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1 Reproductive Parameters of Bering-Chukchi-Beaufort Seas Bowhead Whales

2

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Abstract

Data from Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*), harvested during 1973-2021 by aboriginal subsistence hunters, were used to estimate reproductive parameters: length at sexual maturity (LSM), age at sexual maturity (ASM), pregnancy rate (PR), and calving interval. Sexual maturity (n=187 females) was determined from the presence/absence of corpora in the ovaries, or a fetus. Using sampling bias-corrected logistic regression, LSM was estimated at 13.5 m, 95% CI [13.0, 13.8]. There was a downward trend in LSM over time, statistically significant with one method but marginal with another. A growth model translated this estimate to an ASM estimate of 23.5 years, 95% CI [20.4, 26.7]. Pregnancy rate was determined from mature females (n=125), and from a subset limited to certain autumn-caught whales (n=37) to reduce bias. The PR was estimated at 0.46 globally, 95% CI [0.36, 0.55] and 0.38 for the autumn sample, 95% CI [0.20, 0.51]. Both estimated PRs are consistent with a 3-year calving interval, because the larger estimate includes two cohorts of pregnant whales harvested in spring, and bowhead whale gestation is longer than 12 months. These analyses represent the most conclusive empirical estimates of ASM, LSM, and PR for this bowhead whale stock from the largest available data sets to date.

KEYWORDS

age at sexual maturity, Arctic, birth interval, bowhead whale, calving interval, fetus, length at sexual maturity, pregnancy rate, productivity, reproduction

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Reproductive Parameters of Bering-Chukchi-Beaufort Seas Bowhead Whales

55

56 Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas stock (BCB bowhead whales)
57 were nearly eradicated by Yankee whalers hunting for commercial purposes from 1848-1914 (Bockstoce
58 & Burns, 1993). BCB bowhead whale abundance has subsequently increased substantially, with fourteen
59 reliable abundance estimates since 1978 suggesting that the population has tripled in recent decades (Givens
60 et al., 2016). These whales are still harvested in an aboriginal subsistence hunt by Alaska Natives in 11
61 communities (Suydam & George, 2021), continuing indigenous traditions ongoing for millennia. Many of
62 these harvested whales have been examined by biologists, allowing for the collection of additional extensive
63 biological data useful for studies, including estimating reproductive parameters such as date of conception,
64 length at sexual maturity, interbirth intervals, gross annual reproductive rates, and gestation period (Koski
65 et al., 1993; Reese et al., 2001; Tarpley et al., 2021).

66

67 Studying reproductive data provides insight into the population, its environment, and its management by
68 the International Whaling Commission (IWC). Collecting information on reproductive parameters also
69 facilitates monitoring of the potential impacts of environmental change and/or increasing population
70 density. With atmospheric and ocean warming resulting in a continuing and significant reduction in sea ice
71 duration, extent, and quality, the marine ecosystems of the Bering, Chukchi, and Beaufort Seas are
72 responding with ongoing, ecological transitions (e.g., Huntington et al., 2020). Potential effects to bowhead
73 whales may include changes in reproductive parameters, such as interbirth intervals or annual reproductive
74 rates. Meanwhile, the BCB bowhead whale population has been increasing at a rate of approximately 3.7%
75 per year (Givens et al., 2016). As the population approaches carrying capacity, especially in transitioning
76 ecosystems, we would predict that population parameters such as survival rates or reproductive rates will
77 decline following classic density dependence predictions (although warmer water and declining sea ice may
78 lead to increasing zooplankton abundance and feeding areas, and therefore increased bowhead whale

79 carrying capacity). In addition, pregnancy rate estimates from landed whales are useful in stock assessments
80 and for comparison with empirical estimates of calf production from aerial surveys (Angliss et al., 1995;
81 Clarke et al., 2022; Koski et al., 1993; 2004).

82
83 Accurate reproductive parameter estimates are necessary to determine sustainable subsistence harvest levels
84 for the whaling communities dependent on aboriginal subsistence whaling. In particular, reproductive
85 parameters have been central to the design and simulation testing of the statistical procedure (known as the
86 Bowhead Strike Limit Algorithm) used by the IWC to guide sustainable management of the subsistence
87 hunt (IWC, 2003). The IWC requires that the best available current data on reproduction be regularly
88 evaluated to consider whether this management procedure requires revision.

89
90 In Alaska, scientists and subsistence whalers have collaborated since 1972 to collect biological data from
91 harvested bowhead whales (Albert 2001; George et al., 2011; Suydam & George, 2021). The objectives of
92 this study are to use these data to update the estimated length at sexual maturity (LSM), age at sexual
93 maturity (ASM), pregnancy rate (PR), and calving intervals for BCB bowhead whales, using data sets that
94 are larger, newer, and more carefully screened, and (for LSM and ASM) using improved statistical methods.
95 While we understand that life history statistics are driven by ecological and demographic factors and can
96 change over time, these estimates are currently the most comprehensive empirical estimates to date for this
97 stock.

