









Reproductive parameters of Bering-Chukchi-Beaufort Seas bowhead whales

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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

1 | INTRODUCTION

Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas stock (BCB bowhead whales) were nearly eradicated by Yankee whalers hunting for commercial purposes from 1848 to 1914 (Bockstoce & Burns, 1993). BCB bowhead whale abundance has subsequently increased substantially, with 14 reliable abundance estimates since 1978 suggesting that the population has tripled in recent decades (Givens et al., 2016). These whales are still harvested in an aboriginal subsistence hunt by Alaska Natives in 11 communities (Suydam & George, 2021), continuing indigenous traditions ongoing for millennia. Many of these harvested whales have been examined by biologists, allowing for the collection of additional extensive biological data useful for studies, including estimating reproductive parameters such as date of conception, length at sexual maturity, interbirth intervals, gross annual reproductive rates, and gestation period (Koski et al., 1993; Reese et al., 2001; Tarpley et al., 2021).

Studying reproductive data provides insight into the population, its environment, and its management by the International Whaling Commission (IWC). Collecting information on reproductive parameters also facilitates monitoring of the potential impacts of environmental change and/or increasing population density. With atmospheric and ocean warming resulting in a continuing and significant reduction in sea ice duration, extent, and quality, the marine ecosystems of the Bering, Chukchi, and Beaufort Seas are responding with ongoing, ecological transitions (e.g., Huntington et al., 2020). Potential effects to bowhead whales may include changes in reproductive parameters, such as interbirth intervals or annual reproductive rates. Meanwhile, the BCB bowhead whale population has been increasing at a rate of approximately 3.7% per year (Givens et al., 2016). As the population approaches carrying capacity, especially in transitioning ecosystems, we would predict that population parameters such as survival rates or reproductive rates will decline following classic density dependence predictions (although warmer water and declining sea ice may lead to increasing zooplankton abundance and feeding areas, and therefore increased bowhead whale carrying capacity). In addition, pregnancy rate estimates from landed whales are useful in stock assessments and for comparison with empirical estimates of calf production from aerial surveys (Angliss et al., 1995; Clarke et al., 2022; Koski et al., 1993).

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

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

2 | MATERIALS AND METHODS

BCB bowhead whales are mostly harvested in Alaska during two subsistence whaling seasons: spring (roughly April to mid-June) and fall (roughly late August to October); a few whales are harvested at other times, mainly near St. Lawrence Island (SLI) in early winter (Suydam & George, 2021). Harvested bowhead whales were examined by biologists in several Alaskan communities, with the most frequent and thorough examinations occurring in Utqiagvik (formerly Barrow), Kaktovik and, since 2005, Gambell and Savoonga on SLI. Utqiagvik hunts in spring and fall, Kaktovik in fall, and the SLI communities in spring, but in recent years more in late fall or early winter. The 11 whaling communities mentioned in this article are mapped in Figure 1.

When examining a harvested bowhead whale, biologists routinely took standard cetacean morphometric measurements (e.g., whale length from tip of rostrum to fluke notch, various girths, fluke, and pectoral fin measurements) along with a large array of biological samples to support studies spanning anatomy, genetics, diet, scar-injury frequency, diseases, reproduction, and other topics. Consistent collection of such data began in 1972, although the quantity and nature of the data collected varied from year to year and from whale to whale. Since 1982, harvest monitoring has been conducted by biologists working for, or cooperatively with, the North Slope Borough Department of Wildlife Management (NSB DWM). Information about sexual maturity and pregnancy was obtained from post hoc laboratory analysis where ovaries of harvested bowheads were examined for the presence of corpora lutea (CLs, the progesterone-secreting structure produced after ovulation and maintained through pregnancy), and corpora albicantia (CAs, scars from degenerated corpora lutea at the end of pregnancy). These structures indicate sexual maturity in mammals.

