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

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27   **Abstract**

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29   Data from Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*), harvested during 1973-

30   2021 by aboriginal subsistence hunters, were used to estimate reproductive parameters: length at sexual

31   maturity (LSM), age at sexual maturity (ASM), pregnancy rate (PR), and calving interval. Sexual maturity

32   (n=187 females) was determined from the presence/absence of corpora in the ovaries, or a fetus. Using

33   sampling bias-corrected logistic regression, LSM was estimated at 13.5 m, 95% CI [13.0, 13.8]. There

34   was a downward trend in LSM over time, statistically significant with one method but marginal with

35   another. A growth model translated this estimate to an ASM estimate of 23.5 years, 95% CI [20.4, 26.7].

36   Pregnancy rate was determined from mature females (n=125), and from a subset limited to certain

37   autumn-caught whales (n=37) to reduce bias. The PR was estimated at 0.46 globally, 95% CI [0.36, 0.55]

38   and 0.38 for the autumn sample, 95% CI [0.20, 0.51]. Both estimated PRs are consistent with a 3-year

39   calving interval, because the larger estimate includes two cohorts of pregnant whales harvested in spring,

40   and bowhead whale gestation is longer than 12 months. These analyses represent the most conclusive

41   empirical estimates of ASM, LSM, and PR for this bowhead whale stock from the largest available data

42   sets to date.

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54   **Reproductive Parameters of Bering-Chukchi-Beaufort Seas Bowhead Whales**

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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

99   **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 Utqiaġvik (formerly Barrow), Kaktovik and, since 2005, Gambell and

106   Savoonga on SLI. Utqiaġvik 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.
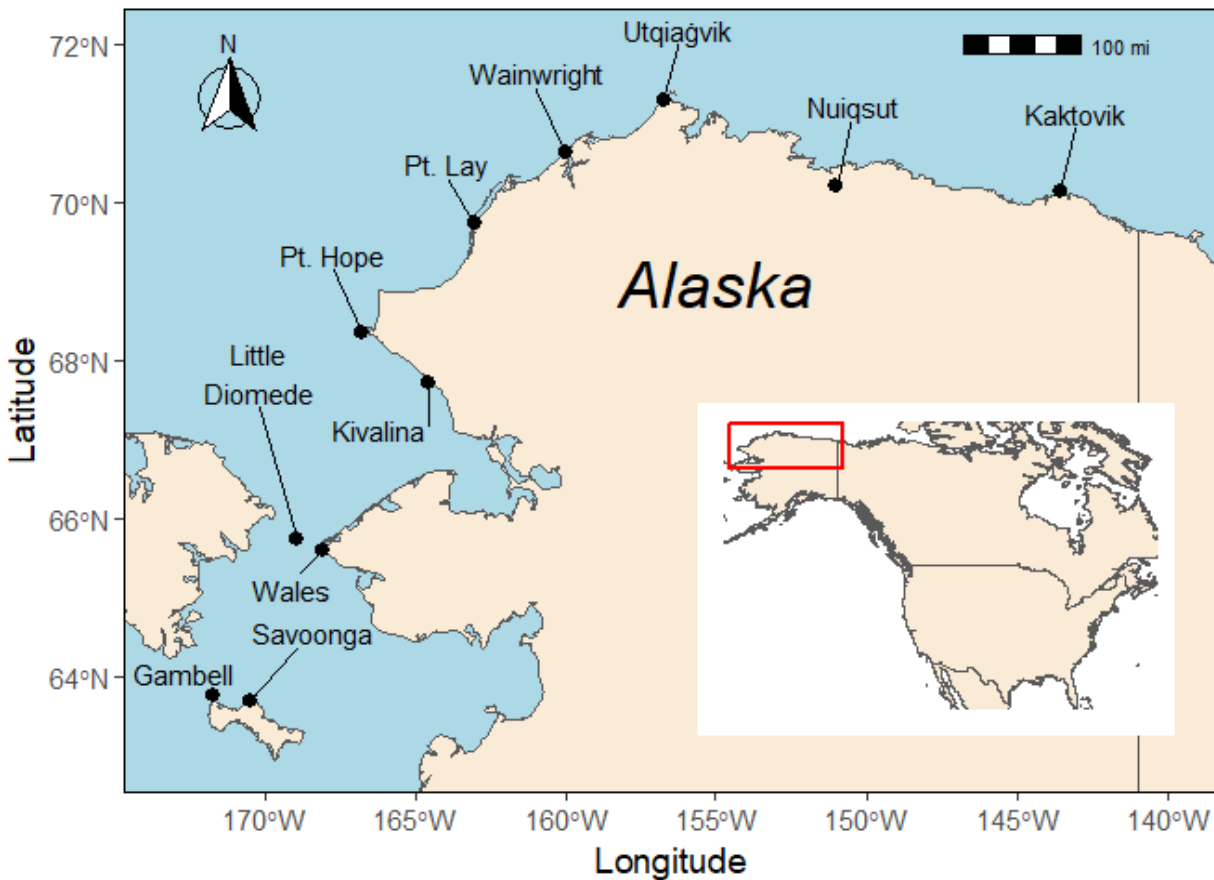
109