98

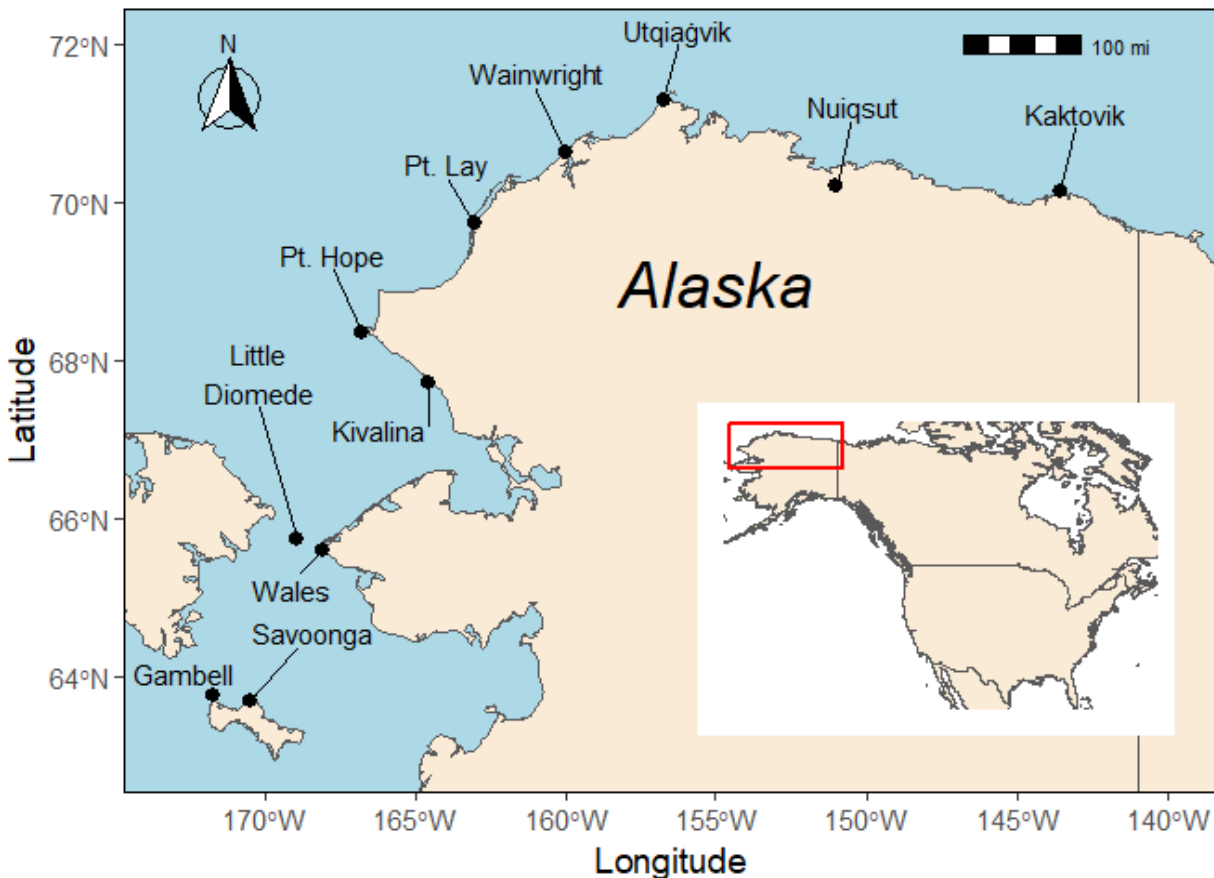
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Materials and Methods

100

101 BCB bowhead whales are mostly harvested in Alaska during two subsistence whaling seasons: spring
102 (roughly April to mid-June) and fall (roughly late August – October); a few whales are harvested at other
103 times, mainly near St. Lawrence Island (SLI) in early winter (Suydam and George, 2021). Harvested
104 bowhead whales were examined by biologists in several Alaskan communities, with the most frequent and
105 thorough examinations occurring in Utqiagvik (formerly Barrow), Kaktovik and, since 2005, Gambell and

106 Savoonga on SLI. Utqiagvik hunts in spring and fall, Kaktovik in fall, and the SLI communities in spring,
107 but in recent years more in late fall or early winter. The 11 whaling communities mentioned in this article
108 are mapped in Figure 1.



109

110 **Figure 1:** Map of Alaska Native bowhead whaling communities.

111

112

113 When examining a harvested bowhead whale, biologists routinely took standard cetacean morphometric
114 measurements (e.g., whale length from tip of rostrum to fluke notch, various girths, fluke, and pectoral fin
115 measurements) along with a large array of biological samples to support studies spanning anatomy,
116 genetics, diet, scar-injury frequency, diseases, reproduction, and other topics. Consistent collection of such
117 data began in 1972, although the quantity and nature of the data collected varied from year to year and from
118 whale to whale. Since 1982, harvest monitoring has been conducted by biologists working for, or
119 cooperatively with, the North Slope Borough Department of Wildlife Management (NSB DWM).

120 Information about sexual maturity and pregnancy was obtained from post hoc laboratory analysis where
 121 ovaries of harvested bowheads were examined for the presence of corpora lutea (CLs, the progesterone-
 122 secreting structure produced after ovulation and maintained through pregnancy), and corpora albicantia
 123 (CAs, scars from degenerated corpora lutea at the end of pregnancy). These structures indicate sexual
 124 maturity in mammals.

125

126 **Length at Sexual Maturity**

127

128 Biologists examined 187 harvested female bowhead whales to determine whether they were sexually
 129 mature. These data are referred to as the sexual maturity dataset (Table 1). To determine maturity, ovaries
 130 were fixed in 10% neutrally buffered formalin for at least 3 weeks, sequentially sliced into 0.5 cm sections,
 131 and visually inspected for the presence of a CL and/or CAs (George et al., 2011). Bowhead whales were
 132 scored as sexually mature if the ovaries showed the presence of a CL or CAs, or if the whale was carrying
 133 a fetus.

134

135 **Table 1:** Whaling community, season, and sexual maturity for 187 Bering-Chukchi-Beaufort Seas bowhead
 136 whales in the sexual maturity data set. The entries in each table cell are written as immature/mature. *
 137 indicates whaling community with spring hunt only; ** indicates a fall hunt only.

138

Community	Season	
	Fall	Spring
Utqiagvik	26/22	23/46
Gambell	0/1	1/8
Point Hope*	NA	4/3
Kaktovik**	7/9	NA
Nuiqsut**	0/4	NA
Savoonga	0/9	4/6
Wainwright*	NA	2/12

139

140

141 In order to estimate the LSM, the first step was to apply a logistic regression model (Hosmer et al., 2013)
 142 to the sexual maturity dataset (n=187). This model estimates the probability that a whale is sexually mature
 143 based on its body length, such that:

144
$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 BL$$

145 where \ln is the natural logarithm, p is the probability that a female bowhead whale with body length BL is
146 sexually mature, and β_0 and β_1 are parameters to be estimated. The second step for estimating LSM was to
147 note that, for a representative sample of whales, the parameter estimates from this model can be used to
148 estimate the length for which a randomly-sampled bowhead whale in the population has probability 0.5 of
149 being mature, or in other words, the length at which 50% of the bowhead whales are mature. Specifically,
150 using the parameter estimates $\hat{\beta}_0$ and $\hat{\beta}_1$, we can let $p = 0.5$ in the logistic regression equation and solve for
151 BL . Thus $LSM = -\hat{\beta}_0/\hat{\beta}_1$. This is analogous to the LD(50) in toxicology, where LD stands for “Lethal
152 Dose,” and LD(50) is the dose at which 50% of animals die (Parasuraman, 2011). In our case, the concept
153 of survival/death is replaced by immature/mature.

154
155 The data set used to fit this logistic regression model is probably not representative of the age distribution
156 in the population. The data are, effectively, the result of a retrospective case-control study: opportunistic
157 samples of mature and immature bowhead whales selected nonrandomly by the hunters (and hence
158 available for analysis by the biologists). We believe that sexually mature whales are overrepresented in our
159 data set compared to corresponding population frequencies. Reasons for this include an IWC prohibition
160 against hunting calves or whales swimming with calves, a tendency for biological examination to be
161 prioritized for pregnant (or potentially pregnant) animals, and perhaps hunter selectivity (some communities
162 prefer larger whales, and others prefer smaller, or they prefer to hunt at specific times, during which only a
163 portion of the age-segregated migration may be passing).

