Frontiers in Marine Science

TYPE Original Research
PUBLISHED 21 January 2026
DOI 10.3389/fmars.2025.1707758

Mating systems, parentage, and reproductive success of beluga whales in Bristol Bay, Alaska

G. O'Corry-Crowe[1]*, L. Quakenbush[2], T. Ferrer[1], J. J. Citta[2]† and A. Bryan[2]

[1]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL, United States,
[2]Alaska Department of Fish and Game, Arctic Marine Mammal Program, Fairbanks, AK, United States

OPEN ACCESS

EDITED BY
Mridula Srinivasan,
NMFS, United States

REVIEWED BY
Evelien De Greef,
University of Manitoba, Canada
A.J. Paijmans,
Bielefeld University, Germany

*CORRESPONDENCE
G. O'Corry-Crowe
gocorryc@fau.edu

†PRESENT ADDRESS
J. J. Citta,
North Slope Borough Department of Wildlife Management, Utqiagvik, AK, United States

RECEIVED 17 September 2025
REVISED 17 November 2025
ACCEPTED 18 November 2025
PUBLISHED 21 January 2026

CITATION
O'Corry-Crowe G, Quakenbush L, Ferrer T, Citta JJ and Bryan A (2026) Mating systems, parentage, and reproductive success of beluga whales in Bristol Bay, Alaska. *Front. Mar. Sci.* 12:1707758. doi: 10.3389/fmars.2025.1707758

An aquatic mode of life and sociality influences mating strategies in cetaceans. In high latitude species, like the beluga whale, extreme seasonality likely imposes additional constraints on parental care, competition, and mate choice. Genetic profiling of 623 biopsy-sampled beluga whales in Bristol Bay, Alaska revealed that both sexes were polygamous, calves associated predominantly with their mothers, variation in reproductive success was slightly greater in fathers, and there was low short-term positive reproductive skew in both sexes. Males were moderately polygynous within and across breeding seasons and females were polyandrous across breeding seasons, (within breeding seasons was undetermined), indicating a polygynandrous mating system. In addition, although the effective population size (N_e) was much lower than census population size (N_c), high levels of genetic diversity and low levels of inbreeding were found within and across generations. Despite larger body size and polygyny, short-term male reproductive success was limited, possibly due to challenges of guarding multiple females and female mating strategies. A long reproductive life, however, may lessen the selective pressure for intense intrasexual competition and strong polygyny within seasons. Polygynandry across breeding seasons leads to long, loose-chain pedigrees that can lower inbreeding and maintain diversity, even in populations with small N_e.

KEYWORDS

mating system, beluga whale, polygynandry, effective population size, longevity, loose-chain pedigree, *Delphinapterus leucas*

1 Introduction

The mating systems and sexual behavior of beluga whales, *Delphinapterus leucas*, in the wild are largely unknown. Their seasonally ice-covered habitat provides unique challenges for this northern whale to secure mates and successfully raise offspring. This environment is also challenging for investigators studying beluga whale reproductive strategies. Much of what we know about beluga whale reproductive behavior comes from studies on captive animals (Hill et al., 2024). By contrast, field observations of mating behaviors are few (Lomac-MacNair et al., 2015; Lydersen et al., 2023), insights into the care of young are confounded by the limited data on care behaviors and kinship (Krasnova et al., 2014; O'Corry-Crowe et al., 2020; Aubin et al., 2021), and opportunities to collect sufficient tissue samples for genetic studies of parentage, mate choice, and reproductive success are rare.

Despite this paucity of information, there are characteristics of beluga whale biology and their habitat that when examined in the context of evolutionary theory, allow us to predict what beluga mating strategies and breeding behavior might be, and how they may influence other population parameters. Such predictions can then be formally tested via genetic analyses of wild populations. We took this approach here.

Firstly, we considered probable beluga reproductive strategies in the context of established evolutionary theory. Sexual selection theory posits that the evolution of mating strategies is driven by competition for mates and mate choice (Darwin, 1871). Furthermore, reduced parental investment by one sex, typically males, increases their potential rate of reproduction, increasing the relative number of reproductively active males to receptive females at any one time (Trivers, 1972). This increases the operational sex ratio (OSR) towards males, which in turn leads to: (1) increased male-male competition, (2) greater variance in male reproductive success (e.g., polygyny), and (3) stronger selection for traits that improve competitive ability (e.g., larger body size, weapons, ornaments) in males (Darwin, 1871; Trivers, 1972; Clutton-Brock, 2007). Choosiness by females further increases male-male competition (Darwin, 1871; Trivers, 1972) and may also reduce the costs of sexual conflict (Harris and Moore, 2005). Females may mate with multiple males (i.e., polyandry) to ensure paternity by quality males (e.g., via sperm competition) or as a bet-hedging strategy to maximize reproductive success by spreading risk (Garcia-Gonzalez et al., 2015; Fromonteil et al., 2023), although the evolution of polygamous mating systems is also influenced by the ability to defend access to multiple mates (Emlen and Oring, 1977).

Within this theoretical context, we note that beluga whales exhibit sexual size dimorphism (SSD), with adult males up to 25% longer and substantially heavier than adult females (Sergeant and Brodie, 1969; Burns and Seaman, 1986; Heide-Jørgensen and Teilmann, 1994; Suydam, 2009; Vos et al., 2020). This male-biased size dimorphism was recently observed to be among the largest in cetaceans and was interpreted as consistent with high inter-male competition and polygyny (Caspar and Begall, 2022). Females have long inter-birth intervals of 2–4 years (Suydam, 2009; Ferguson et al., 2020) which skews the OSR towards males, thereby predicting concomitant increases in male-male competition. Furthermore, belugas have been found with conspecific scarring from tooth rakes which may reflect contest competition (i.e., fighting) for mates (Hamm et al., 2021). Also, age and sex segregation (Kleinenberg et al., 1964; Michaud, 1993; Loseto et al., 2006), including the occurrence of small groupings of adult males within much larger aggregations comprised of all ages and both sexes that can number ≥1,500 individuals (Smith et al., 1994; Chernetskii et al., 2011; O'Corry-Crowe et al., 2020), suggests reduced parental investment by males.

Next, we considered how behavioral, environmental, and life-history characteristics set limits on how beluga reproductive strategies can evolve and operate. We identified five key characteristics: (1) Belugas live in large complex societies (Kleinenberg et al., 1964; O'Corry-Crowe et al., 2020), possibly intensifying reproductive competition (Clutton-Brock and Huchard, 2013), but it could also increase access to multiple mates. (2) The 3-dimensional aquatic environment restrains the form that such competition takes as an individual's ability to monopolize receptive mates is likely limited, which could influence the intensity of sexual selection (Emlen and Oring, 1977). This environmental constraint could favor scramble-competition (e.g., continuous mate-searching) (Foley et al., 2018) over contest-competition (e.g., fighting) for mates. It may also select for cooperative strategies (e.g., male alliances) to secure access to mates as has been observed in other cetaceans (e.g., bottlenose dolphins, *Tursiops* spp.) (Connor et al., 2001; Brightwell and Gibson, 2023). (3) The extreme seasonality of the beluga's environment (i.e., ice cover, food availability) may necessitate specific timing of mating activities to ensure calves are born at a favorable time of year. As such, seasonality could also influence the intensity and form of reproductive competition if mating is restricted to a brief window of time. (4) The possibility of a long post-reproductive lifespan (i.e., reproductive senescence) in female belugas (Suydam, 2009; Ellis et al., 2018; Ferguson et al., 2020) may further skew OSR towards males, further increasing male-male competition. (5) Beluga whales are among the longest-lived mammals, possibly living longer than 90 years (Suydam, 2009; Ferguson et al., 2020), and therefore have long reproductive lives. Such longevity likely provides many mating opportunities over the course of an individual's lifetime.

Finally, we considered how beluga whale mating systems might influence parameters that have implications for individual fitness and population viability, namely, effective population size, N_e, genetic diversity, and inbreeding. N_e determines the rate of loss of genetic diversity within a population via random drift with consequences for heterozygosity, H, and inbreeding (Wang et al., 2016; Waples, 2025). N_e is influenced by demographic factors including historical population sizes, bottlenecks, and founding and mixing events. However, it is also influenced by mating strategies. High variance in reproductive success in one or both sexes, for example, can substantially reduce N_e (Waples, 2025). Small N_e accelerates diversity loss, leading to reduced H across both functional and neutral genetic loci, and increases the likelihood of inbreeding (Wang et al., 2016; Waples, 2025). Higher levels of inbreeding further impacts H with consequences for individual fitness (Charlesworth and Charlesworth, 1987; Charlesworth and Willis, 2009). Here too, mating strategies can play a central role. Avoidance of consanguineous matings, for example, can limit inbreeding (Morrison et al., 2023) and thus, help offset deleterious impacts of diversity loss on fitness. Therefore, if mate choice is not random in beluga whales, and there is high variance in reproductive success in either or both sexes, contemporary N_e could be much smaller than census population sizes, N_c, which could result in low H and elevated likelihoods of inbreeding.

We investigated mating systems, parentage, and reproductive success in a population of beluga whales in Bristol Bay, Alaska (Figure 1) using molecular genetic profiling of 623 wild whales that were biopsy-sampled over a 13-year period. This population is genetically discrete from other populations, movements are limited in range, and genetic and individual exchange with other populations appears to be low to non-existent (O'Corry-Crowe et al., 2018; Citta et al., 2016). Biopsies were collected together with field observations of individual association patterns and age. We used knowledge of beluga whale behavior, ecology, and life-history in the context of evolutionary theory to develop five predictions on beluga mating systems and their influence on a number of population parameters, that we tested as eight formal hypotheses. Definitions of mating systems vary widely and can relate to mating strategies used by males and females over a short (e.g., one or a few breeding seasons) or longer (e.g., entire reproductive life) period (Shuster and Wade, 2003; Klug, 2011; Szala and Shackelford, 2019; Würsig et al., 2023). We investigated short-term strategies as our study spanned a number of years in a species with a very long-lifespan, and we defined three polygamous mating systems: (1) polygyny: one male mates with multiple females within or across breeding seasons, (2) polyandry: one female mates with multiple males within or across breeding seasons, (3) polygynandry: both males and females have more than one mate within or across breeding seasons. As our genetic analyses can only determine the paternity of the single calf born to a female in a given year, we cannot comment on polyandry within seasons, but can identify polyandry across seasons.

1.1 Prediction 1

Based on evidence of SSD, conspecific scaring, and periods of segregation by age and sex, we predict a polygynous mating system in beluga whales where males provide little or no parental care, compete for access to females and have higher variance in reproductive success than females.

