming environment (R Core Team, 2017).

218
 219 Letting $v_{i,a}$ denote the proportion of seals of species i that are age a (determined through Leslie
 220 matrix computations), our next task is to translate these into stable stage proportions (i.e., for
 221 young-of-year, subadults, adult females, and adult males). Letting the subscript $s = M$ denote
 222 male and $s = F$ denote female, we have

$$223 \quad \pi_{i,yoy} = v_{i,0},$$

$$224 \quad \pi_{i,sub} = 0.5 \sum_{a=1}^{39} (1 - m_{i,M,a}) v_{ia} + (1 - m_{i,F,a}) v_{ia}$$

$$225 \quad \pi_{i,am} = 0.5 \sum_a m_{i,M,a} v_{ia}, \text{ and}$$

$$226 \quad \pi_{i,af} = 0.5 \sum_a m_{i,F,a} v_{ia}.$$

227 Note that these calculations implicitly assume that males and females have the same survival
 228 rates.

229

230 2.3 Ribbon and Spotted Seal Analysis

231 Having described a procedure for computing approximate stage frequencies for several Arctic
 232 phocids, we now turn our attention to analyzing possible impacts of age-sex structure on aerial
 233 survey correction factors. In particular, we reexamined haul-out behavior of 115 ribbon seals

234 and 104 spotted seals initially analyzed by London et al. (2022). In addition to examining time-
235 of-day and weather effects, London et al. (2022) estimated sex-age effects on haul-out
236 probabilities, including interactions between sex-age class (young-of-year, subadult, adult
237 female, and adult male) and day of year. In this study, we used their data and a GLMM
238 modeling framework to (1) predict \tilde{a} as in Eq. 1 using a model with an age-sex effect, and (2)
239 predict a_0^* using a model without stable stage adjustments (we ran models for each species
240 separately). To mimic aerial survey conditions during spring in the Arctic, we generated one
241 availability prediction per day for Julian days 91-151 (April 1 - May 30 in non-leap years), at
242 solar noon. To aid in interpretation, we omitted weather effects from GLMMs and only produced
243 predictions for non-pups (availability of pups during Arctic spring is further complicated by the
244 birthing process).

245
246 To see how differences in these estimates might influence abundance estimates from aerial
247 surveys, we calculated potential bias as \tilde{a}/a_0^* . This formulation is motivated by assuming that \tilde{a}
248 is an unbiased estimate of availability, and that abundance can be reasonably calculated using
249 a Horvitz-Thompson-like estimator (cf., Cochran 2007), i.e., $\hat{N} = C/\hat{a}$ (C being a hypothetical
250 aerial survey count).

251

252 2.4 Data and software

253 TDR data and haul-out predictions are currently available at
254 <https://github.com/jmlondon/berchukFits>; Survival and reproductive schedules, and R code to
255 perform stable stage estimation are currently available at
256 <https://github.com/pconn/StableStagePhocid>. Both repositories will be archived to a permanent,
257 publicly available location upon manuscript acceptance.