164
165 To adjust for any nonrepresentative sampling, we redefined LSM, using a method that works regardless of
166 whether sexually mature whales are actually over- or under-represented. In a sample of bowhead whales
167 with an equal number of mature and immature animals, LSM equals the BL for which a random whale from
168 this hypothetical set has a probability $\tau=0.5$ of being mature. We defined \bar{M} as the proportion of whales

169 that were mature in our sample of 120 mature and 67 immature whales, i.e., $\bar{M} = 0.642$. We then derived
170 an adjusted estimated intercept, namely $\hat{\beta}_{0,\tau} = \hat{\beta}_0 - \ln \left\{ \frac{1-\tau}{\tau} \frac{\bar{M}}{1-\bar{M}} \right\}$ (King and Zeng, 2001; Prentice and
171 Pyke, 1979), which effectively adjusted the response curve to account for the imbalanced sample. The
172 corresponding adjusted LSM estimate was $\text{LSM} = -\hat{\beta}_{0,\tau} / \hat{\beta}_1$.

173
174 We calculated a bootstrap confidence interval for LSM using the bootstrap BCa approach (Efron, 1987) as
175 implemented in the `boot` library in R (Canty and Ripley, 2021; R Core Team, 2019). Whales were
176 randomly sampled, with replacement, to obtain 10,000 bootstrap data sets. This method can be replicated
177 for alternate values of τ , for example to determine the length at which 95% of whales are mature by setting
178 $\tau=0.95$. Our results include ASM estimates based on $\tau=0.05$ and $\tau=0.95$, to assess the range of ages at which
179 bowhead whales can mature.

180
181 We used two analyses to assess whether LSM changed over time. In the first analysis, we fit a logistic
182 regression with bowhead whale maturity as the response variable, and predictors of *BL* and year. This
183 approach controls for variation in *BL* (from potential trends in harvest selection) when estimating the effect
184 of year. However, the approach only accounts for a logit-linear trend in LSM and would be more reliable
185 if years were sampled with similar frequency. Moreover, the response variable for this analysis is maturity,
186 not length at maturity. To address these issues, we conducted a second analysis, where we split the data set
187 into quarters (1976-1990, n=47; 1991-2002, n=47; 2003-2012, n=46; 2013-2019, n=47). For each block of
188 years, we estimated LSM using the above methods. We then created a data set with the four LSM estimates,
189 the midpoint of the year blocks, and inverse variance weights (where variance was estimated via the
190 bootstrap, as described above). To these data, we fitted a weighted linear regression of LSM on year to
191 estimate the slope. To estimate the uncertainty in this estimated slope, we applied a nested bootstrap
192 approach by repeating this procedure 100,000 times on quartets of bootstrap samples from each block. A
193 bootstrap 95% confidence interval was then computed using the percentile method (e.g., Givens and

194 Hoeting, 2013). This nested approach requires four lengthy bootstraps within each iteration of the main
195 bootstrap. We used the `foreach` (Wallig et al., 2020a) and `doParallel` (Wallig et al., 2020b) packages
196 in R to make this analysis computationally feasible.

197

198 **Age at Sexual Maturity**

199

200 Wetzel et al. (2017) estimated sex-specific von Bertalanffy II (1938) growth curves for bowhead whales,
201 using a sample of 238 whales landed between 1978 and 2012, and aged by a variety of methods. Further
202 details of the model selection and fitting are given by Lubetkin et al. (2012). We used this fitted model
203 (Wetzel et al., 2017) to translate estimated LSM values to estimated age of sexual maturity (ASM). The
204 LSM corresponding to 5%, 50%, and 95% probability of sexual maturity were estimated using the methods
205 above. From these, corresponding ASMs were derived. Uncertainty was assessed using a nested bootstrap
206 approach that accounted for uncertainty both in the estimated growth curves and the estimated LSMs.
207 Bootstrap confidence intervals were derived using the percentile method (e.g., Givens & Hoeting, 2013).

208

209 **Pregnancy Rate**

210

211 The pregnancy rate analysis was based on data collected from 806 bowhead whales landed during 1972-
212 2021. Gestation in bowhead whales is about 13-14 months with pregnancy occurring in winter (Koski et
213 al., 1993; Nerini et al., 1984; Reese et al., 2001; Tarpley et al., 2021). Therefore, pregnant whales landed
214 in spring may have large term fetuses (e.g., 4-5 m) or very small (e.g., 4 cm) newly implanted fetuses.

215

216 Determining the pregnancy status of a bowhead whale can be difficult as it is affected by: (1) season, i.e.,
217 whether the female is in early or late gestation, (2) the size of the whale, and (3) logistical field conditions
218 during flensing, butchering, and examination. Full and mid-term fetuses are readily conspicuous during the
219 butchering process. Early pregnancies require careful and complete examination of the reproductive tract.

220 If an ovary has a very large (>15 cm diameter) CL, the whale is likely pregnant, or had been recently, even
221 if a fetus is not readily visible. In such cases, careful palpation and subsequent dissection of both uterine
222 horns (which can reach 1.6 m in length) has revealed embryos as small as 4 cm in length.

223
224 To reduce bias incurred when small fetuses were not identified in the field examinations and/or whales
225 were not examined by biologists specializing or experienced in the dissection of reproductive tracts to
226 determine pregnancy status, we retrospectively re-examined all harvest sampling data sheets and created a
227 new variable in the data set indicating whether the whale had been examined by a biologist specifically
228 trained in examining the uterus to detect early term pregnancies via large CLs and other clues such as body
229 condition and pinkish blubber. To assess whether a whale qualified as “examined-by-trained-biologist”, we
230 focused on three sources of information: the examiner and their respective expertise; whether or not the
231 organs were sampled; and the examiner’s notes.

232
233 Of the 806 records in the raw field data set, only 472 bowhead whales that had been examined for pregnancy
234 status (i.e., an active search for pregnancy, including small fetuses, as described above) by a trained
235 biologist were used in the pregnancy rate analysis. Among these, we identified sexually mature whales by
236 cross-referencing the definitive sexual maturity data set (n=187) described above. Whales not included in
237 the latter data set were considered mature if they were pregnant (presence of a fetus), or if their length
238 exceeded LSM (as estimated above).