2.1 | Length at sexual maturity

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

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

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

where \ln is the natural logarithm, p is the probability that a female bowhead whale with body length BL is sexually mature, and β_0 and β_1 are parameters to be estimated. The second step for estimating LSM was to note that, for a representative sample of whales, the parameter estimates from this model can be used to estimate the length for which a randomly sampled bowhead whale in the population has probability .5 of being mature, or in other words, the length at which 50% of the bowhead whales are mature. Specifically, using the parameter estimates $\hat{\beta}_0$ and $\hat{\beta}_1$, we can let $p = .5$ in the logistic regression equation and solve for BL . Thus $LSM = -\hat{\beta}_0/\hat{\beta}_1$. This is analogous to the LD(50) in toxicology, where LD stands for “Lethal Dose,” and LD(50) is the dose at which 50% of animals die (Parasuraman, 2011). In our case, the concept of survival/death is replaced by immature/mature.

The data set used to fit this logistic regression model is probably not representative of the age distribution in the population. The data are, effectively, the result of a retrospective case-control study: opportunistic samples of mature and immature bowhead whales selected nonrandomly by the hunters (and hence available for analysis by the biologists). We believe that sexually mature whales are overrepresented in our data set compared to corresponding

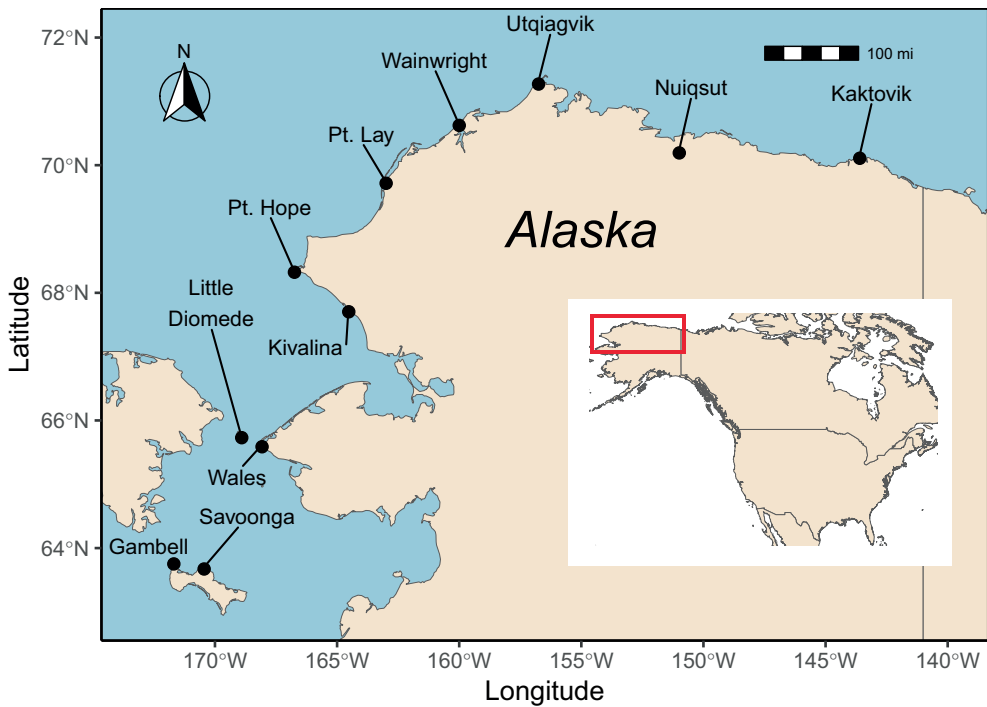


FIGURE 1 Map of Alaska Native bowhead whaling communities.

population frequencies. Reasons for this include an IWC prohibition against hunting calves or whales swimming with calves, a tendency for biological examination to be prioritized for pregnant (or potentially pregnant) animals, and perhaps hunter selectivity (some communities prefer larger whales, and others prefer smaller, or they prefer to hunt at specific times, during which only a portion of the age-segregated migration may be passing).

