# Larger body size leads to greater female beluga fitness at the southern periphery of their range

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## Abstract

Identifying phenotypic characteristics of evolutionarily fit individuals provides important insight into the evolutionary processes that cause range shifts with climate warming. Female beluga whales (Delphinapterus leucas) from the Canadian high Arctic (BB) residing in the core region of the species' geographic range are 14% larger than their conspecifics at the southern periphery in Hudson Bay (HB). We investigated the causal mechanism for this north (core)-south (periphery) difference as it relates to fitness by combining morphometric data with ovarian corpora counted in female reproductive tracts. We found evidence for reproductive senescence in older HB females from the southern peripheral population but not for BB whales. Female beluga whale fitness in the more-northern BB increased faster with age (48% partial variation explained) versus a more gradual slope (25%) in HB. In contrast, body length in HB female beluga accounted for five times more of the total variation in fitness compared to BB whales. We speculate that female HB beluga fitness was more strongly linked with body length due to higher density, as larger body size provides survival advantages during seasonal food limitations. Understanding the evolutionary mechanism of how fitness changes will assist conservation efforts in anticipating and mitigating future challenges to peripheral populations.

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Abstract: Identifying phenotypic characteristics of evolutionarily fit individuals provides important insight into the evolutionary processes that cause range shifts with climate warming. Female beluga whales (*Delphinapterus leucas*) from the Canadian high Arctic (BB) residing in the core region of the species' geographic range are 14% larger than their conspecifics at the southern periphery in Hudson Bay (HB). We investigated the causal mechanism for this north (core)-south (periphery) difference as it relates to fitness by combining morphometric data with ovarian corpora counted in female reproductive tracts. We found evidence for reproductive senescence in older HB females from the southern peripheral population but not for BB whales. Female beluga whale fitness in the more-northern BB increased faster with age (48% partial variation explained) versus a more gradual slope (25%) in HB. In contrast, body length in HB female beluga accounted for five times more of the total variation in fitness compared to BB whales. We speculate that female HB beluga fitness was more strongly linked with body length due to higher density, as larger body size provides survival advantages during seasonal food limitations. Understanding the evolutionary mechanism of how fitness changes will assist conservation efforts in anticipating and mitigating future challenges to peripheral populations.

Key words: age, body length, Delphinapterus leucas, geographic range, ovarian corpora

## Introduction

Evolution occurs through natural selection whereby individuals with greater fitness contribute disproportionately more of their genetic information to future generations. Individuals of a species often cluster into groups of genetically different populations due to differences in environmental selection pressure (Orsini et al. 2008; Coulon et al. 2008; Pauls et al. 2013). Population-level differences are then geographically arranged along a continuum based on where the population is located within the species' range (Kirkpatrick and Barton 1997; Peterson et al. 2011). Sink populations at the periphery of a species' range are constantly in phenotypic flux due to the demographic challenges of an environment that is at the limits of their evolved traits (Gaston 2009; Sheth and Angert 2016). For biological conservation, it is critical to understand the extent of species-level plasticity that allows individuals to track extreme environmental selection pressures at the edge of their geographic range in our rapidly changing world (Hardie and Hutchings 2010; Valladeres et al. 2014).

To test this concept requires a fitness comparison of populations at the core of the species' distribution where individuals are presumably most suitably adapted to their environment as opposed to populations at the periphery where more phenotypic flux occurs. Lifetime reproductive success is a fitness measure estimated as the number of recruited offspring to the next generation that a parent produces over their lifetime (Gustafsson 1986; Brommer et al. 2002). Reproductive success is challenging to estimate in wild populations as long-term studies are often required to monitor an appropriate number of individuals throughout their lives (Newton 1989). Alternatively, researchers have used female reproductive tracts from sustainably hunted individuals to identify the number of ovarian corpora through lab examinations (Lehmann 1993; Nazarova and Evsikoy 2012; Ringsby et al., 2009). The ovaries of many mammals provide an index of reproductive activity that functions as a measure of fitness by recording the history of reproductive events and number of lifetime ovulations (Perrin et al. 1984; Ellis et al., 2018). During ovulation, an oocyte is released from the Graafian follicle with the rupture site forming the corpus luteum (CL), a temporal bright yellow, hormonal gland helping to promote and to maintain implantation of the embryo. Subsequently, this body regresses to the corpus albicans (CA) which is generally considered to persist within the ovarian tissue throughout the life of a female whale even after diminishing in size and color (Mackintosh, 1942; Laws, 1961; Fujino 1963).