239
240 Two estimates of PR were made. Both estimates were computed as the proportion of mature whales that
241 were pregnant, but the estimates differed in determining which whales were mature in cases where the LSM
242 criterion was applied due to the lack of a definitive biological examination of the reproductive tracts and
243 ovaries. The time-variant approach for PR estimation applied four different values for LSM for whales
244 landed in different year blocks to determine maturity, in order to account for any time trend in LSM (above,
245 and Fig. 2). The time-invariant approach for PR estimation used a single LSM value encompassing the

246 entire period of collection (1972-2019). There were 125 whales classified as mature using the first method
 247 and 129 using the second method; see Table 2. (Note that each maturity dataset includes some whales whose
 248 maturity was determined on the basis of LSM, and because the time variant and time invariant approaches
 249 include different LSM criteria for that determination, the numbers of mature whales differ in the two
 250 datasets.) Confidence intervals for PR were estimated using a nested bootstrap. First, a value(s) for LSM
 251 was/were selected at random from the bootstrap distribution(s) obtained in the previous section. Next, a
 252 bootstrap data set was generated by resampling with replacement from the original data set. Then a
 253 bootstrap data set of mature animals was obtained by determining maturity using the criteria given above
 254 and the new LSM value(s). Finally, a bootstrap PR value was calculated from this data set. The percentile
 255 method confidence interval was computed from these bootstrap PR values.

256

257 To assess how much uncertainty in PR was due to uncertainty in LSM, we repeated the bootstrap using a
 258 fixed value of LSM = 13.5 m (from Results), and we also computed a simple normal approximation
 259 confidence interval for a binomial proportion.

260

261 **Table 2:** Pregnancy status for Bering-Chukchi-Beaufort Seas bowhead whales determined to be sexually
 262 mature based on CA in ovaries, presence of a fetus, or exceeding length at sexual maturity (LSM). The
 263 entries in each table cell are written as pregnant/not pregnant. Results presented used a time-variant criterion
 264 for LSM, resulting in 125 mature whales; the use of a time-invariant LSM criterion resulted in the following
 265 changes: Utqiagvik, Fall, 9/20; Savoonga, Spring, 2/3 and a total of 129 mature whales. *indicates whaling
 266 community with spring hunt only; ** indicates a fall hunt only.

267

Community	Season	
	Fall	Spring
Utqiagvik	9/17	26/32
Gambell	NA	4/4
Point Hope*	NA	1/0
Kaktovik**	3/6	NA
Nuiqsut**	2/0	NA
Savoonga	6/1	2/2
Wainwright*	NA	5/5

268

269

270 We used logistic regression and generalized additive models to investigate any potential time trend in PR.
271 We also plotted the empirical autocorrelation function for annual PR to determine whether there are periodic
272 cycles of high/low pregnancy years.

273
274 Estimating PR from landed bowhead whales has several challenges with associated assumptions and biases,
275 including: (i) early pregnancies going undetected, (ii) animals becoming pregnant after the spring field
276 season, (iii) animals giving birth shortly before the spring harvest, (iv) determining if a female is mature,
277 (v) accounting for mature females that were not harvested, because they were accompanied by a calf, as
278 required by IWC regulations, (vi) different behavior patterns of pregnant animals compared with other
279 whales (e.g., remaining on the surface longer, thereby being more susceptible to hunting), (vii) other issues
280 related to hunter selectivity or whale availability, and (viii) possible differences in PR with whale size and
281 age. Our use of the retrospective examined-by-trained-biologist filter directly addresses only the first
282 challenge listed above.

283
284 Some of these biases can be further diminished if only landed whales from the fall season are included.
285 During fall, fetus length ranged from 1.2 to 2 m, which can be readily detected during the butchering
286 process. Furthermore, during fall, there is only one cohort of pregnant females, whereas in spring there are
287 two: early pregnancy and term pregnancy (some of which may have already given birth before harvest).
288 Another source of bias can be reduced if we eliminate six whales landed during fall near Savoonga (on
289 SLI), five of which were pregnant. We suspect that the region north of SLI, where whaling crews from
290 Savoonga traditionally hunt in the fall, is disproportionately frequented by mature pregnant females at that
291 time. Yankee whalers called the region north of SLI in the Bering Strait region and the Chukotka coast the
292 “cow yard” based on the extremely large female whales harvested there: “Cow Yard. Chukchi Sea; an area
293 near Cape Serdtse Kamen, Siberia, where large cow whales were taken, in 1848 and 1849.” (Bockstoce and
294 Batchelder, 1978). In recent years, bowhead whales harvested near Savoonga and Gambell by SLI hunters

295 have frequently been larger than bowhead whales taken by other whaling communities. For these reasons,
296 the SLI fall harvest data should be used cautiously when calculating PR.

297

298 To reduce some of these concerns, we computed the same estimates of PR described above, but using the
299 smaller data set that excludes spring season whales, which belong to two different pregnancy cohorts (early
300 and term), and the six whales harvested during fall near SLI. Limiting the analysis to the remaining fall
301 whales reduces a major bias of missing early pregnancies, but presents its own problems. First, the sample
302 size is greatly reduced ($n=37$). Second, it is unclear whether there may be some population segregation at
303 these times and places, as there is in spring (Moore and Reeves, 1993). For example, differences in habitat
304 use based on size of bowhead whales have been observed in the central Beaufort Sea during late summer
305 and fall (Koski & Miller, 2009). Also, many of the potential biases listed above may remain in this
306 subsample.

307

308 **Results**

309 **Length at Sexual Maturity**

310

311 Of the 187 bowhead whales examined for presence of CA or CL and/or presence of a fetus, 120 were
312 sexually mature. Of these, conclusive evidence of a fetus was found in 66 cases. The left panel of Fig. 2
313 shows the LSM for these 187 whales, which have been jittered for clarity. For estimating LSM, we obtained
314 (uncorrected) logistic regression parameter estimates of $\hat{\beta}_0 = -23.23$ and $\hat{\beta}_1 = 1.77$. The uncorrected LSM
315 was 13.1 m, and applying the correction for sampling bias yielded a final LSM estimate of 13.5 m, 95% CI
316 [13.0, 13.8] (Figure 2 left panel).