To adjust for any nonrepresentative sampling, we redefined LSM, using a method that works regardless of whether sexually mature whales are actually over- or underrepresented. In a sample of bowhead whales with an equal number of mature and immature animals, LSM equals the *BL* for which a random whale from this hypothetical

TABLE 1 Whaling community, season, and sexual maturity for 187 Bering-Chukchi-Beaufort Seas bowhead whales in the sexual maturity data set. The entries in each table cell are written as immature/mature.

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

^aWhaling community with spring hunt only.

^bA fall hunt only.

set has a probability $\tau = 0.5$ of being mature. We defined \bar{M} as the proportion of whales that were mature in our sample of 120 mature and 67 immature whales, i.e., $\bar{M} = 0.642$. We then derived 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 & Zeng, 2001; Prentice & Pyke, 1979), which effectively adjusted the response curve to account for the imbalanced sample. The corresponding adjusted LSM estimate was $\text{LSM} = -\hat{\beta}_{0,\tau} / \hat{\beta}_1$.

We calculated a bootstrap confidence interval for LSM using the bootstrap BCa approach (Efron, 1987) as implemented in the boot library in R (Canty & Ripley, 2021; R Core Team, 2022). Whales were randomly sampled, with replacement, to obtain 10,000 bootstrap data sets. This method can be replicated for alternate values of τ , for example to determine the length at which 95% of whales are mature by setting $\tau = 0.95$. Our results include ASM estimates based on $\tau = 0.05$ and $\tau = 0.95$, to assess the range of ages at which bowhead whales can mature.

We used two analyses to assess whether LSM changed over time. In the first analysis, we fit a logistic regression with bowhead whale maturity as the response variable, and predictors of *BL* and year. This approach controls for variation in *BL* (from potential trends in harvest selection) when estimating the effect of year. However, the approach only accounts for a logit-linear trend in LSM and would be more reliable if years were sampled with similar frequency. Moreover, the response variable for this analysis is maturity, not length at maturity. To address these issues, we conducted a second analysis, where we split the data set into quarters (1976–1990, $n = 47$; 1991–2002, $n = 47$; 2003–2012, $n = 46$; 2013–2019, $n = 47$). For each block of years, we estimated LSM using the above methods. We then created a data set with the four LSM estimates, the midpoint of the year blocks, and inverse variance weights (where variance was estimated via the bootstrap, as described above). To these data, we fitted a weighted linear regression of LSM on year to estimate the slope. To estimate the uncertainty in this estimated slope, we applied a nested bootstrap approach by repeating this procedure 100,000 times on quartets of bootstrap samples from each block. A bootstrap 95% confidence interval was then computed using the percentile method (e.g., Givens & Hoeting, 2013). This nested approach requires four lengthy bootstraps within each iteration of the main bootstrap. We used the “foreach” (Wallig et al., 2020a) and “doParallel” (Wallig et al., 2020b) packages in R to make this analysis computationally feasible.

2.2 | Age at sexual maturity

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

2.3 | Pregnancy rate

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

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

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

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

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

Two estimates of PR were made. Both estimates were computed as the proportion of mature whales that were pregnant, but the estimates differed in determining which whales were mature in cases where the LSM criterion was applied due to the lack of a definitive biological examination of the reproductive tracts and ovaries. The time-variant approach for PR estimation applied four different values for LSM for whales landed in different year blocks to determine maturity, in order to account for any time trend in LSM. The time-invariant approach for PR estimation used a single LSM value encompassing the entire period of collection (1972–2019). There were 125 whales classified as mature using the first method and 129 using the second method; see Table 2. (Note that each maturity data set includes some whales whose maturity was determined on the basis of LSM, and because the time variant and time invariant approaches include different LSM criteria for that determination, the numbers of mature whales differ in the two data sets.) Confidence intervals for PR were estimated using a nested bootstrap. First, a value(s) for LSM was/were selected at random from the bootstrap distribution(s) obtained in the previous section. Next, a bootstrap data set was generated by resampling with replacement from the original data set. Then a bootstrap data set of mature animals was obtained by determining maturity using the criteria given above and the new LSM value(s). Finally, a bootstrap PR value was calculated from this data set. The percentile method confidence interval was computed from these bootstrap PR values.