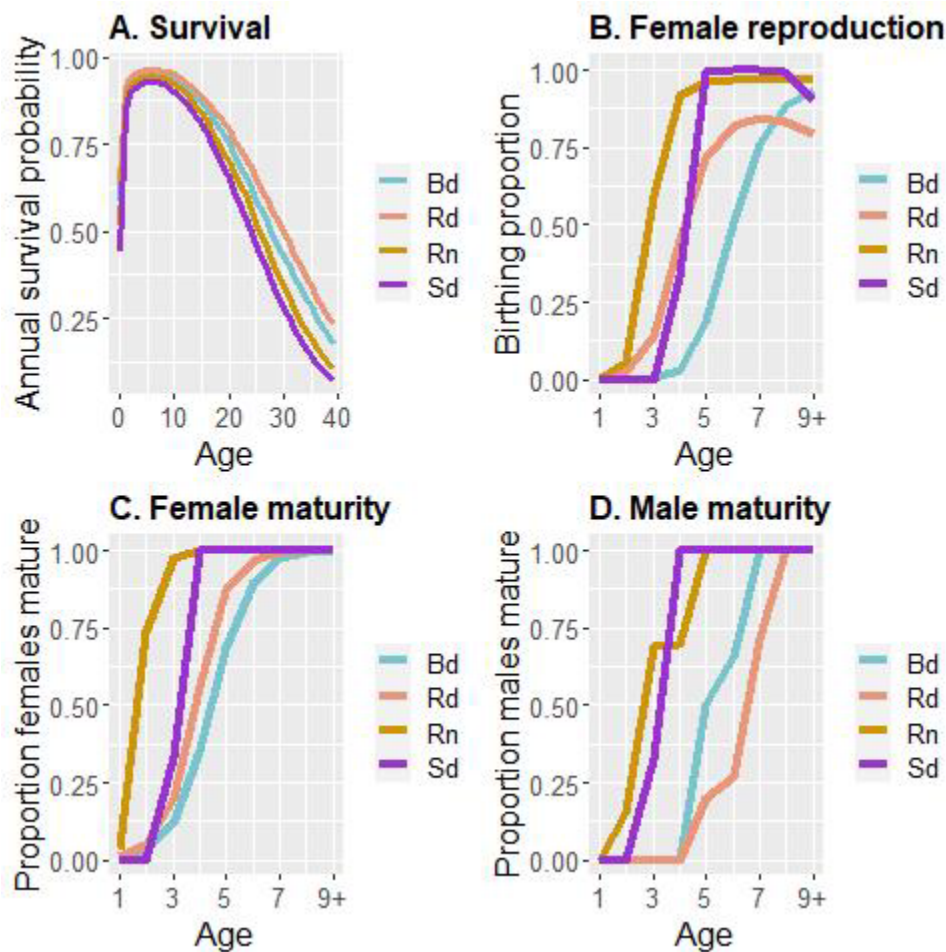
258

259 3. Results

260 3.1 Stable stage distributions

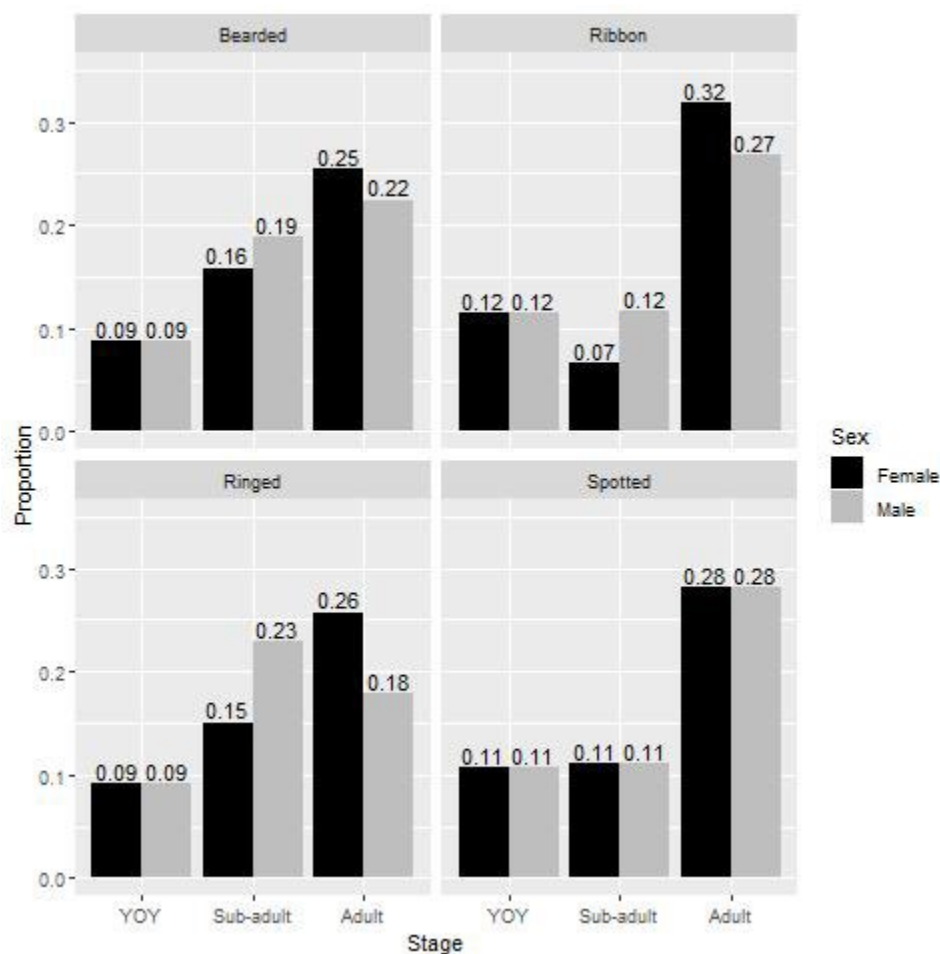
261 Hierarchical meta-analysis models for mortality produced estimates of annual survival for
262 bearded, ribbon, ringed, and spotted seals that increased with age before declining due to
263 senescence (Fig. 1a), as expected given the functional form employed (Trukhanova et al.,
264 2018). Reproductive and sexual maturity schedules differed substantially among species (Figs.
265 1b-1d), with ribbon seals maturing the earliest and bearded and ringed seals maturing the
266 slowest. These translate into very different expected stage proportions (Fig. 2). In particular,
267 ribbon seal populations should primarily be composed of adults owing to early maturation,
268 whereas bearded and ringed seals should have a much higher proportion of subadults.