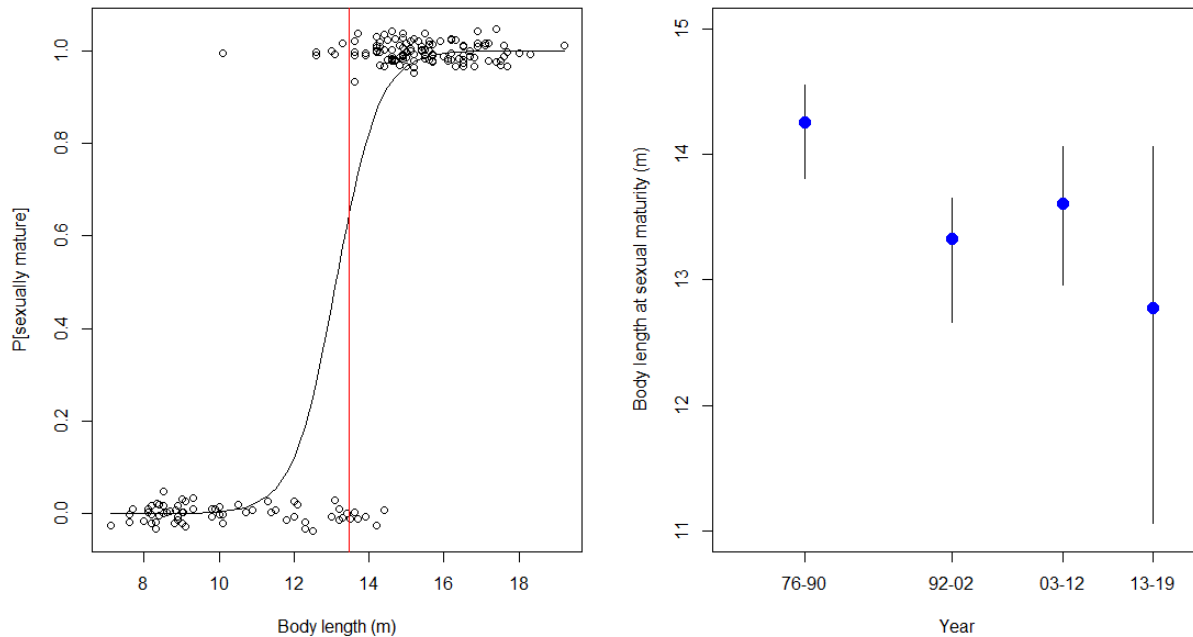
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Figure 2: The left panel shows length at sexual maturity (LSM) data for female bowhead whales, and (corrected) logistic regression fit, with the red vertical line indicating the estimated LSM. The points have been jittered for clarity. The right panel shows year block LSM estimates and corresponding bootstrap confidence intervals. The four LSM estimates (95% confidence intervals) are 14.3 m (13.8, 14.6), 13.3 m (12.6, 13.7), 13.6 m (12.9, 14.1), and 12.8 m (11.0, 14.1) from left to right.

330 Both analyses of time variation in sexual maturity indicated that females are maturing at shorter lengths in
 331 recent years. The logistic regression controlling for *BL*, while estimating a time trend in maturity, yielded
 332 a significant year coefficient (0.065, SE=0.031, $p=0.038$), indicating an increasing probability (over time)
 333 that a female is mature, even after controlling for length. The nested bootstrap approach to estimate the
 334 trend in LSM over time found a regression coefficient of -0.034 (bootstrap 95% confidence interval:
 335 $(-0.10, 0.00)$; a 94.86% symmetric two-sided confidence interval would be entirely negative). Thus, there
 336 is a noteworthy reduction in LSM over time, but not quite as significant as found by the first method. Further
 337 sampling is recommended to see whether this signal strengthens with more years of data. The right panel
 338 of Fig. 2 shows the year block estimates of LSM, with vertical lines indicating bootstrap confidence

339 intervals. The downward trend is evidently due to higher LSM several decades ago and lower LSM in the
340 most recent years.

341

342 **Age at Sexual Maturity**

343

344 Translating LSM to ASM using the fitted growth curve (Wetzel et al., 2017) yielded an estimated ASM of
345 23.5 years, 95% CI [20.4, 26.7]. Similar estimates for the age at which 5% and 95% of bowhead whales are
346 mature were, respectively: LSM = 11.8 m, ASM = 14.8 years, 95% CI [10.3, 20.1]; and LSM = 15.1 m,
347 ASM = 37.8 years, 95% CI [30.1, 47.3].

348

349 **Pregnancy rate and calving interval**

350

351 Using the time-variant approach accounting for the time trend in LSM, and data from all seasons, 58 of 125
352 mature female bowhead whales were pregnant, yielding a PR estimate of 0.46, 95% CI [0.32, 0.51]. For the
353 time-invariant approach with a common LSM for all females in all seasons, 58 of 129 mature females were
354 pregnant, yielding a PR estimate of 0.45, 95% CI [0.36, 0.54].

355

356 Assessing how much uncertainty in PR is due to uncertainty in LSM, we focused on the PR estimate based
357 on time-invariant LSM, so that sources of uncertainty can be isolated more effectively. The analysis using
358 constant LSM = 13.5 m (rather than bootstrap samples from the time-invariant LSM model) and the
359 binomial proportion normal approximation both yielded 95% confidence intervals of [0.36, 0.54] indicating
360 that uncertainty about LSM contributed very little uncertainty to estimates of PR. This is because most
361 females in the data set had maturity determined by a biologist or had a length not near LSM. Maturity status
362 changed for only a few whales when LSM changed.

363

364 We found no statistically significant evidence for a time trend in PR in any model we investigated. The
365 empirical autocorrelation function did not indicate any periodic patterns of low/high pregnancy rates over
366 the years, although the statistical power for this analysis is low.

367
368 As noted above, some potential biases can be reduced by further filtering the data set. Our bias reduction
369 subsample included only fall-harvested bowhead whales that were examined by a trained biologist, and
370 excluded whales harvested near SLI. Using this data set and the time-variant LSM yielded a $PR = 14/37 =$
371 0.38 , 95% CI [0.20, 0.51]. This PR is not directly comparable to the aforementioned estimate because it is
372 counting only one pregnancy cohort, whereas the prior estimate includes two pregnancy cohorts in spring.

373
374 A rough estimate of the calving interval can be derived by inverting the estimate and CI for PR from the
375 bias-reduced fall-only data set (spring should not be used due to the two pregnancy cohorts occurring then,
376 and the fact that some term fetuses of the year could have been born before sampling occurred). The
377 corresponding PR estimate yielded an estimated calving interval of 2.6 years, 95% CI [1.9, 5.0].

378

379

Discussion

380

381 Our analyses provide new estimates of LSM, ASM, and PR in BCB bowhead whales, using more data and
382 some improved methods, compared to previous work. We have also, for the first time, detected a significant
383 temporal trend in LSM.

