Relationship between per capita births of Cook Inlet belugas and summer salmon runs: age-structured population modeling

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Abstract. Anthropogenic disturbances may alter a population's conservation status if the ability of individuals to survive and breed is affected. We used an adaptation of the Heligman-Pollard model to estimate survival at age of Cook Inlet belugas (CIB; *Delphinapterus leucas*), an endangered population in south-central Alaska. We developed an age-structured Leslie matrix model, based on the life history parameters survival and fecundity probability, to evaluate the sensitivity of population size and growth of CIB, to variation in estimate values of Chinook and coho salmon abundance in the Deshka River, a major tributary of the Susitna River. Birth effect (e_b) was regressed against Chinook and coho salmon levels for the year of, the year before, and two years before a beluga calf birth. The effect of a range of modifications of salmon availability was illustrated in CIB with a series of simulations. The maximum annual population growths (λ) were set at 1.036 (3.6%). Ranges of CIB survival and fecundity probabilities indicated small changes in survival probabilities have a greater impact on population growth than similar changes in birth probability. As either survival (e_s) or fecundity (e_b) was reduced, the annual growth declined, with either e_s = 0.961 or e_b = 0.388, causing a decreased annual growth of −0.4%. Regressions of Chinook salmon for the year of, the year before, and two years before a birth were all significant at the 5% level as was coho in the year of and year prior to birth. The mechanism model with the best fit was the sum of Chinook and coho in the year of birth and year prior to birth. Simulations showed that if salmon runs remained at their current levels, the CIB population would likely continue its current slow decline and per capita births would continue to be low. The results from this study suggest reproductive success in CIB is tied to salmon abundance in the Deshka River. Current management practices should consider this when setting research priorities, designing new studies, and developing management actions to achieve CIB population recovery targets.

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INTRODUCTION

Birth and survival probabilities depend on environmental factors that occur in the year of birth or year prior to birth in large cetaceans (Ford et al. 2010). The sources of variability in these probabilities are a central tenet in the ecological management of wildlife species, with drivers of variations that include natural and anthropogenic factors (Shelton and Mangel 2011). For example, variation in prey availability at critical points in the life cycle has been reported to influence population productivity and trajectories of predators (Sidorovich 2006, Ford et al. 2010, Cárdenas-Alayza 2012, Wells et al. 2012). Modeling population dynamics provides a tool with which to assess the consequences of decreased energy intake and thus supports informed conservation and management decisions. Birth and survival probabilities are commonly used in such population models to estimate changes in population abundance incorporating these parameters.

Various modeling methods are used to assess the viability and extinction risks of threatened and endangered populations in relation to mismatches between prey abundance and the corresponding population (Durant et al. 2007, Bell et al. 2017). Matrix models contribute to mechanistic models such as the population consequences of disturbance (PCoD), by linking life history parameters and population consequences to disturbances (i.e., missed feeding opportunities) with changes in population growth rate (King et al. 2015, Tollit et al. 2016). Through evaluation of the asymptotic annual growth, represented by lambda (λ), these models can support population management and assess long-term population viability (Caswell 2001). With initial population status and demographic vital rates such as fecundity and mortality, the Leslie model can simulate future population growth trends and structure as a function of time (Leslie 1945). The Leslie model may also examine the relative effects on population growth of changing birth and survival probabilities to demonstrate the consequences (growth or decline) of current population status and structure under various perturbations (van Groenendael et al. 1988).

An endangered whale population, Alaska belugas (*Delphinapterus leucas*), residing in Cook Inlet (CIB), are designated as one of eight populations in U.S. waters at greatest extinction risk by the National Marine Fisheries Service (NMFS 2015). The CIB population was listed as endangered in 2008 following a 47% population decline during the 1990s due, in part, to unregulated subsistence harvesting (Hobbs et al. 2015a). This decline has continued to an estimated 328 whales in 2016 despite a sharp reduction in subsistence harvesting from 1999, and no hunting since 2005 (Shelden et al. 2017). The lack of significant recovery in the CIB population from overexploitation suggests other factors may be limiting growth (Hobbs et al. 2015a). This CIB population is geographically and reproductively isolated, and faces a potentially increasing number of threats that may preclude recovery to historical numbers (NMFS 2016). As part of the process to downlist from endangered to threatened status, a population estimate of 520 must be achieved, while a population size of 780 animals is one of the requirements to delist from the current endangered status (NMFS 2016).