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

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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
Utqiaġvik	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

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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., $\overline{M} = 0.642$. We then derived

170   an adjusted estimated intercept, namely $\hat{\beta}_{0,\tau} = \hat{\beta}_0 - ln\left\{\dfrac{1-\tau}{\tau} \dfrac{\overline{M}}{1-\overline{M}}\right\}$ (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 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   τ=0.95. Our results include ASM estimates based on τ=0.05 and τ=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: Utqiaġvik, 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
Utqiaġvik	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

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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

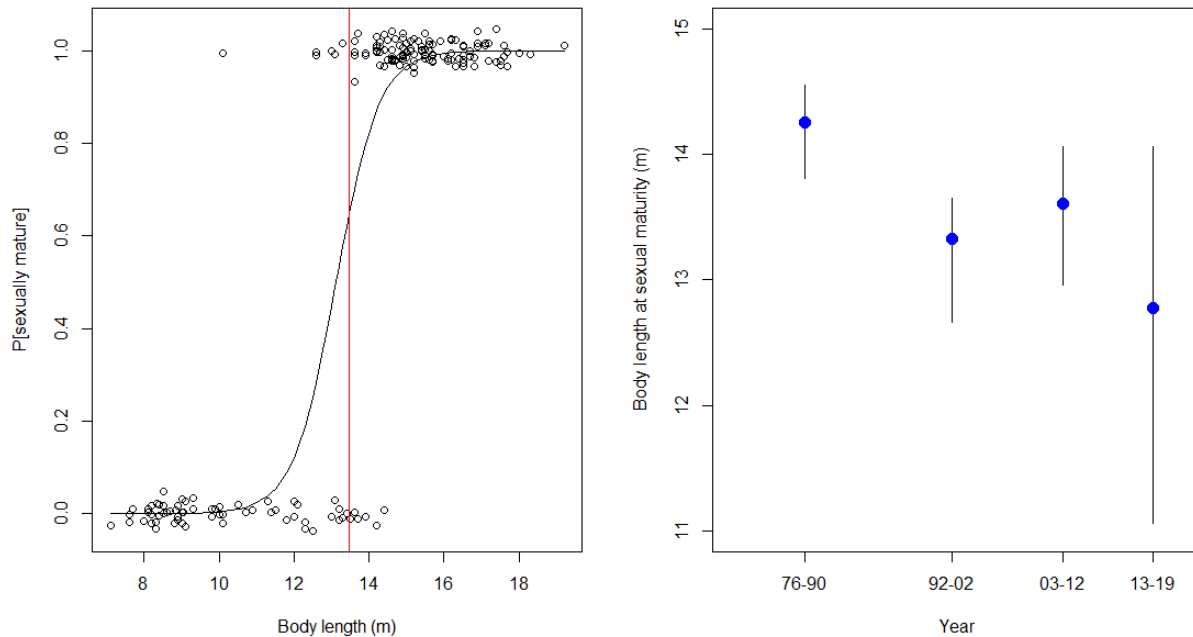316   [13.0, 13.8] (Figure 2 left panel).