384

Length and age at sexual maturity

385

386
387 Our data suggest a large range in length at the initiation of sexual maturity for female bowhead whales. Our
388 estimated LSM of 13.5 m, 95% CI [13.0, 13.8], corresponds to a 50% probability of maturity. The estimated
389 length for which a whale has a 95% chance of being mature is 15.1 m, 95% CI [14.6, 16.1]. The degree of

390 statistical uncertainty here exceeds biological uncertainty: a 15 m whale is certainly mature, especially as
391 the longest immature female in our data set was 14.4 m. The smallest known mature females included two
392 12.6 m pregnant females with a single CL and no CAs observed (indicating it was a first ovulation), and an
393 unusual nonpregnant whale at 10.1 m with no CL and one CA detected. We do not currently understand
394 how the latter whale produced a CA given her short body length unless she was a case of proportionate
395 dwarfism (e.g., Boegheim et al., 2017) or alternatively a diminutive form of a bowhead whale. Best (1985)
396 has reported on the rare occurrence of a diminutive form for Antarctic minke whales (*Balaenoptera*
397 *bonaerensis*).

398

399 Our approach for creation of the sexual maturity dataset relied solely on direct evidence of reproductive
400 capacity. In principle, female sexual maturity could also be evaluated from ovary weight. Tarpley and
401 Hillman (1999) estimated a relationship between ovary weight, body length, and maturity: bowhead
402 whales with an ovary weight exceeding about 3 kg and/or an ovary length over about 30 cm were more
403 likely to be mature (Tarpley et al., 2021). However, the authors cautioned against such metrics as the sole
404 criterion to determine maturity in female bowhead whales, as they found some overlap between the ovary
405 weight of mature and immature whales. We agreed with their caution and therefore relied only on direct
406 observation of a CL, CAs, and/or a fetus, as explained in the Methods.

407

408 Regarding the LSM trend analysis, one might note that the confidence bar for 2013-2019 in Figure 2 is a
409 bit more than double the length as for the other year blocks and ask how this might have influenced our
410 results. First, we note that such a difference in standard deviations is moderate, compared to the radical
411 heteroskedasticity that may complicate some analyses. Indeed, we believe that traditional statistical models
412 requiring variance homogeneity in that respect would be robust to the moderate inconsistency seen here.
413 Fortunately, concern about the degree of heteroskedasticity or the potential statistical robustness of our
414 methods is not warranted here. Specifically, the heterogeneity in variance apparent in Figure 2 is not
415 relevant for the first method we used to assess significance, as traditional logistic regression is based on the

416 binary sexual maturity dataset, a binomial model, and its inherent variance structure, not the block estimates
417 and error bars in Figure 2. The second method (the nested bootstrap), which we prefer, is very well suited
418 to handle heterogeneous variances, as it makes no assumptions about variance structure and directly
419 ‘models’ the heterogeneity between blocks via its resampling structure. We also note that the bootstrapped
420 regression is inverse-variance weighted, so the relative uncertainty in each year bin is accounted for during
421 the estimation.

422

423 Our 95% CI for female bowhead whale LSM is reasonably consistent with the LSM ranges (12.0 m – 14.2
424 m) given in past analyses for BCB bowhead whales (George et al., 2011; Koski et al., 1993). However, our
425 estimate is for landed whales, which may have stretched to some degree during the towing and hauling onto
426 the ice or beach, and because length is measured while the whale is lying in an unnatural position on its
427 back (dorsal surface) for flensing. Applying an empirical, but unpublished, bowhead ‘stretching adjustment’
428 considered by the IWC reduces our estimate of LSM by about 8% to 12.4 m. This is roughly the length of
429 some of the shortest mature females in the landed whale data set and near the low end of lengths observed
430 for the smallest mother-calf pairs (12.2 m) from photogrammetric data (Koski et al., 1993), which can also
431 be subject to some biases (Bierlich et al., 2021). While whales likely stretch somewhat, the stretching
432 adjustment is based on only three measurements of bowhead whales assessed in and out of water and should
433 be applied cautiously.

434

435 We do not have a singular explanation for the downward trend in LSM over time (Fig. 2). Changes in life
436 history traits, namely decreasing ASM (but not body length), have been well documented in several
437 northern and southern baleen whale stocks during the period of heavy exploitation. Proposed underlying
438 key mechanisms in those cases include relaxation of intra- and interspecific competition due to drastic
439 population size decline (commercial catch mortality), and accelerated growth rates of young animals with
440 subsequent earlier maturation (Fujise et al., 2005; Ohsumi, 1986). Since 1990, and particularly since 2010,
441 changing sea ice conditions have likely resulted in improved food availability (George et al. 2015; Moore

442 2016). A reduction in LSM associated with better feeding conditions is a classic density-dependent response
443 in many vertebrates. The time period of our LSM study encompasses many high-density sea ice years in
444 the past (1976-1990), with low ice years increasingly predominant more recently, and particularly since
445 2010. It is reasonable to speculate that the increased access, duration, and productivity of feeding areas (in
446 recent decades) associated with sea ice retreat (Frey et al., 2021; Moore, 2016) may explain why females
447 are mature at shorter body lengths. We cannot directly infer that the age at sexual maturity has decreased
448 accordingly, although this has been documented in other baleen whale stocks (Tulloch et al., 2019).

449

450 Alternatively, a downward trend in LSM may occur if whales reach sexual maturity at a consistent age but
451 are growing more slowly in recent years, thereby being smaller at the age they mature. We have no direct
452 data to support this alternative for bowhead whales, but decreased body length has been noted in North
453 Atlantic right whales (*Eubalaena glacialis*), for which the cumulative impacts from anthropogenic activities
454 (bycatch; noise pollution; vessel traffic) to shifting prey fields are all thought to be contributing factors
455 (Stewart et al., 2022). Future study of this alternative hypothesis is needed. Lastly, we cannot exclude the
456 possibility that historical commercial whaling of BCB bowhead whales induced evolutionary (genetic)
457 changes by selecting against certain life history traits (e.g., Kuparinen & Festa-Bianchet, 2017; Sharpe &
458 Hendry, 2009), although the fact that commercial whaling for BCB bowhead whales ended over 100 years
459 ago makes this hypothesis about the recent observed change less likely.