269



270

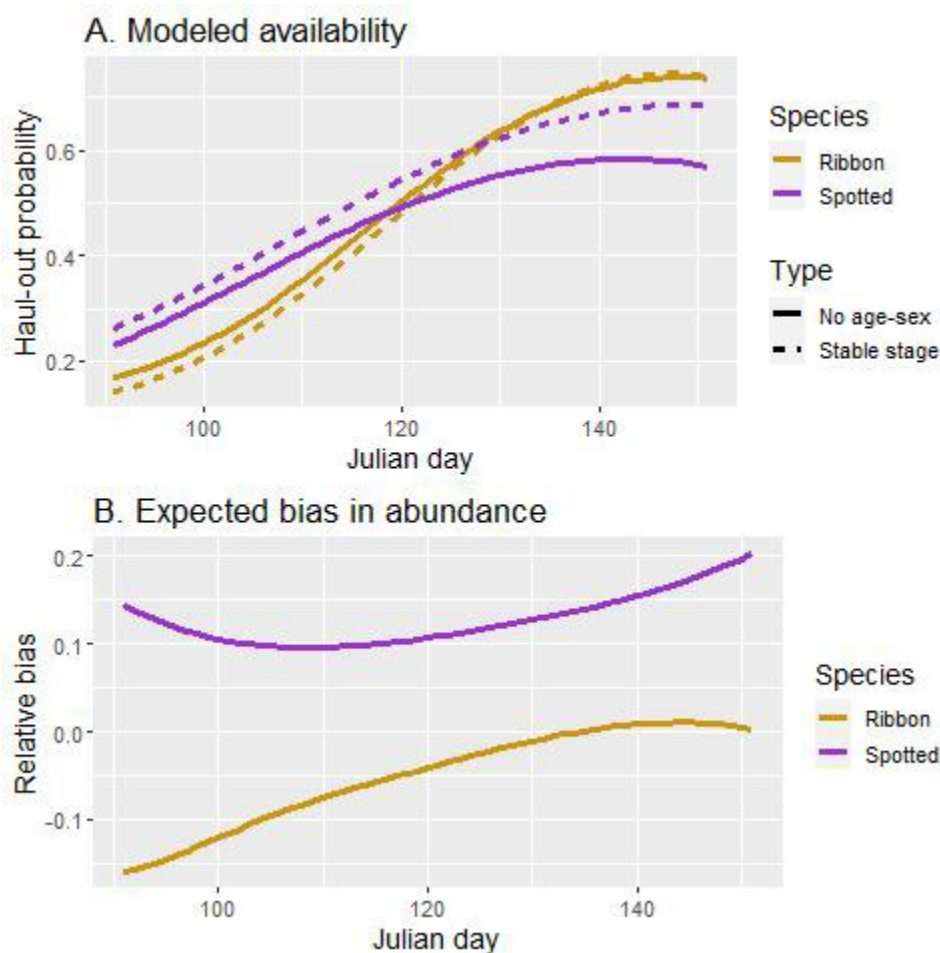
271 Figure 1. Annual survival probability, proportion of reproducing females, and proportion of
272 sexually mature seals as a function of age for four species of ice-associated phocids (bearded
273 seals: Bd; ringed seals: Rd; ribbon seals: Rn; and spotted seals: Sd). These estimates were
274 used in stable stage calculations.



275
276 Figure 2. Stable stage proportions estimated from matrix population models and age-specific
277 sexual maturity schedules for four phocid species. “YOY” stands for young-of-year.