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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.

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

385   **Length and age at sexual maturity**

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

636

637   **REFERENCES**

638

639   Albert, T. F. (2001). The influence of Harry Brower, Sr., an Inupiaq Eskimo Hunter, on the bowhead

640   whale research program conducted at the UIC-NARL faculty by the North Slope Borough. In: D.

641   Norton (Ed*.), Fifty more years below zero: tributes and mediations for the Naval Arctic Research*

642   *Laboratory's first half century at Barrow, Alaska* (pp. 265-278). University of Alaska Fairbanks.

643

644   Angliss, R.P., Rugh, D.J., Withrow, D.E. and Hobbs, R.C. (1995). Evaluations of aerial photogrammetric

645   length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena*

646   *mysticetus*). *Report of the International Whaling Commission, 4*5, 313-24.

647

648   Best, P.B. (1985). External characters of southern minke whales and the existence of a diminutive form.

649   [Scientific Reports of the Whales Research Institute, No.23]. The Whales Research Institute.

650

651   Best, P.B., Brandão, A., and Butterworth, D.S. (2001). Demographic parameters of southern right whales

652   off South Africa. *Journal of Cetacean Research and Management, (Special Issue) 2,* 161-169.

653   https://doi.org/10.47536/jcrm.vi.296

654

655   Bierlich, K.C., Schick, R.S., Hewitt, J., Dale, J., Goldbogen, J.A., Friedlaender, A.S. and Johnston, D.W.

656   (2021). Bayesian approach for predicting photogrammetric uncertainty in morphometric

657   measurements derived from drones. *Marine Ecology Progress Series, 673*, 193-210.

658   https://doi.org/10.3354/meps13814

659

660   Bockstoce, J.R. and Batchelder, C.F. (1978). Gazetteer of Whaler's Place Names. *Names, Journal of the*

661   *American Name Society, 26(3),* 258-270.

662

663   Bockstoce, J.R. and Burns, J.J. (1993). Commercial whaling in the North Pacific sector. In J.J. Burns, J. J.

664   Montague, & C.J. Cowles (Eds.), *The Bowhead Whale* (pp. 563-577). Allen Press.

665

666   Boegheim, I., Leegwater, P., van Lith, H. A., and Back, W. (2017). Current insights into the molecular

667   genetic basis of dwarfism in livestock. *Veterinary Journal, 224,* 64–75.

668   https://doi.org/10.1016/j.tvjl.2017.05.014

669

670   Brandon, J. and Wade, P. R. (2006). Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead

671   whales. *Journal of Cetacean Research and Management, 8(3),* 225-229.

672

673   Burns, J.J. (1993). Epilogue. In J.J. Burns, J. Montague, and C.J. Cowles (Eds.) *The Bowhead Whale* (pp.

674   745-764). Society for Marine Mammalogy.

675

676   Canty, A. and Ripley, B.D. (2021). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-28.

677

678   Clarke, J.T., M.C. Ferguson, S.R. Okkonen, A.A. Brower, and Willoughby, A.L. (2022). Bowhead whale

679   calf detections in the western Beaufort Sea during the open-water season, 2012-2019. *Arctic*

680   *Science, 8(2),* 531-548. https://doi.org/10.1139/as-2021-0020

681

682   Christiansen, F., Dawson, S.M., Durban, J.W., Fearnbach, H., Miller, C.A., Bejder, L., Uhart, M., Sironi,

683   M., Corkeron, P., Rayment, W. and Leunissen, E. (2020). Population comparison of right whale body

684   condition reveals poor state of the North Atlantic right whale. *Marine Ecology Progress Series, 640,*

685   1-16. https://doi.org/10.3354/meps13299

686

687   da Silva, CQ, Gomes, P.V.S., and Stradioto, M.A. 2007. Bayesian estimation of survival and capture

688   probabilities using logit link and photoidentification data. *Computational Statistics and Data*

689   *Analysis*, 51: 6521-6534.