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

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

Estimating PR from landed bowhead whales has several challenges with associated assumptions and biases, including: (1) early pregnancies going undetected; (2) animals becoming pregnant after the spring field season; (3) animals giving birth shortly before the spring harvest; (4) determining if a female is mature; (5) accounting for mature females that were not harvested, because they were accompanied by a calf, as required by IWC regulations; (6) different behavior patterns of pregnant animals compared with other whales (e.g., remaining on the surface longer, thereby being more susceptible to hunting); (7) other issues related to hunter selectivity or whale availability; and (8) possible differences in PR with whale size and age. Our use of the retrospective examined-by-trained-biologist filter directly addresses only the first challenge listed above.

Some of these biases can be further diminished if only landed whales from the fall season are included. During fall, fetus length ranged from 1.2 m to 2 m, which can be readily detected during the butchering process. Furthermore, during fall, there is only one cohort of pregnant females, whereas in spring there are two: early pregnancy and term pregnancy (some of which may have already given birth before harvest). Another source of bias can be reduced

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

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

^aWhaling community with spring hunt only.

^bA fall hunt only.

if we eliminate six whales landed during fall near Savoonga (on SLI), five of which were pregnant. We suspect that the region north of SLI, where whaling crews from Savoonga traditionally hunt in the fall, is disproportionately frequented by mature pregnant females at that time. Yankee whalers called the region north of SLI in the Bering Strait region and the Chukotka coast the “cow yard” based on the extremely large female whales harvested there: “Cow Yard. Chukchi Sea; an area near Cape Serdtse Kamen, Siberia, where large cow whales were taken, in 1848 and 1849.” (Bockstoce & Batchelder, 1978). In recent years, bowhead whales harvested near Savoonga and Gambell by SLI hunters have frequently been larger than bowhead whales taken by other whaling communities. For these reasons, the SLI fall harvest data should be used cautiously when calculating PR.