> *H1. Polygyny: there is a high proportion of paternal half-sibs among calves denoting polygyny within and across breeding events.*

> *H2. Parental care: adult-calf pairings sampled in the field involve a higher number of mothers than fathers.*

> *H3. Variance in reproductive success: there is higher variance in reproductive success in males than females.*

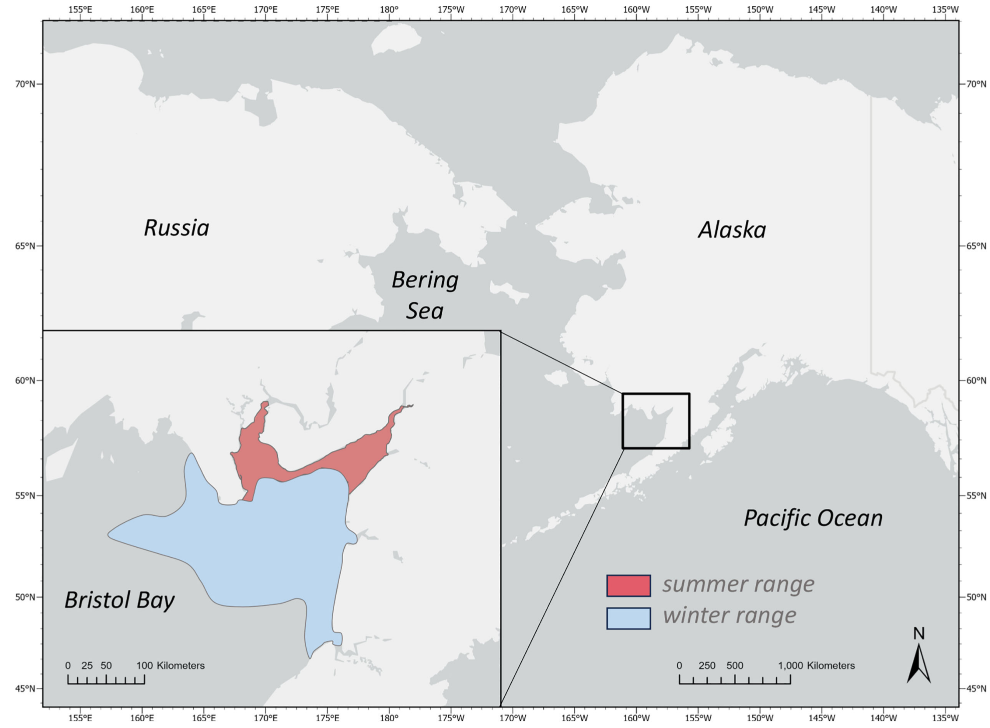

FIGURE 1
The location and range of the Bristol Bay population of beluga whales. The shading indicates the summer and winter range of this population. The winter range includes the summer distribution.

1.2 Prediction 2

Beluga societies are characterized by large seasonal aggregations and fission-fusion dynamics, and beluga females have long inter-birth intervals and a long reproductive life. Re-encounters with former mates therefore, may be unpredictable, while mating with different males may increase fitness over time. We predict females will be polyandrous across breeding seasons, in part as a genetic bet-hedging strategy to spread the risk of mating with low quality males.

> *H4. Polyandry: there is a high proportion of maternal half-sibs among calves denoting polyandry across breeding events.*

1.3 Prediction 3

Belugas are long-lived and likely have long reproductive lifespans, where older animals have higher lifetime reproductive success (i.e., more offspring in the population). We predict that social dominance, competitive ability, and/or experience, may also increase short-term reproductive success with age, such that older animals have more *young* offspring in the population at any one time.

> *H5. Short-term reproductive success and age: older adults have higher short-term reproductive success than younger adults.*

1.4 Prediction 4

We predict that non-random mate choice and high variance in reproductive success in either or both sexes results in current effective population size (N_e) being much smaller than census population size (N_c), currently estimated at ≈2,000 (Citta et al., 2018).

> *H6. Effective population size:* N_e *is* $<< N_c$.

1.5 Prediction 5

We predict that mate choice, substantial variance in reproductive success, and small N_e will result in high levels of inbreeding and loss of diversity in the small Bristol Bay population.

> *H7. Inbreeding: Bristol Bay beluga whales have high inbreeding coefficients.*

> *H8. Genetic diversity: Bristol Bay beluga whales have low genetic heterozygosity.*

2 Materials and methods

Eight hundred skin samples were collected from beluga whales in Bristol Bay, Alaska from 2002-2014. Most (n=721/800; 90.1%) were skin plugs (≤ 8mm diameter) collected from free swimming whales using methods detailed in Citta et al. (2018). The rest were collected from whales that were captured and briefly restrained as part of concurrent satellite tagging projects (n=67; 8.4%) (Citta et al., 2016), and whales that were harvested or recovered dead over the course of the study (n=12; 1.5%). Most samples were collected during a week-long dedicated biopsy effort each spring over an eight-year period (2004-2011; see Supplementary Table S1). Detailed information on the association patterns and grouping behavior of sampled whales was collected at the time of sampling. Furthermore, sampled whales were placed into three broad categories based on their body color as a proxy for age: (1) dark gray to gray (G) representing calves including dependent offspring and juveniles, (2) white-gray (WG) representing young adults, and (3) white (W) representing older adults.

All samples were preserved in 20% DMSO saturated in NaCl, or frozen upon collection and subsequently stored at -20°C. Total DNA was extracted using DNeasy® purification kits (Qiagen) or via salt extraction methods, and samples were PCR-typed for sex, and were genotyped at microsatellite loci on a Genetic Analyzer 3130 (Applied Biosystems) according to previously published methods (O'Corry-Crowe et al., 2010, 2018, 2020; Citta et al., 2018). Each sample was screened for polymorphism at 22 unlinked, hypervariable microsatellite loci (Table 1). Duplicate samples were identified based on multi-locus estimates of probabilities of identity (P_{ID}) in the program CERVUS (v3.0; Kalinowski et al., 2007) and were removed from further analyses (Supplementary Table S1).

Descriptive statistics for each locus, including allele frequencies, number of alleles and heterozygosity, were calculated using the MICROSATELLITE ANALYZER (MSA) program (Dieringer and Schlötterer, 2003) (Table 1). We used the program MICRO-CHECKER (Van Oosterhout et al., 2004) to determine if any of the microsatellite loci suffered from scoring error bias or null alleles. None of the loci exhibited evidence of scoring errors due to stuttering or large allelic dropout and none were found to possess null alleles (Supplementary Table S2). Furthermore, we found 169 samples out of the original 800 to be duplicates from the same individuals because they matched at all seven loci used in an earlier genetic mark-recapture analysis (Citta et al., 2018). Including the additional 15 loci identified a further 8 samples that were exact matches or differed at one locus resulting in a final dataset of 623 individual whales. Thus, in cases where there was a mismatch at one locus among duplicate samples it was likely due to a scoring error. This allowed us to estimate a genotype scoring error rate of 0.856%.

TABLE 1 Details of the microsatellite loci used in the analysis of mating systems in Bristol Bay beluga whales.

Locus name	STR (e.g. CA)	Repeat type	Reference	H obs	H exp	No. of alleles	Citta et al., 2018 O'Corry-Crowe et al., 2018
CS415		dinucleotide	Schlötterer et al. (1991)	0.630	0.629	4	yes
CS417			Schlötterer et al. (1991)	0.849	0.823	8	yes
EV37*Mn*	(AC)24	dinucleotide	Valsecchi and Amos (1996)	0.768	0.768	13	yes
EV94*Mn*	(TC)6[…](AC)20	compound	Valsecchi and Amos (1996)	0.803	0.780	8	yes
DlrFCB3			Buchanan et al. (1996)	0.801	0.799	9	yes
DlrFCB5	(GT)16	dinucleotide	Buchanan et al. (1996)	0.516	0.526	6	yes
DlrFCB17			Buchanan et al. (1996)	0.863	0.889	14	yes
DlrFCB1			Buchanan et al. (1996)	0.770	0.761	6	
DlrFCB10			Buchanan et al. (1996)	0.812	0.815	7	
DlrFCB13			Buchanan et al. (1996)	0.282	0.290	3	
DlrFCB2			Buchanan et al. (1996)	0.513	0.529	6	
DlrFCB11			Buchanan et al. (1996)	0.151	0.150	4	
DlrFCB16			Buchanan et al. (1996)	0.660	0.655	8	
MK6	(GT)17	dinucleotide	Krützen et al. (2001)	0.792	0.777	7	
EV14*Pm*	(GT)11	dinucleotide	Valsecchi and Amos (1996)	0.832	0.802	6	
Tur4_141	(GATA)9	tetranucleotide	Nater et al. (2009)	0.370	0.382	6	
MK9	(CA)17	dinucleotide	Krützen et al. (2001)	0.319	0.332	3	
Tur4_80	(GATA)10	tetranucleotide	Nater et al. (2009)	0.818	0.814	8	
Ttr19	(CA)17	dinucleotide	Rosel et al. (2005)	0.627	0.646	6	
DlrFCB4	(AT)2(CT)4(CA)13	compound	Buchanan et al. (1996)	0.709	0.745	9	
TexVet5	(CA)24	dinucleotide	Rooney and Meritt (1999)	0.656	0.697	7	
KWM12a	(AC)n	dinucleotide	Hoelzel et al. (1998)	0.507	0.503	5	
			mean:	0.639	0.641	6.955	

Estimates of observed and expected heterozygosity and the number of alleles were calculated for the entire dataset (n=623) using the MICROSATELLITE ANALYZER program. Those loci that were used in recent studies cited in the text are listed in the final column.

Some samples had missing genotype scores at one or more loci due to poor amplification and/or ambiguous electopherograms that prevented accurate allele calls. Only individuals scored at ≥19 loci were included in analyses of relatedness, parentage and reproductive success. Previously, we found that six loci were sufficient to yield reliable estimates of high relatedness and close genealogical relationship in other beluga whale populations (O'Corry-Crowe et al., 2020), however we chose the higher threshold of 19 loci in the current study to maximize our ability to discriminate among a number of close relationships, namely parent-offspring, full-sib and half-sib (including grandparent-grandchild) pairings within a small population of belugas (N~2,000) (Citta et al., 2018, 2019) where the probability of allele sharing not by direct descent may be quite high. CERVUS was used to test for deviations from Hardy-Weinberg expectations for each locus.

Likelihood methods were used to infer parentage of and sibship relationships among beluga whale calves from the microsatellite data. The programs COANCESTRY (Wang, 2011) and ML-RELATE (Kalinowski et al., 2006) were used to estimate relatedness, *r*, and genealogical relationship among individuals. COANCESTRY implements seven estimators of *r* that use multilocus genotypic data. We used the allele frequencies of the 22 microsatellite loci to simulate genotypes of pairs of individuals with one of four predefined relationships: parent–offspring (PO), full-sib (FS), half-sib and grandchild–grandparent (HS), and unrelated (U), in order to determine which estimator performed best. We found that of the seven *r* indices compared, the two likelihood estimators, including the dyadic ML estimator, r_{DyadML} (Milligan, 2003), and the moment estimator, r_{QG} (Queller and Goodnight, 1989), performed best and thus were used. We then inferred likely genealogical relationships among pairs of individuals from the r values calculated by COANCESTRY. ML-RELATE also uses a maximum likelihood approach to estimate relatedness. Unlike COANCESTRY, however, it directly estimates the likely relationship between all pairs of individuals for the same four relationship categories: PO, FS, HS and U, and calculates statistical support for the most likely relationship by comparing the difference in the log likelihood of the relationship with the highest likelihood to the log likelihoods of all the other relationships, delta Ln(L). This facilitates comparisons of r and relationships for each pair of individuals.