690

691   Del Monte-Luna, P., Brook, B.W., Zetina-Rejón, M.J. and Cruz-Escalona, V.H. 2004. The carrying

692   capacity of ecosystems. *Global Ecology and Biogeography, 13,* 485-495.

693   https://doi.org/10.1111/j.1466-822X.2004.00131.x

694

695   Efron, B. (1987). Better bootstrap confidence intervals (with discussion). *Journal of the American*

696   *Statistical Association, 82,* 171-200. https://doi.org/10.2307/2289144

697

698   Frey, K.E., Comiso, J.C., Cooper, L.W., Grebmeier, J.M., and Stock, L.V. (2021). Arctic ocean primary

699   productivity: The response of marine algae to climate warming and sea ice decline. [NOAA Arctic

700   Report Card 2020]. https://doi.org/10.25923/vtdn-2198

701

702   Fujise, Y., Hatanaka, H. and Ohsumi, S. (2005). What has happened to the Antarctic minke whale

703   stocks?- an interpretation of results from JARPA. [Unpublished paper JA/J05/JR17 presented to the

704   Scientific Committee of the International Whaling Commission, May 2005]. Available from

705   www.iwc.int.

706

707   George, J.C. (2009). Growth, morphology, and energetics of bowhead whales (*Balaena mysticetus*).

708   [Unpublished Ph.D. dissertation]. University of Alaska Fairbanks. hdl.handle.net/11122/9031

709

710   George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. (1999). Age and

711   growth estimates of bowhead whales (*Balaena mysticetus*) using aspartic acid racemization.

712   *Canadian Journal of Zoology, 77,* 571–80. https://doi.org/10.1139/z99-015

713

714   George, J.C. and Bockstoce, J.R. (2008). Two historical weapon fragments as an aid to estimating the

715   longevity and movements of bowhead whales. *Polar Biology, 31(6),* 751–4.

716   http://dx.doi.org/10.1007/s00300-008-0407-2

717

718   George, J.C., Druckenmiller, M.L., Laidre, K.L., Suydam, R., and Person, B.T. (2015). Bowhead whale

719   body condition and links to summer sea ice and upwelling in the Beaufort Sea. *Progress in*

720   *Oceanography, 136,* 250-262. https://doi.org/10.1016/J.POCEAN.2015.05.001

721

722   George, J.C, Follmann, E., Zeh, J., Sousa, M., Tarpley, R.J., Suydam, R., and Horstmann-Dehn, L.

723   (2011). A new way to estimate whale the age of bowhead whales (*Balaena mysticetus*) using ovarian

724   corpora counts. *Canadian Journal of Zoology, 89,* 840–852. https://doi.org/10.1139/z11-057

725

726   George J.C., Stimmelmayr, R., Suydam, R., Usip, S., Givens, G., Sformo, T., and Thewissen, J.G.M.

727   (2016). Severe bone loss as part of the life history strategy of bowhead whales. *PLoS ONE, 11(6),*

728   e0156753. https://doi.org/10.1371/journal.pone.0156753

729

730   George, J.C., Thewissen, J.G.M., Von Duyke, A., Breed, G.A., Suydam, R., Sformo, T.L., Person, B.T.

731   and Brower Jr., H.K. (2021). Life history, growth, and form. In: J.C. George and J.G.M. Thewissen

732   (Eds.), *The Bowhead Whale,* Balaena mysticetus*, Biology and Human Interactions* (pp. 87-116).