Relating phenotypic characteristics to lifetime reproductive success can provide important insight into evolutionary processes and allow comparisons between populations that may indicate adaptation (Peterson et al. 2019). In general, age is an important determinant of lifetime fitness as older individuals have survived long enough to produce numerous offspring (Sugiyama 1994; Festa-Bianchet et al. 2000; Saino et al. 2012; Potti et al. 2013). Since age-effects directly correlate with fitness, they provide little ecological information that could assist in understanding fitness mechanism. Instead, research needs to assess the relative contribution of variation in phenotypic traits, such as body size, relative to fitness variation (Gaillard et al. 2000), to understand key variables for survival and reproductive success.

Variation in body size is a key characteristic that can exhibit high intra-specific differences in fitness contribution as observed in insects (Sokolovska et al. 2000), pinnipeds (e.g., Le Boeuf & Reiter 1988), ungulates (Clutton-Brock et al. 1988), rodents (Ribble 1992), and birds (Davies et al. 1998). Large mammalian females are generally considered to be capital breeders (Stearns 1992) and, therefore, should illustrate a strong relationship between individual body size and reproductive success. Despite relationships between fitness and body size being investigated across several species groups, this relationship has not been demonstrated in whales likely due to the logistical difficulties of measuring adult body size and counting ovarian corpora in large whales.

There are 21 beluga whale (*Delphinapterus leucas*) populations across the Arctic providing a variety of geographic locations along the continuum of their range (Hobbs et al. 2020). In collaboration with annual

Inuit subsistence harvests across the Eastern Canadian Arctic, Fisheries and Oceans Canada have obtained a large collection of female beluga whale reproductive tracts that include ovaries. To date, this collection has revealed spatial differences in morphology, phylogenetic history, demography and reproduction between individuals wintering in the greater Hudson Bay (HB) region compared to those wintering in Baffin Bay (BB) (Postma 2017; Ferguson et al. 2020). For this study, we chose to compare the HB population which lives at the southern extreme of the beluga whale geographic range (59° latitude) with the BB population (73° latitude) that is considered to be distributed within the core of their range. Our objective was to determine whether spatial differences in fitness occurred between peripheral HB and core BB regions while controlling for age. Specifically, we determined how variation in reproductive fitness, measured as total ovarian corpora counts (TC) relates to body size of female beluga whale from both populations.

#### Methods

We conducted post-mortem gross examinations of 375 female reproductive tracts, collected from three beluga populations (sometimes referred to as stocks; high Arctic n=36, Cumberland Sound n=57, and Hudson Bay n=282) across 17 northern communities within the Eastern Canadian Arctic from 1989 to 2014 (Fig. 1). Ageing was based on examination of dentine and cementum growth layer groups in teeth (Waugh et al. 2018). Whale standard length was measured in the field according to a standard protocol (American Society of Mammalogists, 1961). Body length in whales is strongly correlated with mass (Trites and Pauly 1998).

We combined reproductive morphology data for Cumberland Sound and high Arctic populations into a BB region based on similar growth-age-reproduction relationship (Ferguson et al. 2020). We found no significant differences in whale body length between the two high-latitude populations, Cumberland Sound and high Arctic (ANCOVA:  $F_{2.98} = 0.042$ , p = 0.96), and thus combined them for further analyses.