Parentage was also analyzed using the programs CERVUS and COLONY (Jones and Wang, 2010; Wang, 2022). CERVUS uses a panel of sampled candidate mothers and fathers to assign parentage to sampled offspring. Statistical confidence in the assignments is based on the natural log of the likelihood-odds ratio (LOD) of an individual male or female to one drawn at random where a large difference (Δ) in the LOD score of the male (or female) with the highest score compared to the male (or female) with the second highest score denotes high confidence that the male (or female) with the highest score is the father (or mother). CERVUS can accommodate genotyping errors which has been found to increase success in paternity assignment (Kalinowski et al., 2007) and we also used this program to compare expected heterozygosity between calves and adults. We used COLONY to assign parentage of, and to estimate sibships among, offspring using full likelihood (FL) methods (Wang, 2022). Furthermore, COLONY reconstructs parental genotypes enabling the assignment of a likely mother and father to all offspring whether the parent was sampled or not. Polygamy in both sexes can lead to extended familial clusters where many sibships are half-sibs that link offspring via the shared parent. Thus, an individual offspring may be linked to a maternal half-sib on one hand and a paternal half-sib on the other. These links can form long chains of parent-offspring relationships termed loose-chain pedigrees. Additionally, we used COLONY to reconstruct two-generation pedigrees and identify extended familial clusters and used the program PEDIGREE VIEWER (B. and S. Kinghorn) to generate the pedigree diagrams. We used small paternal and maternal sibship sizes (i.e., the distribution of the likely number of sibships; n_p=n_m = 1, x = 0.25) as priors to reduce false sibship assignments and long, loose pedigrees.

Expected heterozygosity, H_{exp}, for each locus was estimated using CERVUS. Standardized multi-locus heterozygosity, sMLH (Coltman et al., 1999), was also estimated for each individual using the R package INBREEDR (Stoffel et al., 2016). COANCESTRY and COLONY were used to estimate inbreeding coefficients, F, in calves and likely parents and to test for differences in average F among groupings. In COANCESTRY the observed differences were compared to a distribution of differences based on 50,000 randomized bootstrap runs of the data. Finally, we estimated current N_e from the estimated frequency of siblings among offspring in COLONY. This approach is based on the logic that the smaller N_e is the higher the probability that two offspring drawn at random are siblings (Wang, 2009). The estimate of N_e will be biased low if individuals are not drawn from the same generation. We attempted to minimize this bias by running the analysis for short as well as long-term datasets (see below).

There were a number of factors with the study design that needed to be taken into consideration when conducting parentage analysis and estimating reproductive success. Firstly, the three age categories were quite broad, each comprising whales of differing ages, and likely overlapped to some degree. For example, the gray (G) category comprised young offspring and included yearlings, two-year-olds, and likely some older juveniles (neonates were not sampled). The white-gray (WG) category comprised young adults of various ages and may have included some whales that were sexually and/or socially immature and not part of the breeding population. The white (W) category comprised older adults of varying ages that had all reached breeding age. Secondly, because the project spanned more than a decade, some calves sampled early in the study may have reached adulthood and thus entered the breeding population towards the end of the study. Similarly, active breeders at the beginning of the study may have become reproductively senescent or died towards the end of the project. To reduce the likelihood of confounding different generations in assessments of reproductive success, inbreeding, and effective population size (N_e) we re-ran all the analyses originally conducted on the entire 13-year dataset, on a shorter 2-year dataset that comprised samples from the best sampled years (2010 and 2011).

All field activities related to the collection of tissue samples from wild whales were approved by the Alaska Department of Fish and Game's IACUC under protocols 05-12, 06-16, 09-21,10-13R, 2012-020, 2013-020, and 2014-03. All methods of sample collection were carried out in accordance with the guidelines and regulations of the U.S. Endangered Species Act and the U.S. Marine Mammal Protection Act under NMFS ESA/MMPA research permits 782-1719, 14610, and 14245. All activities with wild whales are reported in accordance with ARRIVE guidelines.

3 Results

Of 800 beluga whale samples genotyped, 177 were duplicates, yielding 623 individuals that were genetically profiled (Supplementary Table S1). These individuals were used to estimate population-wide diversity indices (Table 1). Another 100 individuals did not reach our threshold of ≥19 loci scored for the analysis of relatedness and parentage, resulting in 523 individual whales used in those analyses. Almost all (n=513) were successfully typed for sex and assigned an age category in the field based on color. Of these 513 whales, 144 were calves (G for gray), 184 were adult females and 185 were adult males. Roughly half of the adult females were older (W for white) adults (n=84) and half younger (WG for white-gray) adults (n=100). Two thirds of the adult males were Ws (n=126) compared to WGs (n=59). Genotypic proportions for the 523 individuals did not differ significantly from Hardy-Weinberg expectations (p>0.05) at any of the 22 microsatellite loci.

3.1 H1. Are males polygynous?

We documented polygyny in males using both the relatedness and parentage methods (Figure 2). For example, ML-RELATE found

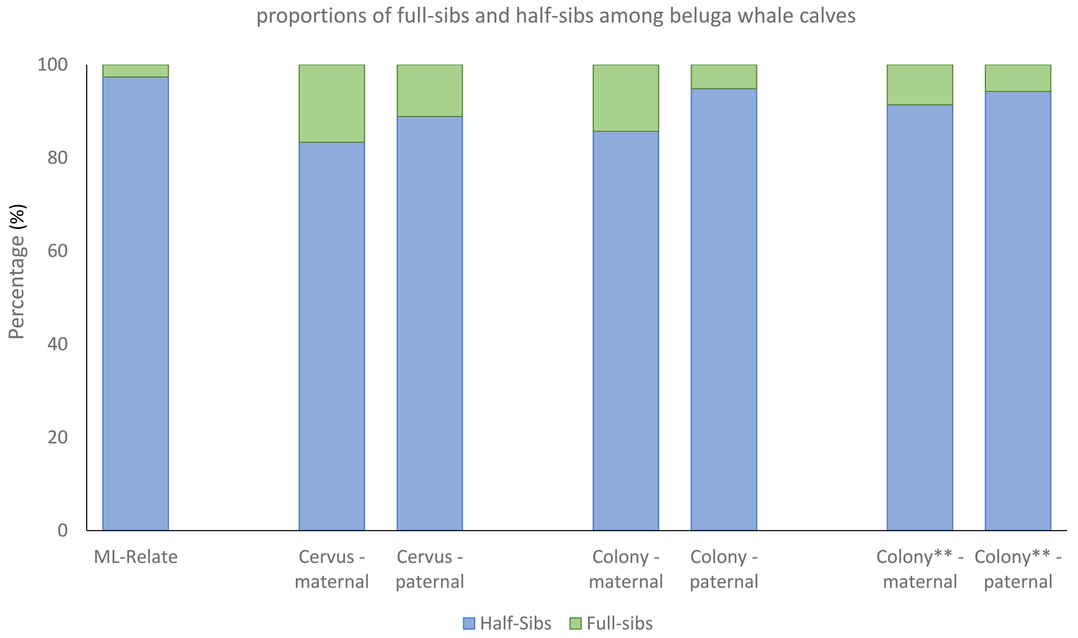

FIGURE 2
Proportions of half-sib and full-sib relationships among beluga whale calves. Sibling relationships were determined based on estimated relatedness among calves (ml-relate) or inferred parentage of calves (cervus and colony), the latter allowing for the determination of maternal and paternal half-sibships. The colony analysis was conducted for sampled parents only and for both sampled and unsampled parents combined (denoted by double asterisks).

that most of the sibships detected among pairs of calves (97.4%) were half-sibs, i.e., shared only one parent. The total number of half-sibs identified by ML-RELATE (n=1,331), however, was artificially high, as many pairs where the relationship HS was found to be more likely than the other three (i.e., FS, PO and U), had *r* values substantially lower than $r = 0.25$, and thus, may have been more distantly related (i.e. cousins). COLONY found that for males, where two or more of their offspring were sampled as calves, 94.2% (n=197/209) of these sibships were half-sibs, indicating that males successfully bred with multiple females.

3.2 H2. Are calves more associated with mothers than fathers?

The ML-RELATE, COANCESTRY, COLONY, and CERVUS analyses found that 9 out of 10 (90%) adult-calf pairs sampled together were mother-calf pairs. The exception was an adult female not closely related to the calf.

3.3 H3. Is there greater variance in reproductive success in males compared to females?

We found substantial variation in estimated reproductive success in both sexes. ML-RELATE revealed that 41.5% of adults sampled were part of a parent-offspring pair. However, limited information on adult age prevented us from determining, in cases where both individuals of the pair were adults, which was the parent, and which was the offspring. This required focusing our analysis on the parentage of sampled calves. All analyses found that the number of offspring per adult was low. Details of the various analyses are presented in Supplementary Material. The COLONY analysis had the highest number of parentage assignments of sampled adults (n=114) and also assigned a likely parent to all offspring (n=144) whether the parent was sampled or not (Table 2). This revealed that fewer fathers contributed to the sampled calves than mothers ($n_{father} = 54$ vs. $n_{mother} = 69$), that successful males had slightly more calves, on average, than successful females ($\bar{x}_{father} = 2.67$ vs. $\bar{x}_{mother} = 2.09$, $p = 0.054$), that the variance in the total number of calves per parent was significantly higher for males compared to females ($V_{father} = 3.36$ vs. $V_{mother} = 1.79$, Levene's test $p = 0.039$; Figure 3A), and that the frequency distribution of the number of sampled calves per parent was positively skewed for both fathers and mothers towards a low number of parents having moderately high numbers of calves ($S_{kp\text{-}father}=1.53$, $S_{kp\text{-}mother}=1.55$; Figure 3A). Parent-calf pairs that were sampled in close association were not strictly independent. Excluding these yielded similar results. Notably, the mean number of calves for fathers ($\bar{x}_{father} = 2.67$) was now significantly higher than that for mothers ($\bar{x}_{mother} = 2.06$, $p = 0.046$; Figure 3A).

Running an analysis over a two-year timeframe, (see Materials and methods), revealed similar findings of low to moderate

TABLE 2 Summaries of inferred parentage of beluga whale calves using cervus and colony.

	CERVUS		COLONY			
			Sampled parents		Sampled and unsampled parents	
	Paternity	*Maternity*	*Paternity*	*Maternity*	*Paternity*	*Maternity*
Assignments	36	62	45	69	144	144
Unassigned	108	82	99	75	0	0
No. of calves	144	144	144	144	144	144
Parent of 1 calf	28	47	6	21	18	30
Parent of 2 calves	4	6	6	11	11	19
Parent of 3 calves		1	5	7	12	12
Parent of 4 calves			3		7	3
Parent of 5 calves				1	2	3
Parent of 6 calves					1	1
Parent of 7 calves					1	1
Parent of 8 calves					1	
Parent of 9 calves					1	
No. of parents	32	54	20	40	54	69
Mean no. of calves per parent	1.13	1.15	2.25	1.73	2.67	2.09

Only parentage assignments with moderate to high confidence are reported for the cervus analysis, while parentage for the colony analysis includes those involving sampled parents and both sampled and unsampled parents. Inferred parentage for the ml-relate and coancestry analyses are in Supplementary Material.

numbers of calves for both males and females, more calves on average, and greater variance in calf number in males compared to females (Figure 3B, Supplementary Material). None of these differences, however, were found to be statistically significant.