Hobbs et al. (2015b) estimated the mean increase in the number of calves per capita for the years 2006–2012 was 3.5% (standard deviation [SD] = 4.3%), based on aerial surveys, compared to a minimum mean mortality of 2% (SD = 1.2%; 2006–2012), derived from carcass counts, and suggested that births were still likely at or below replacement levels. Boat-based photo-identification data, collected during the same years as aerial surveys, indicate that while aerial surveys were performed near peak birthing, post-aerial survey births may have been missed and therefore not taken into account, underestimating calving rates (McGuire and Stephens 2017). Applying a correction method that uses the encounter rate of calves during photo-identification surveys to estimate the fraction of births that occurred after the aerial survey dates, the estimated mean calves per capita is 6.1% during 2006–2012 (R. C. Hobbs and S. A. Norman, *unpublished manuscript*). Assuming adult females comprise 30–35% of the Cook Inlet population, then it is estimated that 17–20% give birth yearly which equals one-half estimated levels for Alaska beluga populations outside of Cook Inlet (Hobbs

et al. 2015*b*; R. C. Hobbs and S. A. Norman, *unpublished manuscript*).

While the CIB population decline and lack of recovery are well-documented (Hobbs et al. 2015*a, c*, Shelden et al. 2017), data on the mechanisms influencing future population trajectories and potential recovery are lacking (Norman et al. 2015). Decreased energy intake was selected from potential factors identified as obstacles to CIB recovery as demonstrated in other odontocete species such as killer whales (*Orcinus orca*; see NMFS 2016: Table 6).

Decreased energy intake (i.e., reduction in prey) was considered a potential threat to CIB recovery of medium concern and of a continuous, intermittent, and seasonal frequency as described in the CIB Recovery Plan (NMFS 2016). However, few data exist regarding its impact or its correlation to estimated annual births and survival. Several factors may result in the reduction of the abundance, quality, availability, or seasonality of CIB prey: competition by fisheries, prey habitat modification or disturbance, and disruption of prey aggregation by noise (NMFS 2016). Key prey species of CIB are eulachon smelt in the spring (*Thaleichthys pacificus*), Chinook (*Oncorhynchus tshawytscha*), and coho (*Oncorhynchus kisutch*) salmon during the summer (Quakenbush et al. 2015). Though CIB forage on a variety of prey species, these fish species were prominent in analyses of stomach contents collected during April through October, coinciding with early pregnancy, calving, and early lactation (Quakenbush et al. 2015). Reduced prey availability (i.e., salmon) was examined in killer whales (Ward et al. 2009, Ford et al. 2010), where a 25% reduction in prey availability reduced survival by 1% (Ford et al. 2010) and fecundity by 15% (Ward et al. 2009).

In this study, we consider that the persistent current decline in the CIB population, after cessation of subsistence hunting, is associated with changes in the abundance levels of prey (i.e., Chinook and coho salmon). A healthy, idealized population model for CIB was developed based on age-structured fecundity and survival data for a growing population of belugas in Bristol Bay (Burns and Seaman 1986, Lowry et al. 2008). The current growth rate of the CIB was modeled with observed fecundity rates for the CIB taken into consideration. Next, we consider the correlation

between the observed fecundity values for the CIB with Chinook and coho salmon abundance in the Deshka River, a primary tributary of the Susitna River, key foraging habitat for CIB. Finally, we assume that the correlations represent a causational mechanism and use the age-structured population model to project population growth or decline under various simulations of Chinook and coho salmon abundance in the Deshka River. Also, survival at age has not been estimated for CIB other than a minimum mortality rate based on annual carcass counts which have been shown to substantially underrepresent mortality in other marine mammal populations (Sharrow 2013, Saavedra et al. 2017). This modeling effort is useful to the CIB population and provides a framework for researchers to further quantify this and other mechanisms possibly impacting the CIB. Further, this study provides fishery managers an estimate of the magnitude of increase in salmon escapement that could be necessary to facilitate the recovery of the CIB.