733   Elsevier Press.

734

735   George, J. C., Zeh, J., Suydam, R. and Clark, C. (2004). Abundance and population trend (1978-2001) of

736   western arctic bowhead whales surveyed near Barrow, Alaska. *Marine Mammal Science 20(4),* 55-

737   773. http://dx.doi.org/10.1111/j.1748-7692.2004.tb01191.x

738

739   Givens, G.H., Edmondson, S.L., George, J.C., Suydam, R., Charif, R.A., Rahaman, A., Hawthorne, D.L.,

740   Tudor, B., Delong, R.A. and Clark, C.W. (2016). Horvitz-Thompson whale abundance estimation

741   adjusting for uncertain recapture, temporal availability variation and intermittent effort.

742   *Environmetrics, 26,* 1-16. https://doi.org/10.1002/env.2379

743

744   Givens, G.H. and Hoeting, J.A. (2013). *Computational Statistics (2ⁿᵈ edition)*. John Wiley and Sons, Inc.

745

746   Hamilton, P.K., Knowlton, A.R., Marx, M.K. and Kraus, S.D. (1998). Age structure and longevity in

747   North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Marine Ecology*

748   *Progress Series*, 171, pp.285-292. https://www.jstor.org/stable/24831743

749

750   Harcourt, R., van der Hoop, J.M., Kraus, S., and Carroll, E.L. (2019). Future directions in *Eubalaena* spp:

751   comparative research to inform conservation. *Frontiers in Marine Science, 30,* January 2019.

752   https://doi.org/10.3389/fmars.2018.00530

753

754   Hosmer Jr, D.W., Lemeshow, S., and Sturdivant, R.X. (2013). *Applied Logistic Regression*. John Wiley

755   & Sons.

756

757   Hunt, K.E., Lysiak, N.S., Moore, M.J., and Rolland, R.M. (2016). Longitudinal progesterone profiles in

758   baleen from female North Atlantic right whales (*Eubalaena glacialis*) match known calving history.

759   *Conservation Physiology, 4(1),* cow014. https://doi.org/10.1093/conphys/cow014

760

761   Hunt, K.E., Lysiak, N.S., Robbins, J., Moore, M.J., Seton, R.E., Torres, L., and Buck, C.L. (2017).

762   Multiple steroid and thyroid hormones detected in baleen from eight whale species. *Conservation*

763   *Physiology, 5(1),* cox061. https://doi.org/10.1093%2Fconphys%2Fcox061

764

765   Hunt, K.E., Stimmelmayr, R., George, J.C., Hanns, C., Suydam, R., Brower, H. Jr., and Rolland, R.M.

766   (2014). Baleen hormones: a novel tool for retrospective assessment of stress and reproduction in

767   bowhead whales (*Balaena mysticetus*). *Conservation Physiology, 2(1),* cou030.

768   https://doi.org/10.1093/conphys/cou030

769

770   Huntington, H.P., Danielson, S.L., Wiese, F.K., Baker, M., Boveng, P., Citta, J.J., De Robertis, A.,

771   Dickson, D.M.S., Farley, E., George, J.C., Iken, K., Kimmel, D.G., Kuletz, K., Ladd, C., Levine, R.,

772   Quakenbush, L., Stabeno, P., Stafford, K.M., Stockwell, D. and Wilson, C. (2020). Evidence

773   suggests potential transformation of the Pacific Arctic ecosystem is underway. *Nature Climate*

774   *Change, 10,* 342–348. https://doi.org/10.1038/s41558-020-0695-2

775

776   International Whaling Commission. 2003. Chair's report of the fifty-fourth annual meeting. Annex C.

777   Report of the aboriginal subsistence whaling subcommittee. *Annual Reports of the International*

778   *Whaling Commission, 2002,* 62-75.