3.4 H4. Are females polyandrous?

Females were mostly polyandrous across breeding seasons (Figure 2). Both cervus and colony found that the majority (83.3-

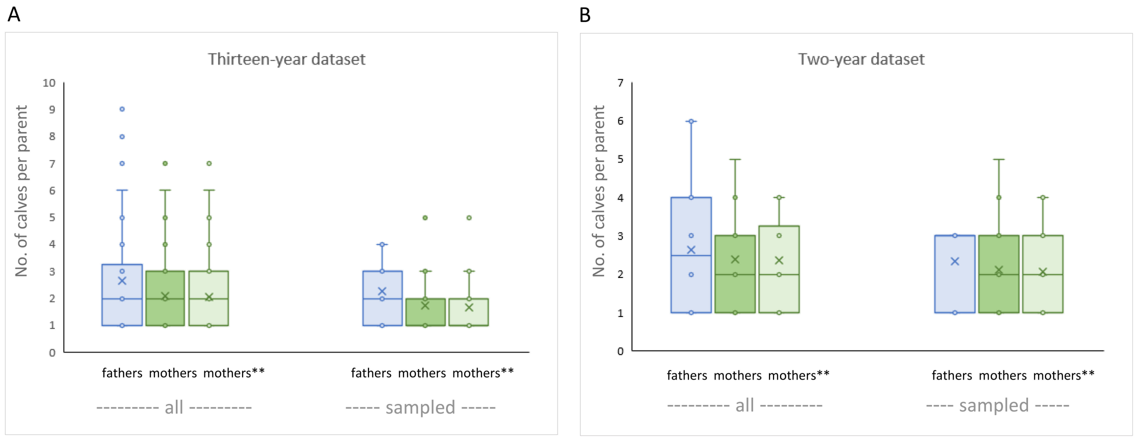

FIGURE 3
Estimated reproductive success of beluga whale fathers and mothers based on parentage assignments of calves using the program colony. Panel **(A)** is for the entire thirteen-year dataset, panel **(B)** for the shorter two-year dataset. Each panel comprises estimates for all parents (i.e. sampled and unsampled) as well as for sampled parents only. The range, central tendency (mean and median) and variance of the number of calves per parent are given for fathers and mothers, and for those mothers where their calves were not co-sampled with them as part of associated cow-calf pairs (see text for details). This latter group is denoted by double asterisks. The box captures the first and third quartiles, the median is represented by a line and the mean by an X, and outliers are defined by the 1.5x IQR rule.

91.4%, COLONY: n=127/139) of maternal sibships were half-sibs and thus, involved different fathers. A small number of full-sibs were identified (Figure 2), indicating that some females successfully bred with the same male more than once. Full siblings from one adult pair were sampled up to six years apart. On three occasions where the sampling of full-sibs was separated by a number of years, another calf was sampled in the interim, and found to be a half sibling to the full-sibs. It should be noted that year-of-sampling may not consistently track year-of-birth.

The high levels of polygamy did not differ between male and female parents (χ^2 p = 0.102). Furthermore, the majority of maternal (73.8%; n=31/42) and paternal (77%; n=30/39) sibships were sampled in different years vs. the same year, with some sampled up to seven years apart. These proportions did not differ between males and female parents (χ^2 p = 0.658). The high proportion of half-sibships from both male and female polygamy resulted in a series of indirect linkages that formed loose-chain pedigrees. For example, in the two-generation pedigree from the COLONY analysis, many offspring were linked either directly by sharing a parent, or indirectly through a shared half-sib (Figure 4). Such indirect linkages tended to result in long loose-chain pedigrees or large clusters of offspring connected in this way (Figure 4).

3.5 H5. Do older adults have higher short-term reproductive success?

We found no difference in the proportion of older (W) adults that were parents of sampled calves compared to the proportion of younger (WG) adults, either for males or females. (e.g., CERVUS χ^2_{male} p = 0.648, χ^2_{female} p = 0.360). However, looking just at the parents, both COANCESTRY and CERVUS found that a significantly higher proportion of older (W) mothers had multiple (n≥2) calves sampled compared to younger (WG) mothers (e.g., COANCESTRY χ^2 p = 0.002). The COLONY analysis found a similar, although non-significant (χ^2 p = 0.076), pattern. The same analyses, by contrast, found no clear differences between older and younger fathers. It should be noted, however, that sample size was low (n=6) for young (WG) fathers.

3.6 H6. Is N_e smaller than N_c?

For Bristol Bay belugas, current N_e estimated from the frequency of siblings among calves in COLONY was small relative to N_c (currently estimated at ≈2,000). From the estimated parentage of the entire calf dataset (n=144), which included sampled and unsampled parents, N_e = 118 (CI:89-154). For offspring where at

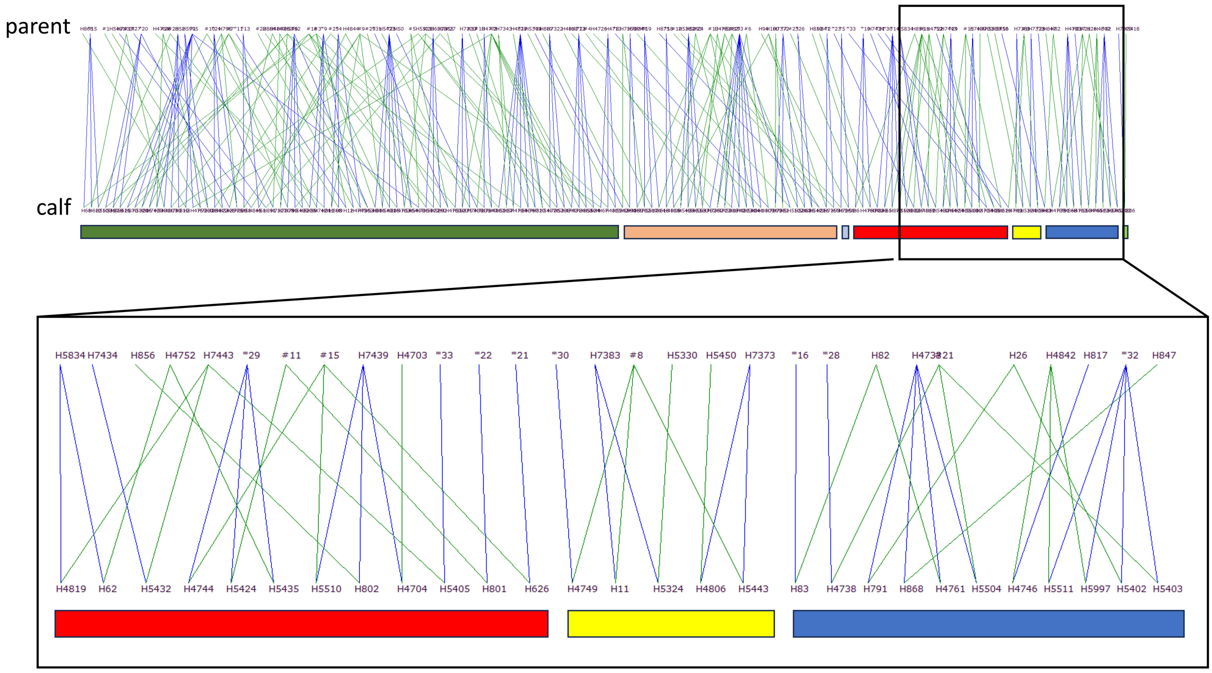

FIGURE 4
A two-generation pedigree of the 144 beluga whale calves and their inferred parents. Each point at the base of the pedigree equates to an individual calf, while each point at the top equates to an individual parent. Offspring are linked to inferred mothers by a green line and to inferred fathers by a blue line. This loose pedigree comprised 7 discrete clusters, the size of which are denoted by the length of the 7 colored ribbons beneath the diagram. For ease of viewing a subset of parent-offspring relationships involving just 28 offspring spanning clusters 4 (red), 5 (yellow), and 6 (blue) is also given. The analysis was conducted in COLONY using a sibship size prior of n_p=n_m=1 and x=0.25. The Figure was generated using PEDIGREE VIEWER. There are slight differences in form between the complete pedigree and the subset. This is because while the pedigrees themselves do not change the order in which individuals are presented in the pedigree view does change somewhat with sample size.

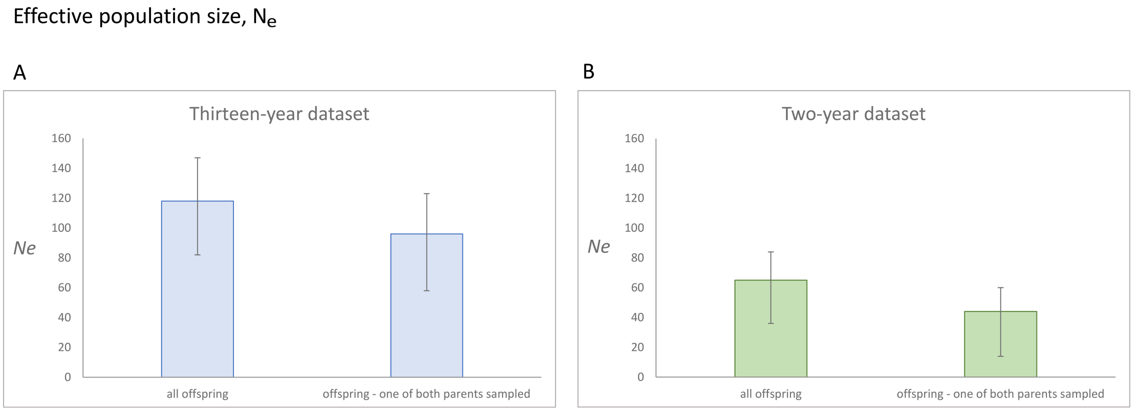

FIGURE 5
Estimated effective population size, N_e, for the Bristol Bay beluga population. Estimates were based on the frequency of sibships in offspring cohorts and were conducted in colony for both the thirteen-year **(A)** and the two-year **(B)** datasets. Values are presented for all offspring assigned parentage whether the parent was sampled or not, and for those offspring where at least one parent was sampled. Upper and lower confidence intervals are included.

least one of the parents was sampled, a slightly lower value was estimated (N_e = 96, CI:69-134) (Figure 5A). To reduce the risk of including possible parent-offspring pairs in the offspring category, and thereby potentially over-estimating frequencies of sibships in offspring cohorts, we re-ran these two analyses on the two-year dataset. This resulted in lower estimates of N_e for the entire calf dataset (N_e = 65, CI:46-94), and for the set of offspring that had at least one parent sampled (N_e = 44, CI:28-74) (Figure 5B).