Materials and Methods

Population model for Cook Inlet beluga

Based on life history data from western Alaska belugas, the maximum value for fecundity probability was 0.333 (Burns and Seaman 1986). Age at first birth was assumed to be seven years (seven growth layer groups [GLGs] in the teeth). Therefore, it was assumed one-third of females first give birth at age seven, one-third at age eight, and one-third at age nine, for a mean age at first birth of eight years which corresponds to 8.3 yr (SD = 2.9) estimated for belugas from western Alaska (Suydam 2009). This corresponds with anecdotal data from hunted CIB in which two females with lengths 320 cm, one found to be pregnant and thought to be multiparous and the second to be lactating (Mahoney and Shelden 2000). Based on age–length data, lengths for these two whales correspond to a whale aged at ten years (Vos et al. 2019). Shelden et al. (2019) found the youngest aged mature female in their sample to be 14 yr old; however, there were no aged females between ages 3 and 13 with reproductive results; thus, this sample is not suitable for estimating mean age at first birth but does provide an upper limit. Pregnancy probabilities by age class, but with age at first birth at 12 yr,

were obtained from a previous study (Burns and Seaman 1986). While some evidence suggests age at first birth may be older than seven, it has been suggested age at first birth may vary with nutritional status. For this study, we use the value from Suydam (2009) as the best available estimate for the healthy population model. The fraction pregnant for the youngest mature females was extended for the CIB down to seven years, resulting in the following birth probabilities for females by age (years), b_x: (0.00 births per year: 0–6, 0.326:7–21, 0.333:22–45, 0.278:46–51, 0.182:52–57, 0.125:58–77, 0.00:78+; Burns and Seaman 1986), which were divided by two to obtain per capita births of calves of both sexes at age.

Beluga was originally aged by counting GLGs in the teeth and assuming a deposition rate of two GLGs/year (Sergeant 1973, Goren et al. 1987). However, recent evidence supports one GLG/year of age (Stewart et al. 2006, Matthews and Ferguson 2014, Read et al. 2018, Waugh et al. 2018, Vos et al. 2019). Mortality probabilities at age, originally based on two GLGs per year of age (Burns and Seaman 1986; Appendix S1: Table S1), were fitted with a Heligman-Pollard model (Heligman and Pollard 1980) using the MortalityLaws package (Pascariu 2018) in the R statistical language (R Core Team 2014). Annual survival was estimated at half-year intervals in the two-GLG model, which could be deconvolved to estimate annual survival for one GLG/year starting from the square root of the higher of the two GLG/year probabilities (Appendix S1: Table S2).

A baseline Leslie matrix model was constructed for a healthy CIB population using the survival probabilities and the per capita births described above. We assume these life history characteristics represent a CIB population with no stressors affecting reproduction or survival. These parameters are used to calculate the stable age distribution and the expected per capita births in an ideal setting in a growing population. The Leslie matrix population projection model describes age group transitions within a population from one age class to the next (Leslie 1945, Caswell 2001).

$$n_{t+1} = \mathbf{A}n_t$$

where n_t is the vector of the number of individuals, n_x, of age x, at time t. Within $\mathbf{n}_t$, the index

indicates the lower bound for the age class so that 0 is animals <1 yr of age, 1 for age $1 \leq$ years < 2, and so on. The matrix $\mathbf{A}$, the population projection matrix, determines the number of individuals born into the youngest age each year by specifying fecundity for each subsequent age group. The matrix also specifies the individual proportion in each age class that survives to enter the next age class, known as the transition probability. Note that in the formulation used here, the birth probability was multiplied by the survival probability from the previous age class to account for survival of the mother during the year of pregnancy. Baseline survival and fecundity vectors were used to construct the baseline transition matrix, multiplying each age-specific component of the survival vector (s_x) by the age class-specific modifying effect (modifier) from the threat of interest (e_s):

$$s_{x,e} = s_x \times e_s.$$

The annual survival and fecundity probabilities consisted of density-independent components (s_e, b_e) set to values <1 to model processes, such as decreased energy (i.e., salmon) intake, that decrease survival or fecundity. Baseline age-specific fecundity probabilities, b_x, were multiplied by e_b, where e was a value between 0 and 1 that represented the effect of a health threat to fecundity:

$$b_{x,e} = b_x \times e_b.$$

The dominant eigenvalue, λ, of $\mathbf{A}$ was calculated to determine the maximum annual growth. An isopleth was constructed based on maximum annual growth displaying the results of fitting changes in per capita calving to salmon abundance.