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

3 | RESULTS

3.1 | Length at sexual maturity

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

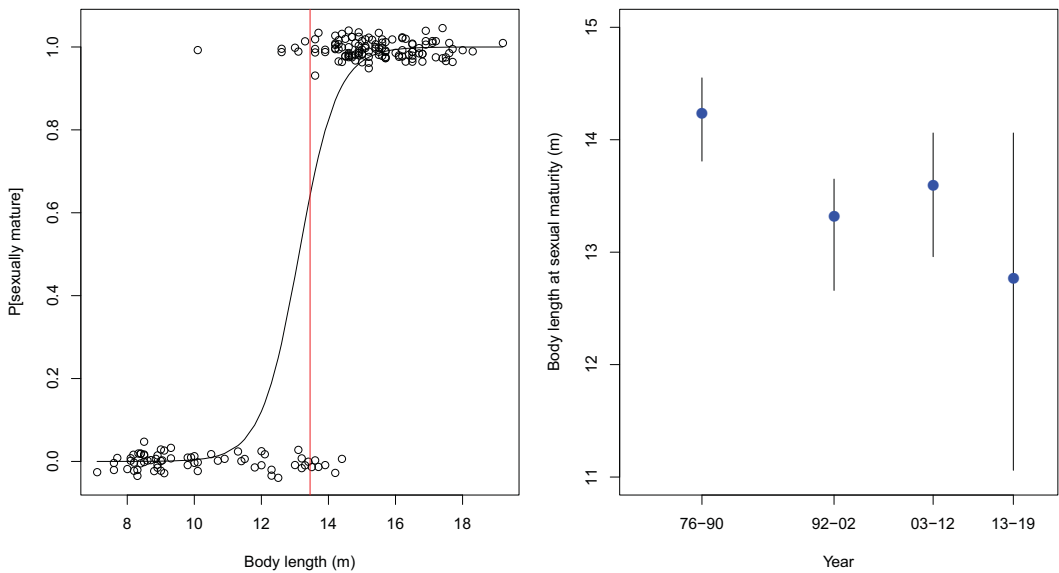


FIGURE 2 The left panel shows length at sexual maturity (LSM) data for female bowhead whales, and (corrected) logistic regression fit, with the red vertical line indicating the estimated LSM. The points have been jittered for clarity. The right panel shows year block LSM estimates and corresponding bootstrap 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, $SE = 0.031$, $p = .038$), 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% CI $[-0.10, 0.00]$; 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 Figure 2 shows the year block estimates of LSM, with vertical lines indicating bootstrap confidence intervals. The downward trend is evidently due to higher LSM several decades ago and lower LSM in the most recent years.

3.2 | Age at sexual maturity

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

3.3 | Pregnancy rate and calving interval

Using the time-variant approach accounting for the time trend in LSM, and data from all seasons, 58 of 125 mature female bowhead whales were pregnant, yielding a PR estimate of 0.46, 95% CI [0.32, 0.51]. For the time-invariant

approach with a common LSM for all females in all seasons, 58 of 129 mature females were pregnant, yielding a PR estimate of 0.45, 95% CI [0.36, 0.54].

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

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

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

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

4 | DISCUSSION

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

4.1 | Length and age at sexual maturity

Our data suggest a large range in length at the initiation of sexual maturity for female bowhead whales. Our estimated LSM of 13.5 m, 95% CI [13.0, 13.8], corresponds to a 50% probability of maturity. The estimated 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 statistical uncertainty here exceeds biological uncertainty: a 15 m whale is certainly mature, especially as the longest immature female in our data set was 14.4 m. The smallest known mature females included two 12.6 m pregnant females with a single CL and no CAs observed (indicating it was a first ovulation), and an unusual nonpregnant whale at 10.1 m with no CL and one CA detected. We do not currently understand how the latter whale produced a CA given her short body length unless she was a case of proportionate dwarfism (e.g., Boegheim et al., 2017) or alternatively a diminutive form of a bowhead whale. Best (1985) has reported on the rare occurrence of a diminutive form for Antarctic minke whales (*Balaenoptera bonaerensis*).

Our approach for creation of the sexual maturity data set relied solely on direct evidence of reproductive capacity. In principle, female sexual maturity could also be evaluated from ovary weight. Tarpley and Hillman (1999) estimated a relationship between ovary weight, body length, and maturity: bowhead whales with an ovary weight exceeding about 3 kg and/or an ovary length over about 30 cm were more likely to be mature (Tarpley et al., 2021). However, the authors cautioned against such metrics as the sole criterion to determine maturity in female bowhead

whales, as they found some overlap between the ovary weight of mature and immature whales. We agreed with their caution and therefore relied only on direct observation of a CL, CAs, and/or a fetus, as explained in the Methods.

Regarding the LSM trend analysis, one might note that the confidence bar for 2013–2019 in Figure 2 is a bit more than double the length as for the other year blocks and ask how this might have influenced our results. First, we note that such a difference in standard deviations is moderate, compared to the radical heteroskedasticity that may complicate some analyses. Indeed, we believe that traditional statistical models requiring variance homogeneity in that respect would be robust to the moderate inconsistency seen here. Fortunately, concern about the degree of heteroskedasticity or the potential statistical robustness of our methods is not warranted here. Specifically, the heterogeneity in variance apparent in Figure 2 is not relevant for the first method we used to assess significance, as traditional logistic regression is based on the binary sexual maturity data set, a binomial model, and its inherent variance structure, not the block estimates and error bars in Figure 2. The second method (the nested bootstrap), which we prefer, is very well suited to handle heterogeneous variances, as it makes no assumptions about variance structure and directly “models” the heterogeneity between blocks via its resampling structure. We also note that the bootstrapped regression is inverse-variance weighted, so the relative uncertainty in each year bin is accounted for during the estimation.