Sample processing is described in more detail in Ferguson et al. (2020), but briefly, ovaries were excised, weighed, measured and preserved in 10% neutral-buffered formalin. For each ovary, we recorded the number of CL and CA (Best, 1968). In cetaceans CLs and CAs form distinct and persistent features, accumulating within the ovary (Perrin et al. 1976) as a record of a female's reproductive history (Slijper 1962; Collet and Harrison et al., 1972). Corpora assessments were performed by one reader to minimize bias in the subjective determination of accessory corpora (Harrison, 1977). As a measure of lifetime reproduction, TC for each beluga whale were assessed by counting all existing CL and CA within the ovaries (hereafter referred to as fitness). For whales with only one ovary (23 of 97 whales from BB and 113 of 210 whales from HB), we doubled the corpora count for the single ovary since beluga whales do not appear to exhibit a left-dominance in ovarian function (Robeck et al. 2010).

TC, body length, and age were normally distributed and parametric models were used without data transformation. Data availability varied among whales for age data [HB: 271 of 282, CS: 55 of 57 and HA: 33 of 36], length data [HB: n=240, CS: n=56 and HA: n=29], and ovary measurements [HB: n=79, CS: n=11 and HA: n=9]. To avoid including sexually immature individuals in our analyses, we excluded whales that were less than 250 cm in length (n=4).

## Statistical analysis

All statistical analyses and graphics were performed using R statistical software (v. 3.6.3). Cooks criteria was used to identify outliers and resulted in the removal of two whales with TC greater than 25 and one whale over 10 years of age without any corpora (all three from HB).

To test the relative effect of body size on fitness between the two regions, we used general linear models (GLM) using a Poisson distribution. We controlled the order of entry of the predictor variables based on our expectation that age would explain the most variation in fitness but that body length would be the variable of interest (i.e., entered first into our model). Age and body length were not significantly correlated for BB ( $r^2 = 0.0075$ ;  $F_{1,19} = 0.143$ , p = 0.71) whereas they were for HB ( $r^2 = 0.086$ ;  $F_{1,79} = 7.40$ , p = 0.008). Here, we follow the "hierarchical analysis procedure" that requires one to structure the analysis and interpretation of partials on the order of entry (Cohen and Cohen 1975). We constructed a GLM that

included all combinations of covariates and interactions (body length, age, region) and then successive steps in backward selection were guided by Variance Inflation Factors (VIF) and information theory using Akaike's information criterion for small sample size (AICc). Covariates with a VIF > 5.0 (Zuur et al., 2009) were used in separate models. We calculated log-likelihood (LL), AICc values, [?]AICc, and AICc weights (wi – relative likelihood of the model) using AICcmodavg package in R (version 2.2-2, Mazerolle, 2019).

Once we had selected the parsimonious models, we tested the effects of body size on fitness while controlling for whale age. We used the partial correlation approach which measured the "unique" contribution of an independent variable to  $\mathbb{R}^2$  when a single variable (age) is added to an earlier set of predictors (body length). Partial correlation is identical to the square of the semipartial correlation of Y (fitness) and length with the effects of age removed.

#### Results

The final dataset included 177 female reproductive tracts: 54 from BB and 123 from HB. Following removal of outliers (see Methods), 144 samples remained for modeling (BB n = 34, HB n = 110).

Female beluga whales from the high-latitude BB region were found to be 4.7% longer ( $F_{2,98} = 11.33$ , p < 0.001) than females from more southern HB (Gompertz asymptotic body length 370.9 cm vs 354.4 cm; Fig. 2) which translated to 13.9% greater body mass (based on growth equations in Heide-Jorgensen and Teilmann, 1994). Whales from both regions had similar age distribution (Fig. 2).

To assess whether body length influenced fitness, we first assessed the influence of region (BB and HB) in a complete model (TC  $\sim$  length\*age\*region). Due to high VIF (>5), we reduced combinations by initially removing the three-way interaction and re-running the model (TC  $\sim$  length\*age + region). Using the backwards step regression approach found support (AICc < 3) for running the models separately by region (coefficient = 3.638 ± 1.035; z-value = 3.516, p = 0.00044) among the available variable combinations. Therefore, we contrasted BB with HB using separate GLM models. To compare fitness, we regressed whale length against TC (Step 1), then we included whale age (Step 2), and finally added the interaction term length\*age (Step 3) (Table 1).