460

461 Table 3 presents sexual maturity estimates for the bowhead whales' "sister taxa", the right whales (Family
462 Balaenidae). These species generally attain sexual maturity at a body length of about 12.5 m, with the
463 possible exception of North Pacific right whales (*Eubalena japonica*), whose length at sexual maturity
464 appears longer, although data from Omura et al. (1969) were limited. LSM for BCB bowhead whales
465 appears to be in the middle of the range estimated for these other species of right whale. When comparing
466 the estimates in Table 3, note that our determination of maturity is based on evidence of a past ovulation,
467 whereas for other right whale populations, LSM is often determined on the basis of calf presence. It could

468 be argued that the estimates are incomparable, due to growth between ovulation and birth. However, Koski
 469 et al. (1992) estimated the growth of bowhead whales with a body length of 12 m of approximately 0.15
 470 m/year, 0.1 m/year for 13 m whales, and less than 0.1 m/year at longer lengths. As such, differences in how
 471 maturity is detected (i.e., based upon the physical examination of harvested whales versus the detection of
 472 a calf) are not enough to explain the variation seen in Table 3.

473

474 **Table 3:** Estimates of length (m) and age (years) at sexual maturity for the right whales (Family:
 475 Balaenidae).

476

Species	Age at Sexual Maturity (years)	Length at Sexual Maturity (m)	Reference
North Atlantic Right Whale	10.1	12.5	Christiansen et al., 2020; Kraus et al., 2007
Bowhead Whale	23.5 95% CI [20.4, 26.7]	13.5 95% CI [13.0, 13.8]	This study
Southern Right Whale	median 7.9 95% CI [7.1, 9.3]	12.5	Best et al., 2001
North Pacific Right Whale	12	15-16	Omura et al., 1969

477

478

479 Our estimate of female bowhead whale ASM was 23.5 years; this is based on the assumption that the age-
 480 length relationship has not changed over time. An analysis to check that assumption is beyond the scope of
 481 this paper, and potentially limited by the range of harvest dates in the BCB bowhead whale age data set
 482 (Wetzel et al., 2017). Previous analysis by Rosa et al. (2013), based on aspartic acid racemization (ARR),
 483 estimated that female ASM was 25.9 years (SE=5.9). Their estimate has a somewhat larger standard error
 484 due to high CVs in the AAR technique for subadult whales. The bowhead whale growth curves derived by
 485 Wetzel et al. (2017) and the LSM analysis in our study are the most careful, comprehensive estimates
 486 available, using the largest available data sets for this species. Therefore, while we propose the female
 487 bowhead whale ASM estimates herein as the most reliable empirical estimates to date, we note that these
 488 ASM estimates arguably should apply to the 1995-2010 period when the bulk of the age data were collected.
 489 It would be interesting to link estimates of ASM and PR to estimates of the BCB bowhead whale population

490 age distribution, but data and models for the latter are limited and such analyses are a matter for future
491 research.

492

493 The estimated ASM for 50% and 95% probability of female bowhead whale sexual maturity (23.5 and 37.8
494 years, respectively) is high, but should be considered in the context of the bowhead whale lifespan. Wetzel
495 et al. (2017) used AAR of bowhead whale lens nuclei to conclude that some bowhead whale lifespans may
496 extend nearly 200 years or beyond. This is consistent with the bowhead whale ages estimated by George et
497 al. (1999), with the fact that late ASM is highly correlated with prolonged longevity in mammals, and with
498 the recoveries of dated, historical weapon fragments in landed whales (George & Bockstoce, 2008). For
499 comparison, the North Atlantic right whale has an estimated ASM of 10.1 (Table 3) with an estimated
500 lifespan of 70 years (Hamilton et al., 1998).

501

502 Our estimated ASM is also consistent with observations that the bowhead whale is a slowly growing species
503 with a correspondingly low metabolic rate that likely contributes to their high ASM compared with other
504 mysticetes (George, 2009; Tarpley et al., 2021). The mean ASM for right whales ranges from about 7 to 10
505 years, which is estimated using longitudinal photo-recapture and determined when a female is first seen
506 with a calf. For example, for North Atlantic right whales, Kraus et al. (2007) reported a mean age of first
507 calving of 10.1 years (individual range 5 to 21). For southern right whales, Best et al. (2001) estimated the
508 median age of first parturition at 7.9 years, 95% CI [7.1, 9.3]. The age at sexual maturity estimates for right
509 whales are less than half those for bowhead whales (Table 3). As noted earlier, slow growth and late
510 reproduction for bowhead whales is well established in the literature and speculations in several papers
511 (Burns et al., 1993; George et al., 1999; 2021) suggest it is related to their low metabolic rates, diverting
512 significant resources to energy storage in the blubber and highly variable, often low-density prey
513 availability at high latitudes (George et al., 2021). We attribute the late age at sexual maturity in bowheads,
514 as compared with other Balaenids, to their slow growth rather than simply being “short for their age”.
515 Maximum lengths for bowheads are similar to or larger than those of other Balaenids (George, 2009).

516

517 **Pregnancy rate and calving interval**

518

519 Our PR estimates suggest that the BCB bowhead whale population is more fecund than its slow life history
520 might otherwise suggest, particularly for a large extremely long-lived balaenid (Kraus & Rolland, 2007).
521 Moreover, our estimated PR for all seasons (0.46) is considerably higher than other estimates for BCB
522 bowhead whales. This is because we made no adjustment to account for the difference between an early
523 fetus and a term fetus in spring, and classified all whales with any sized fetus as pregnant. Tarpley et al.
524 (2016) and Tarpley and Hillmann (1999) estimated pregnancy rates ranging from 0.22 to 0.43 depending
525 on the data set used. In addition, their smallest mature female was 14.2 m (using data through 1992), and
526 their pregnancy rate estimates might be inflated as smaller whales were not included. George et al. (2011)
527 estimated PR = 0.33 for fall whales only; our fall-only PR estimate of 0.38, 95% CI [0.20, 0.51] is consistent
528 with theirs.

529

530 Our modeling of the limited annual data found no clear evidence of a time trend in PR despite substantial
531 demographic change. The estimated 2011 abundance of BCB bowhead whales is 16,820 individuals (95%
532 CI 15,176 to 18,643) (Givens et al., 2016), which is about 3.5 times larger than the 1978 estimate by Zeh
533 and Punt (2005) and may now match or exceed the historical carrying capacity level hypothesized by
534 Brandon and Wade (2006). If the stock is approaching current carrying capacity, then one might expect PR
535 to decrease. However, interpreting vital rates with respect to carrying capacity warrants caution given that
536 it is likely that carrying capacity is not constant (Del Monte-Luna et al. 2004), particularly within a complex
537 and rapidly changing Pacific Arctic (George et al., 2015; Givens et al., 2016) with numerous ecological
538 interactions involved in establishing population trends (Price, 1999; Vucetich and Peterson, 2004).