Time series analyses

We consider the period from 1999 to 2016 during which the estimated CIB population abundance had an average trend of −0.4% (Shelden et al. 2017). Because calving rates may serve as an indicator of population health and recovery potential, data were collected during aerial surveys in August of 2006–2012 (Hobbs et al. 2015b). These data reflect births occurring after the survey period to estimate the per capita births in the population in each year (R. C. Hobbs and S. A. Norman, *unpublished manuscript*; Table 1). Per

capita births are divided by the maximum per capita births estimated from the population model to estimate the Birth Index, BI_{yr} (Table 1). Note that BI_{yr} is an empirical measure of e_b. The birth effect, however, is not constrained to be less than or equal to one; for example, if years of poor salmon abundance are followed by a few good years, then BI_{yr} in the first relatively good years may well exceed a value of one because a larger than average fraction of mature females are available to become pregnant. It was not possible to examine temporal changes in survival due to the lack of comprehensive data on all total deaths each year, and by sex and age class. Alternatively, as a proxy for survival rates, the annual number of CIB carcasses reported each year was obtained for the years 1999–2016 (Muto et al. 2017; NMFS, *unpublished data*).

Annual indices of Chinook and coho salmon abundance were derived from the Alaska Department of Fish and Game (ADFG 2018) estimated escapement in the Deshka River of south-central Alaska (Appendix S1: Table S3). Salmon indices were total escapement estimated from salmon weir counts multiplied by mean weight and energy content (Chinook = 10.9 kg/fish × 1642 kcal/kg;   coho = 3.6 kg/fish × 1366 kcal/kg), with units designated as 10^8 kcal (Bigler et al. 1996, O'Neill et al. 2014). The Deshka is a large tributary of the Susitna River, and salmon spawning in the Deshka will have passed through an important CIB foraging site in the Susitna River delta. Though there are other salmon runs in Cook Inlet, the Deshka River run is

most commonly found in the Susitna Delta and is the only run with a long-enough time series of annual counts to compare to the time interval of interest for this study (Fig. 1). Abundance estimates for eulachon were not available and thus not evaluated in this study. The strength and statistical significance of associations between the BI_{yr} (as well as survival) and salmon abundance indices were assessed by regressing the BI_{yr} and the annual carcass counts against each individual salmon species index, as well as the two species considered together, at various time lags ranging from zero to three years.

Effect models

To model the relationships between birth and survival salmon abundance, we consider each salmon species separately, and the two summed together. For the birth effects, we consider the correlation with salmon abundance in the year of birth, the year prior to birth, which corresponds to feeding during the first trimester of pregnancy, and two years prior which would correspond to the reserves that the female would have prior to mating. For CIB survival, we consider the year of carcass count as well as the year prior to the count. The birth regression model was developed using the data from the period 2006–2012, incorporating the corresponding salmon escapement time series to estimate the BI values in 1999–2005 and 2013–2016. Note that negative estimates of BI are set to zero. The BI values were averaged to estimate the average value of e_b for the whole period 1999–2016 (Table 1). It was not possible to develop an effect model for survival using the carcass count data; therefore, we used the isopleths to estimate the value of e_s, that when applied with the value of e_b estimated above, results in a −0.4% growth rate.

Table 1. Annual birth data for CIB from August aerial surveys (R. C. Hobbs and S. A. Norman, *unpublished manuscript*).

Year	Estimated per capita birth Rate (B_{yr})	CV	Birth Index (BI_{yr})
2006	0.154	0.164	1.266
2007	0.151	1.069	1.246
2008	0.020	0.289	0.165
2009	0.015	0.316	0.127
2010	0.008	0.782	0.069
2011	0.053	0.335	0.436
2012	0.028	0.422	0.232

Notes: CIB, Cook Inlet belugas. Note that the Birth Index estimated for 2006 and 2007 is greater than one this can occur when conditions are poor in the previous years so that more than the average numbers of females are ready to become pregnant in the following good years.