3.7 H7. Is the Bristol Bay population highly inbred?

Low levels of inbreeding were found on average within the Bristol Bay population. For example, mean individual inbreeding coefficients for the entire dataset (n=523) in COANCESTRY averaged F_{TrioML} = 0.058. Furthermore, mean inbreeding coefficients for calves did not differ from those of adults (Supplementary Figure S2; $\bar{x}_{\text{calves}} = 0.055$ v. $\bar{x}_{\text{adults}} = 0.058$, $p = 0.679$). When inbreeding was assessed for parent-calf trios detected by the COLONY analysis (n=64), a similar pattern was found where F values were, on average, low for calves, mothers, and fathers with no significant differences ($\bar{x}_{\text{calves}}$ = 0.053, $\bar{x}_{\text{mothers}}$ = 0.048, $\bar{x}_{\text{fathers}}$ = 0.050 $p \geq 0.696$). Interestingly, there were cases where one or both parents were either more (i.e., $F_{\text{parent}} > F_{\text{calf}}$), or less, inbred than their offspring (Figure 6).

3.8 H8. Do Bristol Bay beluga whales have low heterozygosity?

Estimates of heterozygosity (H_{exp}) at the 22 nuclear markers averaged 0.641 (Table 1), and did not differ between calves (G) and adults (W and WG) (p = 0.978; Figure 7A). Similarly, the distribution of individual multi-locus heterozygosities (sMLH) did not differ between calves and adults (p = 0.637; Figure 7B). A subset of seven microsatellite markers was screened during an earlier study (1989-2001) of Bristol Bay (n=27) and other beluga stocks (O'Corry-Crowe et al., 2018; see map in Supplementary Material), and no significant differences were found in heterozygosity between this earlier period and either the adult (p = 0.934) or offspring (p = 0.524) categories (Figure 7A). Additionally, Bristol Bay heterozygosity was not significantly lower than estimates from Cook Inlet, Eastern Bering Sea, and Anadyr Bay stocks ($p \geq 0.219$), but was for Eastern Chukchi and Beaufort Sea stocks ($p \leq 0.024$; Figure 7). To avoid sMLH distributions being skewed by disparate sample sizes across strata, we conducted population comparisons between Bristol Bay and the Eastern Chukchi only (n=519 for both strata), and found sMLH to be significantly lower in Bristol Bay compared to the Eastern Chukchi Sea population (p = 0.003; Figure 7B).

4 Discussion

This study is the first to report on mating systems, parentage, and reproductive success in a wild population of beluga whales, and how those reproductive strategies influence inbreeding, genetic diversity, and N_e. A number of factors should be considered when assessing our findings: While the broad age categories risked confounding generations, the two-year analysis attempted to minimize this possibility. Although the 13-year study duration meant that some individuals became part of the breeding population sometime after the start of the project, and others likely phased out before the end, it increased our ability to detect progeny and sibships in a species, and sex (i.e., females), with low annual reproductive output. Furthermore, while care is required when interpreting estimates of N_e and inbreeding that are based on a limited number of markers (Putman and Carbone, 2014), the panel of microsatellites used had sufficient power to discriminate first- and second-order relationships and thus, calculate sibship frequencies necessary to estimate contemporary N_e (Wang, 2009; Wang et al., 2016). Marker numbers were also sufficient to calculate confidence intervals for inbreeding coefficients (Wang, 2011).

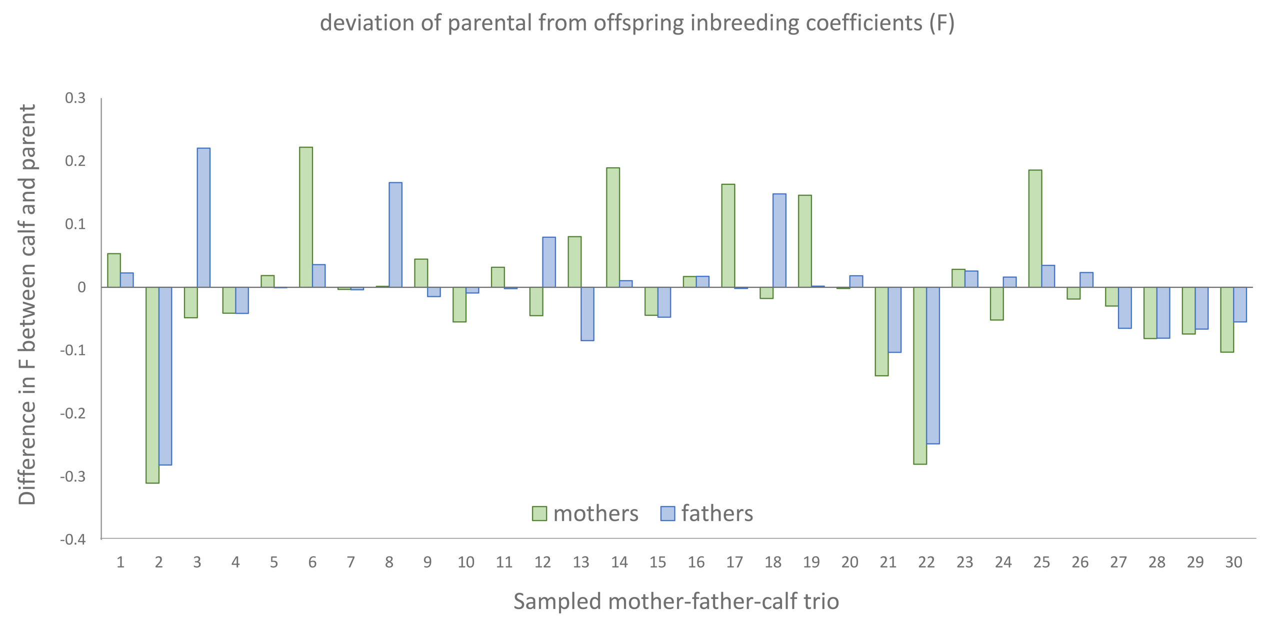

FIGURE 6

Deviation in inbreeding coefficients, F, between beluga whale offspring and their parents. F was calculated using the Trio-ML method in COANCESTRY. Positive bars, for example, indicate that the parent was estimated to have a higher inbreeding coefficient than their calf. A sample of 30 trios are shown.

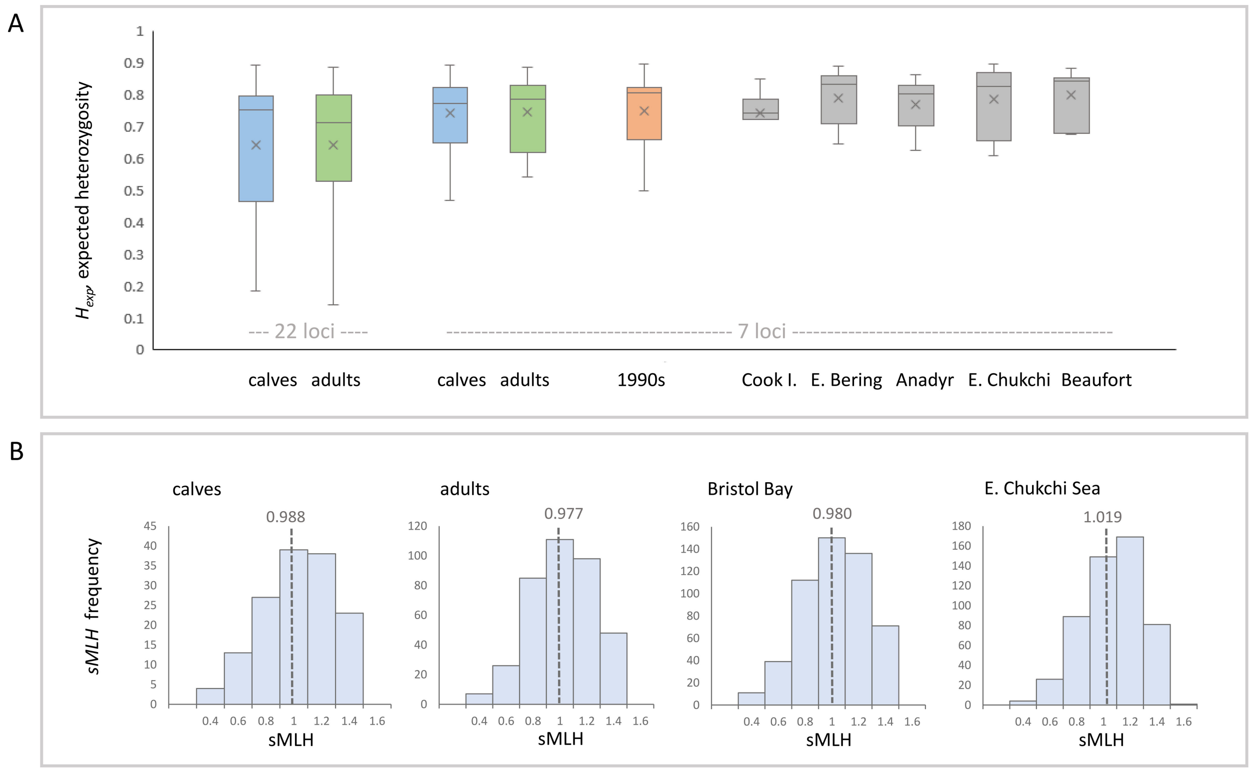

FIGURE 7

Genetic variation, measured as expected heterozygosity, H_{exp}, across microsatellite loci **(A)** and standardized multi-locus heterozygosity, sMLH, across individuals **(B)**, in Bristol Bay beluga whales. Patterns of variation are shown for the entire nuclear marker set (n=22 loci) and a subset (n=7) to allow comparison with an earlier timeframe (1989-2001) in Bristol Bay (labeled in the chart as the '1990s') and across five other beluga whale stocks (See map in Supplementary Figure S1) in the North Pacific Ocean. The seven-locus data for these comparisons are from O'Corry-Crowe et al. (2018).

4.1 Prediction 1. Polygyny

Bristol Bay beluga males are polygynous. A high proportion of calves were paternal half-sibs (H1). Although the sample size was limited (n=10), all the adult-calf dyads were female-calf pairings, indicating that males rarely engage in close affiliative behavior with their young offspring and thus, may provide little direct parental care (H2). Males had a higher maximum number of calves, greater variance in reproductive success than females, and evidence of reproductive skew (H3).

We found, however, limited evidence of individual males fathering a lot of calves, in either the two-year subset or full thirteen-year study (Figure 3), as might be expected in a highly polygynous mating system where successful males can achieve large numbers of paternities in a single, or a few, seasons (e.g., red deer *Cervus elaphus*, Clutton-Brock et al., 1982; Antarctic fur seals *Arctocephalus gazella*, Hoffman et al., 2003; elephant seals *Mirounga leonina*, Fabiani et al., 2004; macaques *Macaca mulatta*, Widdig et al., 2004). While the COLONY analysis estimated that a few unsampled males had fathered up to nine calves over the course of the study, we did not find any sampled males that had more than four confirmed calves, and most fathers had no more than two calves sampled (Table 2). In addition, because the calf category (G) includes a number of age classes, the sampling of more than one calf for an individual male in the same year does not necessarily indicate high reproductive success within a single breeding season. Also, in highly polygynous systems, if the breeding tenure of the most successful males spans multiple years, the likelihood of re-mating with the same females across years increases, even if mating is random, and we would expect a substantial proportion of full-sibs in the population, something we did not observe.