779

780   King, G., and Zeng, L. (2001). Logistic regression in rare events data. *Political Analysis, 9(2),* 137-163.

781   https://doi.org/10.1093/oxfordjournals.pan.a004868

782

783   Koski, W.R., Davis, R.A, Miller, G.W., and Withrow, D.E. (1992). Growth rates of bowhead whales as

784   determined from low-level aerial photogrammetry. *Report of the International Whaling Commission,*

785   *42,* 491-499.

786

787   Koski, W.R, Davis, R.A., Miller, G.W., and Withrow, D.E. (1993). Reproduction. In J.J. Burns, J. J.

788   Montague, and C.J. Cowles (Eds.), *The Bowhead Whale* (pp. 239-269). Allen Press.

789

790   Koski, W.R. and Miller, G.W. (2009). Habitat use by different size classes of bowhead whales in the

791   central Beaufort Sea during late summer and autumn. *Arctic, 62(2),* 137-150.

792   https://www.jstor.org/stable/40513283

793

794   Koski, W.R., Rugh, D.J., Punt, A.E. and Zeh, J. (2006). An approach to minimize bias in estimation of

795   the length-frequency distribution of bowhead whales (*Balaena mysticetus*) from aerial

796   photogrammetric data. *Journal of Cetacean Research and Management*, 8(1): 45-54.

797

798   Kraus, S.D. and Rolland, R.M. (2007). *The Urban Whale: North Atlantic Right Whales at the Crossroads*.

799   Harvard University Press, Cambridge MA.

800

801   Kraus, S. D., Pace III, R.M. and Frasier, T.R. (2007). High investment, low return: The strange case of

802   reproduction in *Eubalaena glacialis*. In S. D. Kraus and R. M. Rolland (Eds.), *The Urban Whale:*

803   *North Atlantic Right Whales at the Crossroads* (pp. 172-199). Harvard University Press, Cambridge,

804   MA.

805

806   Kuparinen, A. and Festa-Bianchet, M. (2017). Harvest-induced evolution: insights from aquatic and

807   terrestrial systems. *Philosophical Transactions of the Royal Society of London, Series B, Biological*

808   *Sciences, 372(1712),* 20160036. https://doi.org/10.1098/rstb.2016.0036

809

810   Lockyer, C. (1987). Observations on the ovary of the southern minke whale. *Sci Rep Whales Res Inst, 38,*

811   75-89.

812

813   Lowe, C.L., Hunt, K.E., Rogers, M.C., Neilson, J.L., Robbins, J., Gabriele, C.M., Teerlink, S.S., Seton,

814   R., and Buck, C.L. (2021). Multi-year progesterone profiles during pregnancy in baleen of humpback

815   whales (*Megaptera novaeangliae*). *Conservation Physiology, 9(1),* coab059.

816   https://doi.org/10.1093/conphys/coab059

817

818   Lubetkin, S.C., Zeh, J. and George, J. (2012). Statistical modeling of baleen and body length at age in

819   bowhead whales. *Canadian Journal of Zoology, 90(8),* 915–31. http://dx.doi.org/10.1139/z2012-057

820

821   Miller, G.W., Davis, R.A., Koski, W.R., Crone, M.J., Rugh, D.J., Withrow, D.E. and Fraker, M.A.

822   (1992). Calving intervals of bowhead whales: an analysis of photographic data. *Report of the*

823   *International Whaling Commission, 42,* 501-506.

824

825   Moore, S.E. (2016). Is it 'boom times' for baleen whales in the Pacific Arctic region? *Biology Letters*

826   12(9), 20160251. https://doi.org/10.1098/rsbl.2016.0251

827

828   Moore, S.E. and Reeves, R.R. (1993). Distribution and movement. In J.J. Burns, J. J. Montague, and C.J.

829   Cowles (Eds.), *The Bowhead Whale* (pp. 313-386). Allen Press.

830

831   Nerini, M., H. Braham, W. Marquette, and Rugh, D. (1984). Life history of the bowhead whale, *Balaena*

832   *mysticetus* (Mammalia: Cetacea). *Journal of Zoology,* 204(4), 443-468.