Population projections

The Leslie matrix model was used to project recovery or decline of the CIB population over 25 yr when the birth rate is as a function of the Deshka salmon (Chinook and coho combined) abundance. Annual values for e_b were calculated from a hypothetical salmon data set using a birth effect model with parameters drawn from the parameter distributions fitted to the CIB BI values, to account for uncertainty in the model parameters. A parameter set is drawn for each of
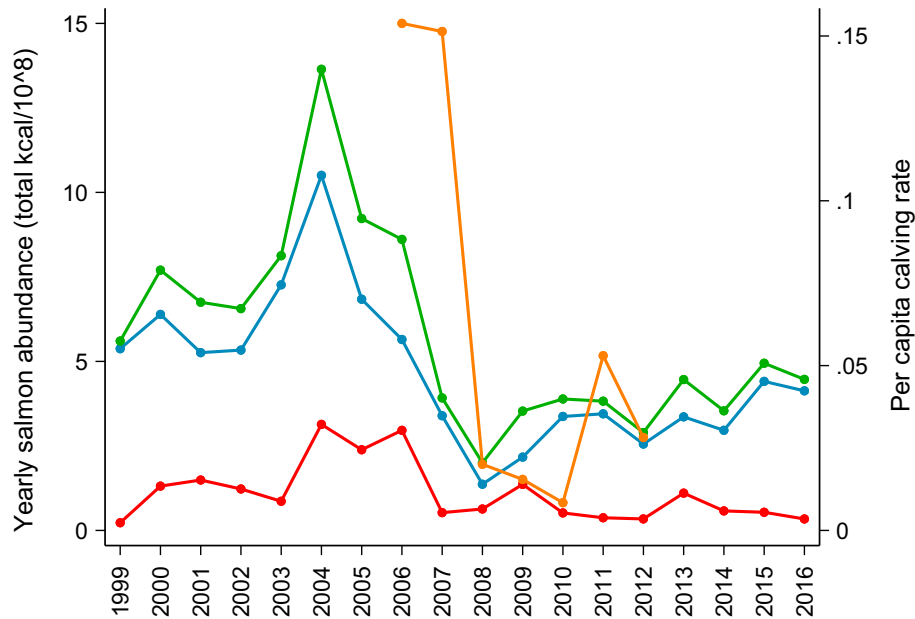
Fig. 1. Deshka River Chinook (blue line), coho (red line), and Chinook + coho (green line) salmon abundance expressed as available energy to Cook Inlet belugas, based on total kcal/10^8 which is represented by yearly weir counts from the Alaska Department of Fish and Game, 1999–2016 (left axis). Per capita birth rates are represented by the orange line (right vertical axis).

the 10,000 simulated populations and used for all of the runs. The residual variance is used for the process error. To prevent biologically unreasonable fecundity values, $e_b(t)$ values were limited to the interval $[0, 3 − (e_b(t − 1) + e_b(t − 2))]$. The optimal birth interval in belugas is three years (Suydam 2009), and consequently at high fecundity rates, one-third of females would become pregnant each year. After a period of low fecundity, more than one-third of the females may be available to begin pregnancies in the first year or two of better salmon abundance, thus resulting in higher than maximum values of e_b; however, this is not sustainable when a general improvement occurs. So that

$$e_b(t) = \text{maximum}(0, \text{minimum}((3 − (e_b(t − 1) + e_b(t − 2)), \text{intercept} + \text{slope} \times \text{SI}(t) + \varepsilon(t)))$$

where $e_b(t)$ is the birth effect in year t, intercept and slope are values specific to that simulation, $\text{SI}(t)$ is the salmon index in year t, and $\varepsilon(t)$ is the process error in year t.

Hypothetical salmon data sets SI for the 2017–2042 projections (25 yr) were created by sampling with replacement from the 1999–2016 salmon data. To preserve the autocorrelation and cross-correlation within the salmon data, three years were drawn from the interval 1999–2016, and then, the ten-year segments of salmon data for both species beginning at each of the years (wrapping around from 2016 to 1999 for the years after 2006) were pieced together to create a 30-yr time series. A random start point in the first five years was chosen so that the joints between segments would not all occur at 10 and 20 yr. A set of 10,000 of these salmon time series was developed. To test the response of the population to an increase in salmon, increases ranging from 0.0 (no increase) to 1.0 (salmon abundance doubled) were considered, and for each simulation, all of the salmon index values in the set of time series were multiplied by the increase factor (1.0 + increase) to create salmon time series at higher average abundance.

The initial age structures for the simulations were set up using the stable age distribution for the population growing at −0.4%. The age classes aged 28 and older were then reduced by 60% to account for the depletion of the population in the 1990s by subsistence hunting. In the

mid-1990s, there was a period of high removals by subsistence hunting, in which the population was reduced by 47%, mostly by removals of older adults (Mahoney and Shelden 2000, Vos et al. 2019). Hunting was at much lower levels prior to 1990, and since 1998, only five whales have been taken. Thus, we treated hunting as a single event with the lowest impacted age class at 28 yr (age 10 yr + 2017–1999). The variability of salmon abundance in the years prior to 2017 would affect size of the initial cohort of each age class. To account for this, each age class of the distribution was multiplied by a birth effect for each of the 79 yr prior to 2016. The birth effects for the years 2006–2012 were the per capita birth data in R. C. Hobbs and S. A. Norman (*unpublished manuscript*; Table 1). Birth effects for 1999–2005 and 2013–2016 were based on the existing salmon data, while those effects prior to 1999 were generated using the same approach as above. Thus, the proportional size of age class is as follows:

$$P(a) = (0.996^{-a}) \times S(a) \times e_b(2017\text{-age}) \\ \times (0.4 \text{ if } a > 27)$$

where $P(a)$ is the proportion of the population at age a; (0.996^{-a}) accounts for the larger initial cohort sizes at older ages; $S(a)$ is the survival to age a; $e_b(2017\text{-age})$ is the age effect for the birth year, and (0.4 if $a > 27$) accounts for the high mortality rate in the mid-1990s. The proportions of the population in each age class developed above were divided by the sum of the proportions over all ages to get an initial age distribution for each simulated population. The number of individuals in each age class was determined using the age class probability in a binomial draw from 328, the population estimate for 2016. This resulted in variation in the initial population sizes that approximated the uncertainty in the population estimate.

Thus, for each of the 10,000 populations, there was an initial population, a model relating salmon abundance to birth rate and a time series of salmon data, with the only difference between the simulations being the relative increase of the available salmon after 2017. Simulations over 25 yr, ranging from no increase in salmon (multiplier = 1) to a 100 percent increase (multiplier = 2) for each species separately and combined together, were conducted to estimate

the increase or decline in birth rates and abundance of CIB. The program R was used for all analyses (R Core Team 2014), and code is provided in Data S1.

RESULTS

Leslie matrix

Annual survivorship in the one GLG/yr age estimate was at a maximum (97.3%) at ages 23 and 24 and dropped off at the extremes with first-year survival at 76.2% (Fig. 2; Data S1). The decrease in survival to age (i.e., cumulative survival) was curvilinear, with the greatest decreases occurring from 0 to 5 yr of age (Fig. 2). When combined with the age-specific per capita births, the Leslie matrix yields a λ of 1.036 for maximum annual growth of 3.6%. Using the stable age distribution, with the age-specific birth rates, the population per capita maximum birth rate (B_{max}), during the period of −0.4% growth, is estimated to be 0.121 births per nonage zero (i.e., born that year) individual in the population, and from the stable age distribution, we estimate 0.53 deaths per capita.

Ranges of CIB survival and fecundity probabilities indicate a small change in survival has a greater impact on population growth than a similar change in per capita births (Table 2, Fig. 3).
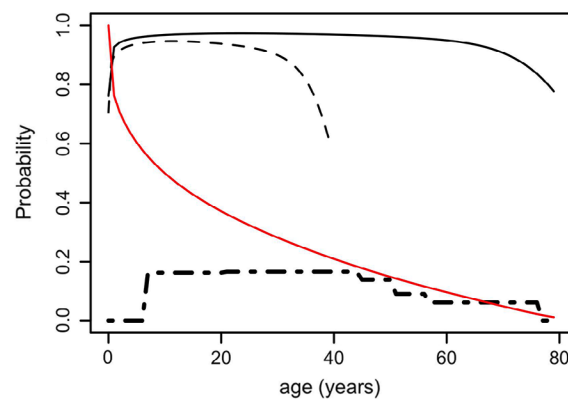

Fig. 2. Cook Inlet beluga baseline cumulative or survival to age (red line) and annual (solid line) survival probabilities based on the one growth layer group (GLG)/yr age estimation. The annual survival, based on two GLGs/yr from Burns and Seaman (1986), is included for comparison (dashed line). Per capita age-specific births are represented by the dot-dash line.

For example, the isopleth for CIB annual growth at 0.02 indicates that an approximate 2% decline in survival, with no reduction in per capita births, has nearly an equivalent effect as a 40% decline in per capita births assuming no reduction in survival probability.

Optimal 3.6% yearly growth was used as the base rate, achieved when survival (e_s), and fecundity (e_b), effects were both equal to one, which is assumed to be the case in Bristol Bay. As either parameter was reduced, annual growth declined, with either $e_s = 0.961$ or $e_b = 0.388$, causing a decreased growth rate of -0.4%, representing the range of differences between the CIB at -0.4% per yr, and that of the presumed healthy population at 3.6% per yr. Annual growth from -5% to 3% is also presented (Fig. 3) to demonstrate the ranges of survival and fecundity effects that result in a corresponding increase or decrease in population growth. The two effect (e) values each resulting in -0.4% growth, when added together, have a nearly additive effect, reducing the growth rate to -4.2%, or a total of -7.8% below maximum growth.