The effect of length on fitness was assessed using partial correlations to remove variation attributable to length and age. For BB, length explained 2.4% of variation while controlling for age, whereas age explained 48.2%. For HB, length explained 8.4% of the variation in fitness while controlling for age, whereas age explained 24.7%. For BB, the rate of increase in fitness with age was 1.5 times greater than HB (0.50 versus 0.33 TC per year, t = -2.17, p = 0.031; Fig. 3), while the rate of increase in fitness with length was similar (t = 0.53, p = 0.96; Fig. 4). However, HB whales had a significant grade shift to overall higher fitness for similar body lengths (t = 2.95, p = 0.0037). Length explained 5% of the total variation in BB (2.4% / (2.4% + 48.2%) \* 100%) compared to 25% of total fitness explained for HB (8.4% / 8.4% + 24.7%) \* 100%). Assessing the pattern of changes in fitness with age, HB beluga whales showed an asymptote in pregnancies at ages greater than approximately 45 years; whereas, the BB populations did not show this pattern (Fig. 5).

#### Discussion

Using a quantitative assessment of the effect of beluga whale body size on female fitness, we found that a southern population at the periphery of the species' geographic range was more strongly influenced by body size than population distributed within the core of their range. If this finding holds for other species facing similar selective pressures from climate warming, then our results provide critical information on the mechanism of redistribution and underscore the limits to opportunities for adaptive evolution in changing environments. Here, body size was more important as a predictor of overall fitness (~five times greater) for female HB beluga whales living at the southern edge of their distribution compared to BB whales living in core regions within the species distribution.

Sexual selection is a major evolutionary force selecting for larger male body size for polygynous mating systems which predominate in mammalian species (Ralls 1977). Beluga males are generally 13-14% larger

than females and this ratio did not appear to differ among populations across North America despite spatial variation in relative whale size (Luque and Ferguson 2010). For females, fecundity selection is a major driver of body size, an adaptation that needs to be balanced with survival (Pincheira-Donoso and Hunt, 2017). For example, selection for large female body size is eventually counterbalanced by opposing selective forces that may include (1) increased risk from predation, parasitism, or starvation because of their large size (e.g., reduced agility, increased detectability, higher energy requirements, heat stress) and (2) a longer development time to attain larger size which may result in a later age of sexual maturity and decreased lifetime reproductive success (Blanckenhorn 2000).

Linear increases in age with fitness are expected as the number of offspring born to a female accumulates over time; however, non-linear effects such as a decline in reproduction with advancing age are more challenging to explain or confirm. For a limited number of wild cetaceans, lifetime reproductive success of females has been shown to asymptote at older age when they stop reproducing (Perrin et al., 1976; Mizroch 1981; March and Kasuya 1984). The number of beluga CAs has been found to increase up to approximately 40 years of age (Brodie 1972, Heide-Jorgensen and Teilmann 1994, Suydam 2009, Ferguson et al. 2020). We were able to detect a decline in pregnancy rate of older females (>40 y) as reflected in TC, but this only appeared to occur in the population at the southern limit of the species' distribution. However, as with some other beluga populations (Sergeant, 1973), we did not document an obvious decline in corpora with age, although we had few old females in our hunt sample which may have been due to a sampling bias or to a demographic pattern for whales of the BB region. This demographic pattern in BB beluga may indicate a growing young population recovering from past overexploitation (Wade et al., 2012) or an evolved life-history adaptation of a population selected for life in core range (i.e., source vs sink; Kozłowski 1993).