These findings suggest that polygyny is not as strong, nor male-male competition as intense, when compared to highly polygynous species, at least for this population of beluga whales. While conspecific tooth-rake scarring suggests aggressive contest competition in beluga whales, there is no evidence as yet that it is sex-biased (Hamm et al., 2021), or that it primarily reflects agonistic or affiliative behavior. Also, we rarely observed such scars in the Bristol Bay population. Furthermore, while a recent study concluded that SSD in belugas was among the highest in cetaceans, and thus, indicative of a polygynous mating system (Caspar and Begall, 2022), the degree of SSD differs among beluga populations (Supplementary Table S4), is moderate in Bristol Bay (=1.15) (Lensink, 1961; Suydam, 2009; Supplementary Table S4), and may not always indicate male competitive ability. There is growing evidence that niche partitioning between males and females can also contribute to sexual dimorphism (Bauld et al., 2022). Beluga males have been found to use different areas (Loseto et al., 2006; Hauser et al., 2014; Citta et al., 2016) and target different prey (Szpak et al., 2020) than females, suggesting that character displacement due to inter-sexual competition may influence SSD in belugas. Unlike some other cetacean species (e.g., Bigg's killer whale *Orcinus orca*) (Bigg et al., 1990), beluga whales form complex fission-fusion societies where closely related individuals are not always, or even frequently, found together (O'Corry-Crowe et al., 2020). If affiliation in beluga whales does not require close physical proximity, it is possible that fathers provide parental care through other means, such as vigilance, group defense, or active or passive instruction of older calves and juveniles.

In addition, the aquatic environment could limit the extent of polygyny in cetaceans by restricting a male's ability to guard multiple females from other males, and facilitating female choice by improving their ability to evade coercive advances by males (Würsig et al., 2023). Cooperation among males, however, may increase individual reproductive success and reduce reproductive skew by improving an individual male's ability to sequester and guard females (e.g., lions *Panthera leo*) (Bygott et al., 1979). Male alliances have been recorded in other cetacean species and linked to improved reproductive success (e.g., bottlenose dolphins *Tursiops* spp.) (Connor et al., 2000; Wiszniewski et al., 2012; Brightwell and Gibson, 2023). Groups of predominantly unrelated adult male belugas have been documented in several populations, although their possible role in reproduction remains unclear (O'Corry-Crowe et al., 2020). The only confirmed case of beluga whale mating behavior in the wild involved a sexual encounter between 19 males and a single female in Svalbard, Norway (Lydersen et al., 2023), which included cooperative behavior and aggressive mating attempts by multiple males, resulting in injury to the female. More research is required to assess the prevalence of this behavior and to investigate competition and reproductive cooperation in beluga whales.

4.2 Prediction 2. Polyandry

Bristol Bay beluga females are polyandrous across breeding seasons (H4). Breeding with multiple males may be a female bet-hedging strategy (Garcia-Gonzalez et al., 2015) to spread risk, for example by avoiding low quality males, and thus, optimize fitness across a long reproductive lifespan. The observation of full-sibs, often multiple years apart, shows that males and females can successfully re-mate with the same partner. However, the low incidence of full-sibs could reflect a female tendency to choose different males across consecutive breeding seasons. Bristol Bay belugas thus have a polygynandrous mating system, at least across breeding seasons, where both males and females successfully breed with multiple mates. Although it has been suggested by others (Hill et al., 2024; Kelley et al., 2014), this study is the first to provide definitive evidence of polygynandry in beluga whales. Field studies of female mating behavior are required to determine whether they also mate with multiple males within a season, and thus, whether beluga mating systems are polygynandrous over shorter time frames. A recent study investigating group structure and kinship proposed that beluga whale societies are communities comprised of whales spanning all ages and both sexes, and can number in the hundreds or possibly thousands (O'Corry-Crowe et al., 2020). If mating occurs while such large communities are concentrated in space and time, many opportunities may arise for both males and females to mate with multiple members within a season.

4.3 Prediction 3. Reproductive longevity and age

Although young adults were just as likely to be parents as older adults, older mothers were more likely to have more young calves in the population (H5). This indicates that while female belugas are limited by the number of offspring they can produce in the short term, breeding success (e.g., calf survival) may be higher in older, more experienced mothers who may also be larger, in better condition, and more successful at choosing fitter males. Lifetime ovarian reproductive activity, for example, has been found to increase in some regions with body size as well as age (Ferguson et al., 2021). It may also reflect competition among females for mates. This can be just as intense as that among males, even in predominantly polygynous species, though the form that the intrasexual competition takes may differ between the sexes (e.g., social status vs. direct fighting) (Clutton-Brock and Huchard, 2013).

Breeding lifespan is an important determinant of reproductive success (Lukas and Clutton-Brock, 2014). This is especially true for polygynous mammals, where social hierarchies and the costs of intense competition may greatly limit the reproductive lifespan of males. For example, a review of 61 mammal species with short to moderate male tenures (≤ 12 years) found a strong negative relationship between the potential for males to monopolize multiple females and male reproductive tenure (Lukas and Clutton-Brock, 2014). Beluga whales, by contrast, likely have much longer reproductive lifespans, although their fully aquatic mode creates unique challenges for monopolizing multiple mates.

Our limited ability to determine specific ages focused our analysis on the parentage of young offspring (i.e., gray calves), rather than all offspring, and revealed that both older and younger adults typically had few calves present in the population at any one time (especially younger females). The physiological demands of reproduction (i.e., one calf every 2–4 years) can explain these low numbers in females, however, physiological limitations likely do not exist for most males. That both older and young fathers had at most, only a few young offspring in our sample set may indicate that adult male belugas of any age tend not to father many offspring in a single breeding season, or even a few concurrent ones. This provides further evidence that extreme polygyny and high male reproductive skew over the short term are unlikely, at least for this population of beluga whales. Furthermore, if male belugas do have long reproductive lifespans, this might indicate that they tend to play a long game, fathering low numbers of offspring per year across a long reproductive life. Such a strategy may entail scramble competition and the guarding of individual females, rather than intense contest competition and the guarding of multiple females. Female belugas are facultative induced ovulators (Steinman et al., 2012), and as such, require some stimulus to ovulate. There is some evidence from belugas in managed care that when multiple adult females are present, an adult male will spend up to 7 days during the breeding season with one female before switching to another (Hill et al., 2024). Male-male cooperation may still enhance mating success, and variance in male lifetime reproductive success could still result. Low male reproductive skew over the short term may also reflect a polyandrous female mating system, where mating with multiple males within a season ensures paternity by quality males (e.g., via sperm competition). In addition to induced ovulation (Steinman et al., 2012), female belugas have complex genitalia, including vaginal folds, that may serve to control paternity (Kleinenberg et al., 1964; Orbach et al., 2023). In other mammalian species, promiscuous mating by females has also been found to confuse paternity, reducing harassment and the risk of infanticide by males (e.g., chimpanzees *Pan troglodytes*) (Pieta, 2008).

4.4 Predictions 4 and 5. Effective population size, inbreeding, and heterozygosity

N_e is influenced by both historical and contemporary processes (Waples, 2022, 2025, see Introduction). An earlier genetic study found that a number of beluga whale populations had low ancestral N_e relative to current sizes and likely went through a period of sudden expansion following the last glacial maximum (O'Corry-Crowe et al., 2010). A recent genomic study found that a number of populations in the Eastern Arctic experienced declines in N_e during and subsequent to the last glacial period, and that recent estimates for some endangered populations are below $N_e = 400$ (Müller et al., 2025). These investigations were characterized by small sample sizes and focused on how demographic history over long timeframes (i.e., 10^2–10^6 years) shape N_e.

By contrast, we used large sample sizes to investigate how beluga whale mating systems shape current N_e. While caution is required when assessing such estimates of N_e, as beluga whale generations span several years and may overlap, complicating sibship frequency calculations (and thus estimates may be biased low, see Supplementary Material), estimated contemporary N_e in the Bristol Bay population was substantially smaller than N_c (H6). This was driven primarily by the moderate variance in reproductive success recorded in both males and females. To investigate this further, we modeled the impact of different mating systems on N_e in an idealized population, using sampled Bristol Bay adult males and females as parents (see Supplementary Material), and found that low to moderate variance in reproductive success, even in a monogamous mating system where some mated pairs are more successful than others, can dramatically reduce contemporary N_e (Supplementary Figure S3). Our findings highlight how mating systems must be considered alongside historical demographic processes when interpreting spatial and temporal patterns of N_e and using this parameter in conservation strategies.

The small contemporary N_e in Bristol Bay could increase inbreeding and decrease genetic diversity (Waples, 2022), yet average inbreeding coefficients were low (H7) and levels of nDNA heterozygosity had not changed over recent decades (H8). Furthermore, heterozygosity in the Bristol Bay population is comparable to levels observed in other, much larger, populations (Figure 7) (O'Corry-Crowe et al., 2018).

The mating system in the Bristol Bay population may explain this unexpected finding. Low reproductive rates and reproductive skew limits the number of sibships in offspring cohorts. Mate choice may further reduce relatedness among siblings and the level of inbreeding. High rates of re-mating by female red deer with the same males, or with males whom a female relative has mated with (intra-lineage polygyny), have been associated with high levels of pairwise relatedness and inbreeding (Stopher et al., 2012). In belugas, frequent mate switching by both sexes would indicate that a high proportion of sibships will be half-sibs ($\bar{r}$ = 0.25) and a low proportion will be full-sibs ($\bar{r}$ = 0.38). While this can result in long loose-chain pedigrees (Figure 4), few offspring will be highly related. Thus, the possibility of two highly related individuals (e.g., full-sibs) mating by chance is very low, minimizing the frequency of highly inbred offspring, and the risk of diversity loss in the population. Social factors could also reduce likelihoods of inbreeding. Elements of beluga societies may be matrifocal, where maternal relatives form strong bonds (Kleinenberg et al., 1964; O'Corry-Crowe et al., 2020). Such bonds, however, do not require exclusive associations only with maternal kin (O'Corry-Crowe et al., 2020). Frequent associations among unrelated females could reduce the likelihood of intra-lineage polygyny, while large community size, kin-recognition, and active avoidance of consanguineous mating could limit inbreeding and genetic diversity loss further.