Birth effect model

Birth Index was regressed against Chinook and coho salmon levels for the year of birth, the year before, and two years before birth (Table 3). Regressions of Chinook salmon for the year of, the year before, and two years before a beluga's birth were all significant at the 5% level, as was

Table 2. Estimated annual population growth in the Cook Inlet beluga population, incorporating health modifiers into the matrix model due to decreased energy intake.

Threat	Population growth (%)	Change from baseline (%)	Fraction of baseline (%)
Model with no effects (baseline)	3.6	0.000	100.0
Model with effects			
Fecundity affected	0.8	−2.8	97.3
Survival affected	2.3	−1.3	98.7
Fecundity and survival affected	−0.4	−4.0	96.1

Notes: The change in fecundity is based on the estimate for the period 1999–2016 ($e_b = 0.538$). The change in survival ($e_s = 0.9877$) is hypothesized, assuming the reduced energy intake is responsible for the current rate of decline.

coho in the year of a beluga's birth and the year prior. The mechanism model with the best fit based on R^2 values was the sum of Chinook and coho in the year of birth, and the year prior to a birth, we used this to model birth effect for the simulations. To estimate mean fecundity (e_b) for the period 1999–2016, assuming that salmon abundance is the key influence, we used the calving indices from 2006 to 2012 (Table 3), and the mechanism model with the salmon data for 1999–2005 and 2013–2016. A yearly e_b was calculated, and then used to estimate the mean value of e_b for the whole period 1999–2016 (Table 4). The estimated mean value of e_b through the period 1999–2016 was 0.538 which is t higher than the mean of 0.504 during 2006–2012.

Survival effect model

Carcass counts were available for all years between 1999 and 2016, averaging 8.7 yr^{-1} and ranging between 3 and 20 in a year. The age-structured model estimated that the population should average 15.6 mortalities, suggesting that half of the carcasses are discovered yearly. Regression of the carcass counts against the salmon data over the period 1999–2016 yielded one significant positive correlation between the carcass counts and the size of the Chinook salmon run in the same year (Table 4).

Inserting the estimated e_b value into the age-structured model, we have an annual growth of 0.8%, which is greater than the trend for 1999–2016 (vertical arrow, Fig. 3). We hypothesize a survival effect e_s of 0.9877 (horizontal arrow, Fig. 3), which when combined with the birth effect, results in a decline of -0.4% per yr (diagonal arrow, Fig. 3). We include this survival effect in the population projections so that the model with unchanged salmon levels is consistent with the observed -0.4% growth.

Population simulations

The simulations showed that if the salmon runs remained at their current levels, the population would likely continue its current lack of growth and per capita births would continue to be low (Fig. 4). The per capita birth rate increases within two years of the increase in salmon. Furthermore, the three-year birth interval is evident in both the 50% and 100% increases in salmon because the sudden increase in prey availability
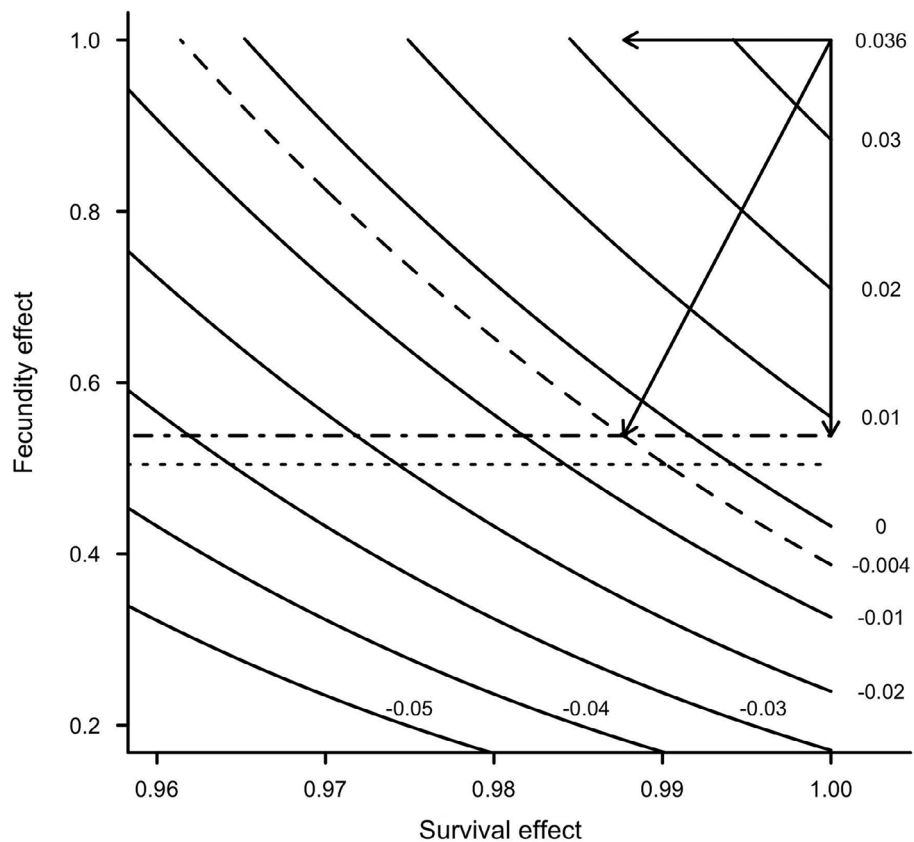
Fig. 3. Isopleths for values of survival and fecundity for annual growth in a simulated model of Cook Inlet, Alaska belugas (−5% to +3.6%). Isopleths show the relationship between changes in fecundity and survival that result in the same population growth rate. The long dashed line represents the current beluga population decline of −0.5%. The fecundity effect was estimated from Cook Inlet belugas survey data 2006–2012 (short dashes) and from the salmon data 1999–2016 (dot-dash line vertical arrow). The survival effect (horizontal arrow) is hypothesized assuming that the reduced salmon availability is responsible for current annual decline (diagonal arrow).