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

We do not have a singular explanation for the downward trend in LSM over time (Figure 2). Changes in life history traits, namely decreasing ASM (but not body length), have been well documented in several northern and southern baleen whale stocks during the period of heavy exploitation. Proposed underlying key mechanisms in those cases include relaxation of intra- and interspecific competition due to drastic population size decline (commercial catch mortality), and accelerated growth rates of young animals with subsequent earlier maturation (Fujise et al., 2005; Ohsumi, 1986). Since 1990, and particularly since 2010, changing sea ice conditions have likely resulted in improved food availability (George et al. 2015; Moore, 2016). A reduction in LSM associated with better feeding conditions is a classic density-dependent response in many vertebrates. The time period of our LSM study encompasses many high-density sea ice years in the past (1976–1990), with low ice years increasingly predominant more recently, and particularly since 2010. It is reasonable to speculate that the increased access, duration, and productivity of feeding areas (in recent decades) associated with sea ice retreat (Frey et al., 2021; Moore, 2016) may explain why females are mature at shorter body lengths. We cannot directly infer that the age at sexual maturity has decreased accordingly, although this has been documented in other baleen whale stocks (Tulloch et al., 2019).

Alternatively, a downward trend in LSM may occur if whales reach sexual maturity at a consistent age but are growing more slowly in recent years, thereby being smaller at the age they mature. We have no direct data to support this alternative for bowhead whales, but decreased body length has been noted in North Atlantic right whales (*Eubalaena glacialis*), for which the cumulative impacts from anthropogenic activities (bycatch, noise pollution, vessel traffic) to shifting prey fields are all thought to be contributing factors (Stewart et al., 2021). Future study of this alternative hypothesis is needed. Lastly, we cannot exclude the possibility that historical commercial whaling of BCB bowhead whales induced evolutionary (genetic) changes by selecting against certain life history traits (e.g., Kuparinen & Festa-Bianchet, 2017; Sharpe & Hendry, 2009), although the fact that commercial whaling for BCB bowhead whales ended over 100 years ago makes this hypothesis about the recent observed change less likely.

Table 3 presents sexual maturity estimates for the bowhead whales' "sister taxa," the right whales (Family Balaenidae). These species generally attain sexual maturity at a body length of about 12.5 m, with the possible exception of North Pacific right whales (*Eubalena japonica*), whose length at sexual maturity appears longer, although data from Omura et al. (1969) were limited. LSM for BCB bowhead whales appears to be in the middle of the range estimated for these other species of right whale. When comparing the estimates in Table 3, note that our determination of maturity is based on evidence of a past ovulation, whereas for other right whale populations, LSM is often determined on the basis of calf presence. It could be argued that the estimates are incomparable, due to growth between ovulation and birth. However, Koski et al. (1992) estimated the growth of bowhead whales with a body length of 12 m of approximately 0.15 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 maturity is detected (i.e., based upon the physical examination of harvested whales versus the detection of a calf) are not enough to explain the variation seen in Table 3.

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

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

Our estimated ASM is also consistent with observations that the bowhead whale is a slowly growing species with a correspondingly low metabolic rate that likely contributes to their high ASM compared with other mysticetes (George, 2009; Tarpley et al., 2021). The mean ASM for right whales ranges from about 7–10 years, which is estimated using longitudinal photo-recapture and determined when a female is first seen with a calf. For example, for North Atlantic right whales, Kraus et al. (2007) reported a mean age of first calving of 10.1 years

TABLE 3 Estimates of length (m) and age (years) at sexual maturity for the right whales (Family Balaenidae).

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)

(individual range 5–21). For southern right whales, Best et al. (2001) estimated the median age of first parturition at 7.9 years, 95% CI [7.1, 9.3]. The age at sexual maturity estimates for right whales are less than half those for bowhead whales (Table 3). As noted earlier, slow growth and late reproduction for bowhead whales is well established in the literature and speculations in several papers (Burns, 1993; George et al., 1999, 2021) suggest it is related to their low metabolic rates, diverting significant resources to energy storage in the blubber and highly variable, often low-density prey availability at high latitudes (George et al., 2021). We attribute the late age at sexual maturity in bowheads, as compared with other Balaenids, to their slow growth rather than simply being “short for their age.” Maximum lengths for bowheads are similar to or larger than those of other Balaenids (George, 2009).