5 Conclusion

This study revealed how a polygynandrous mating system, where males optimize their fitness through moderate short-term reproductive success over a long reproductive lifespan, and females optimize theirs through polyandry to ensure mate quality, spread risk and avoid conflict, can limit inbreeding and diversity loss, even in small populations. The social and seasonal behavior of beluga whales, including their tendency to aggregate in large numbers at certain times of year, likely has a strong influence on mate availability, the competition for and defense of mates, mate choice and parental investment in offspring, while a long reproductive life may lessen the selective pressure for intense intrasexual competition and strong polygyny within seasons. Our findings emphasize the importance of understanding mating systems in small populations of long-lived, slow reproducing species like beluga whales that not only face the inherent risks of low N_e, but also a growing number of external threats due to environmental change and increasing human activities.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

Ethics statement

The animal study was approved by the Alaska Department of Fish and Game's IACUC under protocols 05-12, 06-16, 09-21,10-13R, 2012-020, 2013-020, and 2014-03. All methods of sample collection were carried out in accordance with the guidelines and regulations of the U.S. Endangered Species Act and the U.S. Marine Mammal Protection Act under NMFS ESA/MMPA research permits 782-1719, 14610, and 14245. All activities with wild whales are reported in accordance with ARRIVE guidelines. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

GO: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. LQ: Data curation, Funding acquisition, Project administration, Supervision, Writing – review & editing. TF: Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – review & editing. JJC: Data curation, Methodology, Validation, Writing – review & editing. AB: Data curation, Methodology, Writing – review & editing.

Funding

The author(s) declared financial support was received for this work and/or its publication. Financial support for sample collection was provided by the Alaska Beluga Whale Committee, the Alaska Department of Fish and Game (ADF&G), and the National Marine Fisheries Service. Financial support for sample analysis was provided by the North Pacific Research Board, NOAA Grant #N17NMF4720051, and Harbor Branch Oceanographic Institute at Florida Atlantic University (HBOIFAU).

Acknowledgments

We thank the many people who assisted us in the collection of samples, for their generosity in providing their insights on beluga whales and for their continued support of this research, especially the Bristol Bay Native Association Marine Mammal Council, the Alaska Beluga Whale Committee (ABWC), and our field crew in Kvichak Bay including H. Aderman, N. Apokedok, B. Apokedok, G. Tallekpallek, G. Wilson, and L. Hughes; our field crew in Nushagak Bay including F. Bartman, T. Bavilla, B. Lopez, M. Olsen, T. Olsen, A. Roehl, and B. Tinker. Invaluable lab assistance was provided by B. Potgieter. We thank HBOI-FAU and ADF&G for providing administrative support. Samples were collected pursuant to NMFS ESA/MMPA research permits 782-1719, 14610, and 14245 and ADF&G IACUC protocols 05-12, 06-16, 09-21,10-13R, 2012-020, 2013-020, and 2014-03. We thank Steve Jackson and Thermo Fisher for technical assistance and for DNA sequencing and fragment analysis support.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1707758/full#supplementary-material

References

Aubin, J. A., Michaud, R., and Vander Wal, E. (2021). Prospective evolutionary drivers of allocare in wild belugas. *Behaviour* 158, 727–756. doi: 10.1163/1568539X-bja10094

Bauld, J. T., Abernathy, K. A., Newton, J., Lehmann, D., Jones, I. L., and Bussière, L. F. (2022). Can diet niche partitioning enhance sexual dimorphism? *Ecol. Evol.* 12, e9599. doi: 10.1002/ece3.9599

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., and Balcomb, K. C.III (1990). Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm. Special Issue* 12, 383–405.

Brightwell, K., and Gibson, Q. (2023). "Inter- and intrapopulation variation in bottlenose dolphin mating strategies," in *Sex in Cetaceans*. Eds. B. Würsig and D. N. Orbach (Cham, Switzerland: Springer Nature Switzerland AG), 251–279.

Buchanan, F. C., Friesen, M. K., Littlejohn, R. P., and Clayton, J. W. (1996). Microsatellites from the beluga whale Delphinapterus leucas. *Mol. Ecol.* 5, 571–575.

Burns, J. J., and Seaman, G. A. (1986). "Investigation of belukha whales in coastal waters of western and northern Alaska," in *II. Biology and Ecology. Final report submitted to MMS and NOAA, Out. Contin. Shelf Environ. Assess. Prog.* (Fairbanks: Alaska Department of Fish and Game).

Bygott, J. D., Bertram, B. C. R., and Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature* 282, 839–841. doi: 10.1038/282839a0

Caspar, K. R., and Begall, S. (2022). Sexual dimorphism in toothed whales (Odontoceti) follows Rensch's rule. *Mamm. Biol.* 102, 523–529. doi: 10.1007/s42991-022-00239-1

Charlesworth, D., and Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. System* 18, 237–268. doi: 10.1146/annurev.es.18.110187.001321

Charlesworth, D., and Willis, J. H. (2009). The genetics of inbreeding depression. *Nat. Rev. Genet.* 10, 783–796. doi: 10.1038/nrg2664

Chernetskii, A. D., Krasnova, V. V., and Bel'kovich, V. M. (2011). Studies of the structure of the Solovetsky reproductive gathering of beluga whales (Delphinapterus leucas) in the White Sea using the photo Identification method. *Oceanology* 51, 275–280. doi: 10.1134/S0001437011020044

Citta, J. J., Frost, K. J., and Quakenbush, L. (2019). Aerial surveys of Bristol Bay beluga whales, Delphinapterus leucas, in 2016. *Mar. Fish. Rev.* 81, 98–104. doi: 10.7755/MFR.81.3-4.5

Citta, J. J., O'Corry-Crowe, G., Quakenbush, L. T., Bryan, A. L., Ferrer, T., Olson, M. J., et al. (2018). Assessing the abundance of Bristol Bay belugas with genetic mark-recapture methods. *Mar. Mamm. Sci.* 34, 666–686. doi: 10.1111/mms.12472

Citta, J. J., Quakenbush, L. T., Frost, K. J., Lowry, L., Hobbs, R. C., and Aderman, H. (2016). Movements of beluga whales (Delphinapterus leucas) in Bristol Bay, Alaska. *Mar. Mamm. Sci.* 32, 1272–1298. doi: 10.1111/mms.12337

Clutton-Brock, T. (2007). Sexual selection in males and females. *Science* 318, 1882–1885. doi: 10.1126/science.1133311

Clutton-Brock, T. H., Guinness, F. E., and Albon, S. D. (1982). *Red Deer: Behavior and Ecology of Two Sexes* (Chicago: University of Chicago Press).

Clutton-Brock, T. H., and Huchard, E. (2013). Social competition and selection in males and females. *Philos. Trans. R. Soc. B* 368, 20130074. doi: 10.1098/rstb.2013.0074

Coltman, D. W., Pilkington, J. G., Smith, J. A., and Pemberton, J. M. (1999). Parasite mediated selection against inbred soay sheep in a free-living, island population. *Evolution* 53, 1259–1267. doi: 10.2307/2640828

Connor, R. C., Heithaus, M. R., and Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proc. R. Soc. Lond. B* 268, 263–267. doi: 10.1098/rspb.2000.1357

Connor, R. C., Read, A. J., and Wrangham, R. (2000). "Male reproductive strategies and social bonds," in *Cetacean societies: field studies of whales and dolphins*. Eds. J. Mann, R. Connor, P. Tyack and H. Whitehead (University of Chicago Press, Chicago, IL), 247–269.

Darwin, C. R. (1871). *The Descent of Man, and Selection in Relation to Sex* (London: John Murray).

Dieringer, D., and Schlötterer, C. (2003). Microsatellite Analyser (MSA): a platform independent analysis tool for large microsatellite data sets. *Mol. Ecol. Notes*. 3, 167–169. doi: 10.1046/j.1471-8278.2003.00351.x

Ellis, S., Franks, D. W., Nattrass, S., Currie, T. E., Cant, A. C., Giles, G., et al. (2018). Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed Whales. *Sci. Rep.* 8, 12833. doi: 10.1038/s41598-018-31047-8

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223. doi: 10.1126/science.327542

Fabiani, A., Galimberti, F., Sanvito, S., and Hoelzel, A. R. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behavi. Ecol.* 15, 961–969. doi: 10.1093/beheco/arh112

Ferguson, S. H., Willing, C., Kelley, T. C., Boguski, D. A., Yurkowski, D. J., and Watt, C. A. (2020). Reproductive parameters for female beluga whales (Delphinapterus leucas) of Baffin Bay and Hudson Bay, Canada. *Arctic* 73, 405–420. doi: 10.14430/arctic71435

Ferguson, S. H., Yurkowski, D. J., Hudson, J. M., Edkins, T., Willing, C., and Watt, C. A. (2021). Larger body size leads to greater female ovarian reproductive activity at the southern periphery of their range. *Ecol. Evol.* 11, 17314–17322. doi: 10.1002/ece3.8367

Foley, A. M., Hewitt, D. G., DeYoung, R. W., Schnupp, M. J., Hellickson, M. W., and Lockwood, M. A. (2018). Reproductive effort and success of males in scramble-competition polygyny: Evidence for trade-offs between foraging and mate search. *J. Anim. Ecol.* 87, 1600–1614. doi: 10.1111/1365-2656.12893

Fromonteil, S., Marie-Orleach, L., Winkler, L., and Janicke, T. (2023). Sexual selection in females and the evolution of polyandry. *PloS Biol.* 21, e3001916. doi: 10.1371/journal.pbio.3001916

Garcia-Gonzalez, F., Yasui, Y., and Evans, J. P. (2015). Mating portfolios: bet-hedging, sexual selection and female multiple mating. *Proc. R. Soc B* 282, 20141525. doi: 10.1098/rspb.2014.1525

Hamm, J. R., Lilley, M. K., and Manitzas Hill, H. M. (2021). Conspecific scarring on wild belugas (Delphinapterus leucas) in Cunningham inlet. *Behaviour* 158, 663–683. doi: 10.1163/1568539X-bja10086

Harris, W. E., and Moore, P. J. (2005). Female mate preference and sexual conflict: females prefer males that have had fewer consorts. *Am. Nat.* 165, S64–S71. doi: 10.1086/429352

Hauser, D. D., Laidre, K. L., Suydam, R. S., and Richard, P. R. (2014). Population-specific home ranges and migration timing of Pacific Arctic beluga whales (Delphinapterus leucas). *Polar. Biol.* 37, 1171–1183. doi: 10.1007/s00300-014-1510-1

Heide-Jørgensen, M. P., and Teilmann, J. (1994). Growth, reproduction, age structure and feeding habits of white whales (Delphinapterus leucas) in West Greenland waters. *Meddr. Grønland Biosci.* 39, 195–212. doi: 10.7146/mogbiosci.v39.142550

Hill, H. M. S., Lilley, M. K., Ham, J. R., and Robeck, T. (2024). A review of beluga (Delphinapterus leucas) sexual behavior and reproductive physiology leading to conception. *Theriogenology Wild* 4, 13. doi: 10.1016/j.therwi.2024.100071

Hoelzel, A. R., Potter, C. W., and Best, P. B. (1998). Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proc. R. Soc. Lond. Ser. B. Biol. Sci.* 265, 1177–1183.