It is not clear why female beluga fitness should be more strongly correlated with body size in a population of smaller-bodied whales living near the southern periphery of their geographic range. One possibility is due to differences in trends in population abundance since the greater relative density of beluga whales occurs in the peripheral population (Luque and Ferguson 2010). Over evolutionary time, food limitations may have selected for relatively smaller-bodied whales, compared to core populations that are regulated by density-independent ice entrapments (Heide-Jørgensen et al. 2002, Luque and Ferguson 2010). Larger-sized females may be important in peripheral populations because greater fat storage capability provides survival advantages during seasonal food limitation (Lindsteadt and Boyce 1985) and increased nursing duration for improved offspring growth and survival (Beauplet and Guinet 2007).

Another consideration is the contrasting demographic history between the two regions and how long-term changes in population dynamics can drive differences in fitness. The peripheral population is possibly at carrying capacity (Hammill et al. 2017) compared to the much lower abundance of the core populations. The pristine, pre-commercial whaling abundance of the BB population was estimated using modeling of harvest levels to be double that of the most recent population abundance estimate from 1996 of 21,213 belugas (Innes et al. 2002; Innes and Stewart 2002). Although, the population growth trend has been interpreted as suggesting an increasing population, the high Arctic population as a whole is still considered depleted due to past commercial whaling (Hobbs et al., 2020). Similarly, the Cumberland Sound population is considered depleted due to past overharvesting from commercial whaling practices (Sergeant and Brodie 1975) with a current abundance estimated at 1.381 or 15% of the original estimated population size (Watt et al. 2020). In contrast, the western Hudson Bay population is considered to be possibly the largest in the world at a minimum size of 54,473 beluga whales (Matthews et al. 2017). Although considerable commercial harvesting of WHB beluga occurred over the past century (Mitchell and Reeves 1981), the population is considered to be currently at or near carrying capacity (Hobbs et al., 2020). Demographic rates differed between the beluga populations studied here and research has shown that long-term population dynamics can not only fluctuate over time but can sometimes drive large differences in fitness (Ozgul et al. 2006; Boyce et al., 2006) as evidenced in this study.

Cohort effects that include the individual advantages and disadvantages attributed to environmental conditions or maternal conditions passed on from mother to offspring may also influence fitness variation between BB and HB beluga whale populations (Lindström 1999, Descamps et al. 2008, Rickard et al. 2010). If commercial whaling had a significantly higher impact on the core population compared to the more southern beluga whale population, a greater disruption on the social structure of BB beluga whales could have reverberating effects on the survival or reproduction of a particular cohort. Cohort effects may include morphological differences but could also include less tangible effects such as social status generating variation in future performance among individuals born in different years (Beckerman et al. 2002). Similar to social status, differences in genetic or population health between the BB and HB populations could explain the observed spatial variation in beluga whale fitness. Experience of whales could explain differences in fitness (Connor 2007) but was not measured in this study and would be logistically challenging to measure in the wild. The effects of inbreeding on fitness in natural populations can be deleterious (Kruuk et al. 2002) and there is a general linear relationship between population size and population fitness (Reed 2005). The Cumberland Sound population is currently approximately 1,000 individuals which is problematic in maintaining population fitness compatible with long-term persistence (Berger 1990).

Despite the large number of whale samples provided by Inuit hunters from across Nunavut, the number of intact female reproductive tracts sampled with ovaries was modest. As a result, our sample sizes were not large enough to allow for consideration of other covariates that may explain fitness variation, such as comparison between time periods that may relate to environmental shifts. In addition, since hunters are somewhat selective in the size of harvested whales, there is the possibility of bias in the whales hunted (e.g., health), although we would expect this possible bias to be similar throughout Nunavut and our two study populations. Another data uncertainty is whether CA in older females become progressively smaller and more difficult to detect (Suydam 2009). Interpreting TC of beluga whales is made difficult because of the occurrence of accessory corpora (Burns and Seaman 1986) and it is possible that younger females may produce more accessory corpora than older ones (Brodie 1971; Harrison et al. 1972; Perrin et al. 1984). Again, we expect these possible biases would be consistent between both regions and are unlikely to affect overall patterns.