4.2 | Pregnancy rate and calving interval

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

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

Calving intervals are of particular interest biologically, with implications for potential recovery rates of the BCB bowhead whale population and management applications. A large body of information on bowhead whale reproduction shows no evidence of calving intervals of <3 years (e.g., Koski et al., 1993; Rugh et al., 1992; Tarpley et al., 2021). Considerable evidence from past studies suggests BCB bowhead whales reproduce on a 3- to 4-year calving interval. Miller et al. (1992) estimated interbirth intervals using photographic data, where they noted two photographic recaptures at 4 years and three recaptures at 7 years for mothers with young calves. Their data are open to a number of interpretations, because these mothers were not seen every year, and their estimates of interbirth intervals ranged from 3.3 to 5.8 years, with 3.3–4.5 years as the most likely range. Miller et al. (1992) did not find any 3-year intervals, but considered them likely. These authors as well as Rugh et al. (1992) suggested that the 7-year intervals could be real or could represent a combination of 3- and 4-year intervals. Using another method based on the frequency of bowhead whale females with calves in their photographic sample, Miller et al. (1992) estimated a calving interval of 3.3 years. George et al. (2011) examined a sample of mature females using presence of a CL, CA, and/or fetus, and estimated an ovulation rate value of 0.332 per year and a PR of 0.326 per year, implying intervals between ovulations and pregnancies of 3.0 and 3.1 years. Rolland et al. (2018) analyzed progesterone spikes in the baleen plates of three large mature females, as well as annual cycles in the stable carbon isotopes to estimate time intervals between hormone spikes (Schell & Saupe, 1993). Using this approach, one of their analyses yielded estimated calving intervals ($n = 11$) ranging from 2.10 to 5.31 with a mean of 3.11 years (Tarpley et al., 2021). Analysis of baleen hormone cycles is perhaps the most promising direct technique to investigate reproductive history in bowhead whales and other baleen whales (e.g., Hunt et al., 2014, 2016, 2017; Lowe et al., 2021).

Other evidence, such as the current rate of population increase (Givens et al., 2016), percent calves in surveys (Clarke et al., 2022; Koski et al., 2006), the current harvest rate, and survival rate (da Silva et al., 2007; Schweder et al., 2010; Zeh et al., 2002), all suggest that a 3-year interval is the most plausible.

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

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

The weight of evidence based on all these sources suggests the BCB bowhead whale calving interval is 3–4 years with a possibility of rare 2-year intervals. We suggest that estimating bowhead whale calving intervals derived from the pregnancy rate estimates of harvested whales is useful, but some of the other methods discussed above, including baleen hormone cycles and aerial surveys, are more direct and less susceptible to biases.

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

DEDICATION

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

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AUTHOR CONTRIBUTIONS

John C. George: Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing. **Geof H. Givens:** Conceptualization; formal analysis; methodology; software; visualization; writing – original draft; writing – review and editing. **Lara Horstmann:** Investigation; resources; writing – original draft; writing – review and editing. **Robert Suydam:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing. **Kayla Scheimreif:** Data curation; investigation; writing – review and editing. **Raphaela Stimmelmayer:** Funding acquisition; investigation; writing – original draft; writing – review and editing. **Gay Sheffield:** Investigation; writing – original draft; writing – review and editing. **Todd L. Sformo:** Investigation; writing – review and editing. **Brian Person:** Investigation; writing – review and editing. **Andrew Von Duyke:** Investigation; writing – review and editing. **Leandra Sousa:** Investigation; writing – review and editing. **Rita Acker:** Investigation; writing – review and editing. **Raymond Tarpley:** Investigation; resources; writing – review and editing.

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