Hoffman, J. I., Boyd, I. L., and Amos, W. (2003). Male reproductive strategy and the importance of maternal status in the Antarctic fur seal Arctocephalus gazella. *Evolution* 57, 1917–1930. doi: 10.1111/j.0014-3820.2003.tb00598.x

Jones, O. R., and Wang, J. (2010). Colony: a program for parentage and sibship inference from multilocus genotype data. *Mol. Ecol. Resou.* 10, 551–555. doi: 10.1111/j.1755-0998.2009.02787.x

Kalinowski, S. T., Taper, M. L., and Marshall, T. C. (2007). Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* 16, 1099–1006. doi: 10.1111/j.1365-294x.2007.03089.x

Kalinowski, S. T., Wagner, A. P., and Taper, M. L. (2006). ml-relate: a computer program for maximum likelihood estimation of relatedness and relationships. *Mol. Ecol. Notes* 6, 576–579. doi: 10.1111/j.1471-8286.2006.01256.x

Kelley, T. C., Stewart, R. E. A., Yurkowski, D. J., Ryan, A., and Ferguson, S. H. (2014). Mating ecology of beluga (Delphinapterus leucas) and narwhal (Monodon monoceros) as estimated by reproductive metrics. *Mar. Mamm. Sci.* 31, 479–500. doi: 10.1111/mms.12165

Kleinenberg, S. E., Yablokov, A. V., Bel'kovich, B. M., and Tarasevich, M. N. (1964). *Beluga (Delphinapterus leucas) Investigation of the Specie* (Moscow: Academy of Sciences of the USSR).

Klug, H. (2011). "Animal mating systems," in *eLS* (Chichester: John Wiley & Sons, Ltd). doi: 10.1002/9780470015902.a0022553

Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., and Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (Delphinapterus leucas) in natural environment. *Biol. Bull.* 41, 349–356. doi: 10.1134/S1062359014040062

Krützen, M., Valsecchi, E., Connor, R. C., and Sherwin, W. B. (2001). Characterization of microsatellite loci in Tursiops aduncus. *Mol. Ecol. Notes* 1, 170–172.

Lensink, C. J. (1961). *Status report: beluga studies* (Juneau: Div. Biol. Res., Alaksa Dep. Fish and Game), 20.

Lomac-MacNair, K. S., Smultea, M. A., Cotter, M. P., Thissen, C., and Parker, L. (2015). Socio-sexual and probable mating behavior of cook Inlet beluga whales, Delphinapterus leucas, observed from an aircraft. *Mar. Fish. Rev.* 77, 32–39. doi: 10.7755/MFR.77.2.2

Loseto, L. L., Richard, P., Stern, G. A., Orr, J., and Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Can. J. Zool.* 84, 1743–1751. doi: 10.1139/z06-160

Lukas, D., and Clutton-Brock, T. (2014). Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proc. R. Soc B* 281, 20140418. doi: 10.1098/rspb.2014.0418

Lydersen, C., Langenberger, K., and Kovacs, K. M. (2023). An observation of white whale (Delphinapterus leucas) mating behaviour in the wild. *Polar. Res.* 42, 9. doi: 10.33265/polar.v42.8875

Michaud, R. (1993). Distribution estivale du béluga du St.-Laurent: synthèse 1986 à 1992. *Can. Tech. Rep. Fish. Aquat. Sci.* 1906, 28.

Milligan, B. G. (2003). Maximum-likelihood estimation of relatedness. *Genetics* 163, 1153–1167. doi: 10.1093/genetics/163.3.1153

Morrison, R. E., Ndayishimiye, E., Stoinski, T. S., and Eckardt, W. (2023). Multiple mechanisms for inbreeding avoidance used simultaneously in a wild ape. *Proc. R. Soc B* 290, 20231808. doi: 10.1098/rspb.2023.1808

Müller, C., de Greef, E., Watt, C. A., Ferguson, S. H., Lesage, V., Parent, G. V., et al. (2025). Exploring contemporary and historic effective population sizes in Atlantic beluga whale populations. doi: 10.1101/2025.09.19.677402. preprint.

Nater, A., Kopps, A. M., and Kruetzen, M. (2009). New polymorphic tetranucleotide microsatellites improve scoring accuracy in the bottlenose dolphin Tursiops aduncus. *Mol. Ecol. Resour.* 9, 531–534.

O'Corry-Crowe, G. M., Lydersen, C., Heide-Jørgensen, M. P., Hansen, L., Mukhametov, L. M., Dove, O., et al. (2010). Population genetic structure and evolutionary history of North Atlantic beluga whales (Delphinapterus leucas) from West Greenland, Svalbard and the White Sea. *Polar. Biol.* 33, 1179–1194. doi: 10.1007/s00300-010-0807-y

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., et al. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (Delphinapterus leucas). *PloS One.* doi: 10.1371/journal.pone.0194201

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T., Lydersen, C., Kovacs, K., et al. (2020). Group structure and kinship in beluga whale societies. *Sci. Rep.* doi: 10.1038/s41598-020-67314-w

Orbach, D. N., Gorter, U., and Mesnick, S. (2023). "Sexual anatomy of female cetaceans: art and science contribute insights into functionality," in *Sex in Cetaceans*. Eds. B. Würsig and D. N. Orbach (Cham, Switzerland: Springer Nature Switzerland AG), 85–102. doi: 10.1007/978-3-031-35651-3_5

Pieta, K. (2008). Female mate preferences among Pan troglodytes schweinfurthii of Kanyawara, Kibale National Park, Uganda. *Int. J. Primatol.* 29, 845–864. doi: 10.1007/s10764-008-9282-5

Putman, A. I., and Carbone, I. (2014). Challenges in analysis and interpretation of microsatellite data for population genetic studies. *Ecol. Evol.* 4, 4399–4428. doi: 10.1002/ece3.1305

Queller, D. C., and Goodnight, K. F. (1989). Estimating relatedness using molecular markers. *Evolution* 43, 258–275. doi: 10.1111/j.1558-5646.1989.tb04226.x

Rooney, A. P., and Meritt, D. B. (1999). Microsatellite diversity in captive bottlenose dolphins (Tursiops truncatus). *J. Hered.* 90.

Rosel, P. E., Forgetta, V., and Dewar, K. (2005). Isolation and characterization of twelve polymorphic microsatellite markers in bottlenose dolphins (Tursiops truncatus). *Mol. Ecol. Notes* 5, 830–833.

Schlotteröer, C., Amos, B., and Tautz, D. (1991). Conservation of polymorphic simple sequence loci in cetacean species. *Nature* 354, 63–65.

Sergeant, D. E., and Brodie, P. F. (1969). Body size in white whales, Delphinapterus leucas. *J. Fish. Res. Board Can.* 26, 2561–2580. doi: 10.1139/f69-251

Shuster, S. M., and Wade, M. J. (2003). *Mating Systems and Strategies* (Princeton, NJ: Princeton University Press).

Smith, T. G., Hammill, M. O., and Martin, A. R. (1994). Herd composition and behaviour of white whales (Delphinapterus leucas) in two Canadian arctic estuaries. *Meddelelsser Grønland. Biosci.* 39, 175–184. doi: 10.7146/mogbiosci.v39.142546

Steinman, K. J., O'Brien, J. K., Monfort, S. L., and Robeck, T. R. (2012). Characterization of the estrus cycle in female beluga (Delphinapterus leucas) using urinary endocrine monitoring and transabdominal ultrasound: evidence of facultative induced ovulation. *Gen. Comp. Endocrinol.* 175, 289–397. doi: 10.1016/j.ygcen.2011.11.008

Stoffel, M. A., Esser, M., Kardos, M., Humble, E., Nichols, H., David, P., et al. (2016). inbreedR: an R package for the analysis of inbreeding based on genetic markers. *Meth. Ecol. Evol.* 7, 1331–1339. doi: 10.1111/2041-210X.12588

Stopher, K. V., Nussey, D. H., Clutton-Brock, T. H., Guinness, F., Morris, A., and Pemberton, J. M. (2012). Re-mating across years and intralineage polygyny are associated with greater than expected levels of inbreeding in wild red deer. *J. Evol. Biol.* 25, 2457–2469. doi: 10.1111/j.1420-9101.2012.02626.x

Suydam, R. S. (2009). *Age, Growth, Reproduction, and Movements of Beluga Whales (Delphinapterus leucas) from the Eastern Chukchi Sea* (Ann Arbor, MI: University of Washington).

Szala, A., and Shackelford, T. K. (2019). "Polygynandry," in *Encyclopedia of Animal Cognition and Behavior*. Eds. J. Vonk and T. K. Shackelford (Springer, Switzerland). doi: 10.1007/978-3-319-47829-6_1904-1

Szpak, P., Julien, M. H., Royle, T. C. A., Savelle, J. M., Yang, D. Y., and Richards, M. P. (2020). Sexual differences in the foraging ecology of 19th century beluga whales (Delphinapterus leucas) from the Canadian High Arctic. *Mar. Mamm. Sci.* 36, 451–471. doi: 10.1111/mms.12655

Trivers, R. L. (1972). "Parental investment and sexual selection," in *Sexual selection and the descent of man*. Ed. B. Campbell (Heinmann, London), 136–179.

Valsecchi, E., and Amos, W. (1996). Microsatellite markers for the study of cetacean populations. *Mol. Ecol.* 5, 151–156.

Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., and Shipley, P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes* 4, 535–538. doi: 10.1111/j.1471-8286.2004.00684.x

Vos, D. J., Shelden, K. E. W., Friday, N. A., and Mahoney, B. A. (2020). Age and growth analyses for the endangered belugas in Cook Inlet, Alaska. *Mar. Mamm. Sci.* 36, 293–304. doi: 10.1111/mms.12630

Wang, J. (2009). A new method for estimating effective population sizes from a single sample of multilocus genotypes. *Mol. Ecol.* 18, 2148–2164. doi: 10.1111/j.1365-294X.2009.04175.x

Wang, J. (2011). Coancestry: a program for simulating, estimating and analyzing relatedness and inbreeding coefficients. *Mol. Ecol. Resour.* 11, 141–145. doi: 10.1111/j.1755-0998.2010.02885.x

Wang, J. (2022). *Colony: a program for parentage and sibship inference from multilocus genotype data Version 2.06: User's guide* (Zoology Society of London), 73.

Wang, J., Santiago, E., and Caballero, A. (2016). Prediction and estimation of effective population size. *Heredity* 117, 193–206. doi: 10.1038/hdy.2016.43

Waples, R. S. (2022). What is Ne anyway? *J. Hered.* 113, 371–379. doi: 10.1093/jhered/esac023

Waples, R. S. (2025). The idiot's guide to effective population size. *Mol. Ecol.*, e17670. doi: 10.1111/mec.17670

Widdig, A., Bercovitch, F. B., Streich, W. J., Sauermann, U., Nürnberg, P., and Krawczak, M. A. (2004). longitudinal analysis of reproductive skew in male rhesus macaques. *Proc. R. Soc Lond. B* 271, 819–826. doi: 10.1098/rspb.2003.2666

Wiszniewski, J., Corrigan, S., Beheregaray, L. B., and Möller, L. M. (2012). Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (Tursiops aduncas). *J. Anim. Ecol.* 81, 423–431. doi: 10.1111/j.1365-2656.2011.01910.x

Würsig, B., Rich, J., and Orbach, D. N. (2023). "Sex and behavior," in *Sex in Cetaceans*. Eds. B. Würsig and D. N. Orbach (Cham, Switzerland: Springer Nature Switzerland AG), 1–28. doi: 10.1007/978-3-031-35651-3