278
279 3.2 Aerial survey correction factors for ribbon and spotted seals
280 Estimates of haul-out probabilities for spotted and ribbon seals differed depending on whether
281 age-sex class was ignored (treating the marked sample as representative of the population)
282 versus accounted for in predictions using stable stage weighting (Figure 3). In particular,

283 weighted predictions were almost always higher than model predictions ignoring age-sex class.
284 This is largely because samples of satellite tagged seals comprised higher proportions of
285 subadults than expected for the population based on stable stage proportions. For spotted
286 seals, 41% of non-pup telemetry observations were from subadults, whereas stable stage
287 proportions suggested that 28% of non-pups should be subadults. For ribbon seals, 32% of
288 non-pup records came from subadults compared to the 24% expected from stable stage
289 proportions. Depending on the day of the survey, omitting stable-stage weighting adjustments
290 could be expected to bias aerial survey abundance estimates of non-pups by -16 to 0% for
291 ribbon seals (mean -5%), and by 10-20% (mean 13%) for spotted seals (Figure 3).



292
293 Figure 3. Availability and expected bias in abundance for models that do and do not adjust for
294 age-sex effects. Panel (A) gives a comparison of predicted haul-out probabilities for subadult

295 and adult ribbon and spotted seals for models ignoring age-sex structure (solid lines) with
296 models that account for age-sex structure and adjust predicted haul-out behavior by stable age
297 proportions (dashed lines). Panel (B) summarizes the expected bias in abundance estimates
298 when age-aggregated availability estimates are used (assuming that the age- and sex-
299 adjustment model is true).

300

301 **4. Discussion**

302 In this paper, we showed that estimates of availability needed for aerial survey correction factors
303 can be biased when the age-sex composition of satellite tagged seals differs from the
304 population and when age-aggregated availability estimates are used. We also illustrate how
305 matrix population models and estimates of stable stage composition can be used to adjust
306 estimates to remove these biases. Use of matrix population models and stable stage
307 composition implicitly involves another set of assumptions – namely that life history schedules
308 are accurate and that there have not been any major perturbations to the system (e.g., wide
309 scale recruitment failures, extreme stochasticity in vital rates). Nevertheless, we believe stable
310 stage proportions obtained in this manner are an improvement over the raw age proportions
311 obtained via opportunistic sampling that might favor capture of the most vulnerable (and often
312 younger) individuals. When assumptions underlying matrix population models are in doubt,
313 researchers may want to conduct sensitivity analyses to investigate the effects of alternative
314 age- and sex-class proportions on resultant availability estimates.

315

316 Where possible, our stable stage estimates relied on reproductive schedules developed from
317 recent harvest collections (i.e., Alaska Dept. of Fish and Game, 2020; Quakenbush et al. 2020).
318 However, ribbon seal and bearded seal reproductive schedules (and ages of male sexual
319 maturity) relied on dated estimates from the Russian literature (i.e., Fedoseev, 1965; Fedoseev,
320 2000; Tikhamorov, 1966). Although these schedules work to illustrate our modeling approach,

321 they may need to be updated for specific locations and time periods where surveys are
322 conducted. For example, there is some indication that the age of ringed seal sexual maturity
323 may have decreased in the last several decades (Krafft et al., 2006; Quakenbush et al., 2020); it
324 would thus be useful to continue (and perhaps expand) sampling of Alaska Native subsistence
325 harvests in Alaska to update our analysis with more recent data. For ringed seals, there is also
326 some thought that mature, sexually reproducing seals preferentially select landfast ice in the
327 Chukchi Sea, and that immature seals preferentially select pack ice habitat in the Bering Sea
328 (Crawford et al., 2019; but see Kelly, in press). This raises an interesting question about habitat
329 partitioning. If younger individuals select different habitats than older individuals, and if haul-out
330 probabilities differ between the two groups, there is an argument that one should use an adult-
331 biased correction factor in one area, and an immature-biased correction factor in the other. To
332 make such regionally different availability predictions, researchers would need spatially explicit
333 information on population age-sex composition, which may be difficult to collect.

334
335 Our finding that age-sex variation in seal behavior can cause biases in population dynamics
336 parameters is not new. For instance, Härkönen et al. (1999) showed that skewed sampling of
337 age-sex classes can result in biased estimates of population growth, survival, and fecundity in
338 harbor seals. Similarly, Lonergan et al. (2013) illustrate how temporal variability in sex-ratios
339 (with different haul-out probabilities for each sex) might confound inference about abundance
340 and trend at a harbor seal haul-out site. When sample sizes allow, it thus seems prudent to
341 account for age- and sex-based variation in behavior when applying population corrections
342 based on biased samples of tagged seals. Our approach illustrates one possible approach for
343 doing so. In cases where sample sizes do not allow for robust characterization of age-sex
344 effects on availability, we advise increased caution when interpreting abundance estimates from
345 aerial surveys of marine mammals.

346

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354

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