539

540 Calving intervals are of particular interest biologically, with implications for potential recovery rates of the
541 BCB bowhead whale population and management applications. A large body of information on bowhead

542 whale reproduction shows no evidence of calving intervals of less than 3 years (e.g., Koski et al., 1993;
543 Rugh et al., 1992; Tarpley et al., 2021). Considerable evidence from past studies suggests BCB bowhead
544 whales reproduce on a 3- to 4-year calving interval. Miller et al. (1992) estimated interbirth intervals using
545 photographic data, where they noted 2 photographic recaptures at 4 years and 3 recaptures at 7 years for
546 mothers with young calves. Their data are open to a number of interpretations, because these mothers were
547 not seen every year, and their estimates of interbirth intervals ranged from 3.3 to 5.8 years, with 3.3 to 4.5
548 years as the most likely range. Miller et al. (1992) did not find any 3-year intervals, but considered them
549 likely. These authors as well as Rugh et al. (1992) suggested that the 7-year intervals could be real or could
550 represent a combination of 3- and 4-year intervals. Using another method based on the frequency of
551 bowhead whale females with calves in their photographic sample, Miller et al. (1992) estimated a calving
552 interval of 3.3 years. George et al. (2011) examined a sample of mature females using presence of a CL,
553 CA, and/or fetus, and estimated an ovulation rate value of 0.332 per year and a PR of 0.326 per year,
554 implying intervals between ovulations and pregnancies of 3.0 and 3.1 years. Rolland et al. (2018) analyzed
555 progesterone spikes in the baleen plates of 3 large mature females, as well as annual cycles in the stable
556 carbon isotopes to estimate time intervals between hormone spikes (Schell & Saupe, 1993). Using this
557 approach, one of their analyses yielded estimated calving intervals (n=11) ranging from 2.10 to 5.31 with
558 a mean of 3.11 years (Tarpley et al., 2021). Analysis of baleen hormone cycles is perhaps the most
559 promising direct technique to investigate reproductive history in bowhead whales and other baleen whales
560 (e.g., Hunt et al., 2014, 2016, 2017; Lowe et al., 2021). Other evidence, such as the current rate of population
561 increase (Givens et al., 2016), percent calves in surveys (Clarke et al., 2022; Koski et al., 2006), the current
562 harvest rate, and survival rate (da Silva et al., 2007; Schweder et al., 2010; Zeh et al., 2002), all suggest that
563 a 3-year interval is the most plausible.

564

565 Our relatively high PR estimates can be reconciled with the available evidence about calving intervals. We
566 have not observed a case of a lactating pregnant bowhead whale in fall, which would suggest the possibility
567 of a 2-year calving interval, although ovulation and pregnancy during lactation has been observed in other

568 baleen whales (Kraus & Rolland, 2007; Lockyer, 1987) and various dolphins (West et al., 2007).
569 Hypothetically, if the true interbirth interval is 3 years, pregnancy status is detected without error, hunting
570 in each season is not biased with respect to pregnancy status, and no whale gives birth before being landed
571 in the spring, then we would expect a third of fall whales to be pregnant, and two-thirds of spring whales.
572 Consequently, using the spring/fall harvest proportions from our data set (81 of 125 samples from spring
573 equals 64.8%), the expected PR using our approach would be $(0.648)(2/3)+(0.352)(1/3) = 0.55$. Thus, our
574 estimated PR of 0.46 for all seasons is not inconsistent with a 3-year interbirth interval, and the fact that
575 our estimate is less than 0.55 is likely partly because some term fetuses are born prior to harvest in the
576 spring, and some calving intervals are likely longer than 3 years. The estimate (PR = 0.38, 95% CI [0.20,
577 0.51]) from our fall bias reduction subsample also supports a 3-year calving interval, as both the point
578 estimate and interval are consistent with a PR of 0.33, while simultaneously avoiding the confounding effect
579 of two pregnancy cohorts. Northern Atlantic right whales, a close relative of bowhead whales, show high
580 variation in calving intervals likely associated with nutrition, female body condition, and feeding
581 opportunities (Harcourt et al., 2019). As summarized by Kraus and Rolland (2007), the mean calving
582 interval for this stock of right whales was 3.67 years with a range from 2 to 8+ years.

583
584 The bowhead calf ratio (# calves/total sightings) determined from the Aerial Surveys of Arctic Marine
585 Mammals undertaken by NOAA and BOEM (2012-2019) was 7.9% for July-October combined (Clarke et
586 al., 2022). It has long been known from earlier ice-based and aerial surveys that calf production varies
587 widely among years, and that these differences are real and not an artifact of sampling or survey effort
588 (George et al., 2004; Koski et al., 2006). If half of the BCB population are females, and about 40% are
589 mature (Angliss et al., 1995), then a 3-year calving interval suggests calf production should be
590 approximately 7%.

591
592 The weight of evidence based on all these sources suggests the BCB bowhead whale calving interval is 3
593 to 4 years with a possibility of rare 2-year intervals. We suggest that estimating bowhead whale calving

594 intervals derived from the pregnancy rate estimates of harvested whales is useful, but some of the other
595 methods discussed above, including baleen hormone cycles and aerial surveys, are more direct and less
596 susceptible to biases.

597

598 Altogether, we interpret our LSM, ASM, and PR results as positive biological indicators for BCB bowhead
599 whales to date. The stock is robust and growing, despite an ongoing subsistence harvest mortality (landed
600 whales plus likely deaths from struck-and-lost whales) of about 55 whales per year, and seems to exhibit
601 strong productivity even as sea ice loss in the Pacific Arctic and other environmental changes continue to
602 occur. Nonetheless, we are aware that continued climate change will likely impose stress to BCB whales in
603 the future, e.g., through changes in prey distribution, increases in ship collisions, entanglement in fishing
604 gear, and competition with sub-Arctic mysticetes (Moore, 2016). Furthermore, we recognize that some
605 other stocks of bowhead whales (e.g., the Okhotsk Sea stock) are currently at high risk, in part due to climate
606 warming. Indeed, we strongly recommend that the trends and drivers in bowhead ASM and LSM be
607 carefully monitored in the future to better understand the relationship and trends in these important life
608 history traits regarding their biological and management implications.

609

610 **DEDICATION**

611 Shortly after revising this paper, our dear friend and longtime patriarch of bowhead whale science in Alaska,
612 John Craighead “Craig” George, perished in a rafting accident on the Chulitna River in Alaska. Craig was
613 deeply dedicated to family, community, and the Arctic. Unfailingly warm and kind to all, and insatiably
614 curious about the world he lived in, Craig will be sorely missed and forever remembered.

615

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636

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