833   https://doi.org/10.1111/j.1469-7998.1984.tb02381.x

834

835   Ohsumi, S. (1986). Yearly change in age and body length at sexual maturity of a fin whale stock in the

836   eastern North Pacific. [Scientific Reports of the Whales Research Institute, No.37]. The Whales

837   Research Institute.

838

839   Omura, H., Ohsumi, S., Nemoto, T., Nasu, K. and Kasuya, T. (1969). Black right whales in the North

840   Pacific. [Scientific Reports of the Whales Research Institute, No.21]. The Whales Research Institute.

841

842   Parasuraman, S. (2011). Toxicological screening. *Journal of Pharmacology and Pharmacotherapeutics,*

843   *2(2),* 74-79. https://doi.org/10.4103/0976-500x.81895

844

845   Prentice, R.L., and Pyke, R. (1979). Logistic disease incidence models and case-control studies.

846   *Biometrika, 66(3),* 403-411. https://doi.org/10.2307/2335158

847

848   Price, D. (1999). Carrying capacity reconsidered. *Population and Environment, 21,* 5–26.

849   https://doi.org/10.1007/BF02436118

850

851   R Core Team 2019. R: A language and environment for statistical computing. R Foundation for Statistical

852   Computing, Vienna, Austria. https://www.R-project.org/

853

854   Reese, C.S., Calvin, J.A., George, J.C. and Tarpley, R.J. (2001). Estimation of fetal growth and gestation

855   in bowhead whales. *Journal of the American Statistical Association, 96,* 915-923.

856   https://doi.org/10.1198/016214501753208618

857

858   Rolland, R.M., Lysiak, N.S., Graham, K.M., Burgess, E.A., Hunt, K.E., Fuller, R. and Hannigan, R.

859   (2018). Assessing stress and reproduction in bowhead whales (*Balaena mysticetus*) using baleen

860   hormones. [Unpublished Final Report for the North Slope Borough/Shell Baseline Studies Program,

861   Contract #2015-102. Available from North Slope Borough, Alaska, Department of Wildlife

862   Management, PO Box 69, Utqiaġvik AK 99723].

863

864   Rosa, C., Zeh, J., George, J. C., Botta, O., Zauscher, M., Bada, J. and O'Hara, T.M. (2013). Age estimates

865   based on aspartic acid racemization for bowhead whales (*Balaena mysticetus*) harvested in 1998–

866   2000 and the relationship between racemization rate and body temperature. *Marine Mammal Science,*

867   *29(3),* 424–445. https://doi.org/10.1111/j.1748-7692.2012.00593.x

868

869   Rugh, D.J., Miller, G.W., Withrow, D.E. and Koski, W.R. (1992). Bowhead whale calving intervals

870   established through photographic reidentifications. *Journal of Mammalogy,* 73, 487-490.

871   https://doi.org/10.2307/1382014

872

873   Schell, D.M. and Saupe, S.M. (1993). Feeding and growth as indicated by stable isotopes. In J.J. Burns, J.

874   J. Montague, and C.J. Cowles (Eds.), *The Bowhead Whale* (pp. 491-509). Allen Press.

875

876   Schweder, T., Sadykova, D., Rugh, D., and Koski, R. 2010. Population estimates from aerial

877   photographic surveys of naturally and variably marked bowhead whales. *Journal of Agricultural,*

878   *Biological, and Environmental Statistics*, 15:1-19.

879

880   Sharpe, D.M. and Hendry, A.P. (2009). Life history change in commercially exploited fish stocks: an

881   analysis of trends across studies. *Evolutionary applications, 2(3),* 260–275.