Understanding the evolutionary mechanisms of shifting adaptation of marine mammals in a warming planet will assist conservation efforts in anticipating and possibly ameliorating future demographic challenges (Hazen et al., 2013). Life history variation and population processes are key evolutionary guides that assist in setting priorities in species conservation (Saether et al. 1996). Evolution can occur on contemporary timescales (e.g., decades; Reznick and Ghalambor 2001) and is associated with habitat loss and overharvesting (Wilcove et al. 1998; Conover 2000). Thus, habitat degradation might influence the potential of a population to adapt in response to shifting distributions of prey and predators (Norman et al. 2015). For example, increasing anthropogenic stress from contaminants, noise, and conflicts with fisheries may exacerbate fitness costs to beluga whales (SLE). Certain harvesting strategies, such as selecting large size, can result in the evolution of life-history traits, and result in negative impacts on population demography (Festa-Bianchet 2003; Stockwell et al. 2003). Furthermore, contemporary evolution might reduce fitness through interactions between population size and strength of selection making most conservation efforts risky unless they are able to measure and account for changes in fitness (Fernandez and Caballero 2001). More work is required to understand relationships between fitness and population characteristics, such as individual body growth patterns, sociality, genetics, and possible cohort effects to strengthen conservation efforts ultimately aimed at maintaining individual fitness of populations and ensure long-term persistence.

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Table 1: Regression of female beluga total corpora counts as a measure of fitness on body length (cm) and age (y) for Baffin Bay (N=20) and Hudson Bay (N=80).

Baffin Bay:

Step Variable  $r R^2$  added  $B SE_BBeta$ 

1 Length 0.095 0.009 -0.228 0.117 0.0259

2 Age 0.711 0.505\*\*\* -2.442 1.333 0.4955\*\*\*

3 Length X Age (0.785) 0.112\* 0.00783 0.00353 -

(Constant) 81.18 44.44

Hudson Bay:

Step Variable  $r R^2$  added  $B SE_BBeta$ 

1 Length .289 0.084 -0.0481 0.0.0179 0.0259

2 Age 0.575 0.331\*\*\* 0.3138 0.05847 0.3380\*\*\*

3 Length X Age (0.643) 0.403\*\*\* 0.00621 0.00189 -

(Constant) 54.8 19.5

\*p<.05; \*\*p<.01; \*\*\*p<.001; For Baffin Bay model cumulative  $R^2 = .707$  and adjusted  $R^2 = .672$ . For Hudson Bay, cumulative  $R^2$  squared = .413 and adjusted  $R^2$ squared = .390. B and SE<sub>B</sub> are from the final model at Step 3, and Beta is from the model at Step 2 (all main effects, but no interaction term).

### Figures

Figure 1. Study area delineating the three beluga whale populations and 16 Nunavut, Canada communities where hunt sampling took place.

Figure 2. Comparing female beluga whale age (top) and (length) distributions between Baffin Bay (red) and Hudson Bay (blue) populations.

Figure 3. Linear relationship between female fitness and age comparing Baffin Bay (red; fitness = 0.0441 + 0.0272(age) - 7.72 + 9.99; r<sup>2</sup> = 0.078, p = 0.115) and Hudson Bay (blue; fitness = 0.0339 + 0.0154(age) - 1.898 + 5.233; r<sup>2</sup> = 0.043, p = 0.030) beluga whale populations.

Figure 4. Linear relationship between female fitness and body length comparing Baffin Bay (red; fitness = 0.5029 + 0.0496(length) - 3.749 + 1.326;  $r^2 = 0.766$ , p < 0.001) and Hudson Bay (blue; fitness = 0.3311 + 0.0367(length) - 0.1331 + 1.135;  $r^2 = 0.439$ , p < 0.001) beluga whale populations.

Supplementary Figure. Non-linear relationship between female fitness and body length comparing Baffin Bay (red) and Hudson Bay (blue) beluga whale populations.

Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.