882   https://doi.org/10.1111/j.1752-4571.2009.00080.x

883

884   Stewart, J.D., Durban, J.W., Knowlton, A.R., Lynn, M.S., Fearnbach, H., Barbaro, J., Perryman, W.L.,

885   Miller, C.A., and Moore, M.J. (2021). Decreasing body lengths in North Atlantic right whales.

886   *Current Biology, 31(14)*, 3174-3179. https://doi.org/10.1016/j.cub.2021.04.067

887

888   Suydam, R. and George, J.C. (2021). Current indigenous whaling. In J.C. George and J.G.M. Thewissen

889   (Eds.), *The Bowhead Whale* Balaena mysticetus*: Biology and Human Interactions* (pp. 519-535).

890   Academic Press.

891

892   Tarpley, R.J. and Hillmann, D.J. (1999). Observations on ovary morphology, fetal size and functional

893   correlates in the bowhead whale *Balaena mysticetus*. [Unpublished Final Report to the Department of

894   Wildlife Management, North Slope Borough, Box 69, Utqiaġvik, AK 99723].

895

896 Tarpley, R.J., Hillmann, D.J., George, J.C. and Thewissen, J.G.M. (2021). Female and male reproduction.

897 In J.C. George and J.G.M. Thewissen (Eds.), *The Bowhead Whale* Balaena mysticetus*: Biology and*

898 *Human Interactions* (pp. 185-212). Academic Press.

899

900 Tarpley, R.J., Hillmann, D.J., George, J.C., Zeh, J.E. and Suydam, R.S. (2016). Morphometric correlates

901 of the ovary and ovulatory corpora in the bowhead whale, *Balaena mysticetus*. *The Anatomical*

902 *Record, 299(6),* 769–797. https://doi.org/10.1002/ar.23337

903

904 Tulloch V.J.D., Plagányi, É.E., Brown, C., Richardson A.J., and Matear, R. (2019). Future recovery of

905 baleen whales is imperiled by climate change. *Global Change Biology, 25(4),* 1263–1281. doi:

906 10.1111/gcb.14573. https://doi.org/10.1111/gcb.14573

907

908 Von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth laws, II).

909 *Human Biology* 10(2): 181-213.

910

911 Vucetich, J. and Peterson, R. (2004). The influence of top-down, bottom-up and abiotic factors on the

912 moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society B: Biological*

913 *Sciences, 271(1535),* 183-189. http://doi.org/10.1098/rspb.2003.2589

914

915 Wallig, M., Microsoft, and Weston, S. (2020a). foreach package for R.

916 https://github.com/RevolutionAnalytics/foreach

917

918 Wallig, M., Microsoft, Weston, S. and Tenenbaum, D. (2020b). doParallel package for R. https://cran.r-

919 project.org/web/packages/doParallel/index.html

920

921   West, K.L., Oftedal, O.T., Carpenter, J.R., Krames, B.J., Campbell, M., and Sweeney, J.C. (2007). Effect

922   of lactation stage and concurrent pregnancy on milk composition in the bottlenose dolphin. *Journal of*

923   *Zoology, 273(2),* 148-160. https://doi.org/10.1111%2Fj.1469-7998.2007.00309.x

924

925   Wetzel, D. L., Reynolds III, J. E., Mercurio, P., Givens, G. H., Pulster, E. L., and George, J. C. 2017. Age

926   estimation for bowhead whales (*Balaena mysticetus*) using aspartic acid racemization with enhanced

927   hydrolysis and derivatization procedures. *Journal of Cetacean Research and Management, 17,* 9-14.

928

929   Zeh, J., Poole, D., Miller, G., Koski, W., Baraff, L. and Rugh, D. (2002). Survival of bowhead whales,

930   *Balaena mysticetus*, estimated from 1981-1998 photoidentification data. *Biometrics, 58,* 832-40.

931

932   Zeh, J.E. and Punt, A.E. (2005). Updated 1978-2001 abundance estimates and their correlations for the

933   Bering-Chukchi-Beaufort Seas stock of bowhead whales. *Journal of Cetacean Research and*

934   *Management, 7(2),* 169-175.