results in a pulse that initially synchronizes the cycle in the simulated populations (Fig. 4). The model predicted that if salmon levels of both species increased by 50%, the CIB population would increase with 48% probability of reaching 520 individuals (downlisting size) within 25 yr and per capita births would be near their maximum value at least 50% of the time (Fig. 5). Doubling the salmon run (100%) would result in a 73% probability of reaching a 520-individual population size in 25 yr and per capita births above 10% in 50% of the years, and rarely falling below 5% (Fig. 5). If Chinook salmon increased 20% or more, the current decline would likely be reversed and the population would increase, while only increasing the coho run would be less

effective (Fig. 5). Average birth effect e_b doubled with the doubling of both salmon runs, with the majority of the change resulting from the increase in Chinook salmon availability (Fig. 5). The average per capita births for CIB nearly doubled, but less than the birth effect, because higher annual population growth results in an increased fraction of subadults in the population.

DISCUSSION

Though other sources of anthropogenic disturbance such as noise or environmental threats such as predation by killer whales may contribute to sub-optimal birth rates, a strong correlation is evident for both salmon species in the

Table 3. Regression of various models of the influence of Chinook and coho runs in the Deshka River on per capita births of CIB between 2006 and 2012.

Model	Estimate	SE	t value	Pr(>|t|)	R^2
Coho (yr)	0.419	0.088	4.789	0.005	0.785
Coho (yr-1)	0.558	0.068	8.165	0.000	0.916
Coho (yr-2)	0.352	0.150	2.351	0.066	0.430
Chinook (yr)	0.295	0.038	7.863	0.001	0.910
Chinook (yr-1)	0.246	0.030	8.290	0.000	0.919
Chinook (yr-2)	0.140	0.027	5.089	0.004	0.806
Chin + Coho	0.183	0.022	8.428	0.000	0.921
(Chin + Coho) (yr-1)	0.177	0.015	11.980	0.000	0.960
Chin + Coho + (Chin + Coho) (yr-1)	0.093	0.006	16.817	0.000	0.979
(Chin + Coho) ((yr-1) + (yr-2))	0.069	0.011	6.359	0.001	0.868

Notes: CIB, Cook Inlet belugas; SE, standard error; yr, year of birth; yr-1, year prior to birth corresponding to first-trimester pregnancy; yr-2, two years prior to birth corresponding to summer prior to conception the following spring. Time-lagged series of each salmon species were considered separately; then, plausible combinations of the more significant fits were considered for a projection model. Salmon counts were multiplied by average weight and by energy density (Chinook = 10.9 kg/fish × 1642 kcal/kg, coho = 3.6 kg/fish × 1366 kcal/kg); units were 10^8 kcal.

Table 4. Regression of various models of the influence of Chinook and coho runs in the Deshka River on annual carcass counts of CIB between 1999 and 2016.

Model	Estimate	SE	t value	Pr(>|t|)	R^2
Coho (yr)	0.69	1.35	0.52	0.61	0.02
Coho (yr-1)	1.12	1.33	0.84	0.41	0.04
Chinook (yr)	1.05	0.48	2.16	0.05	0.23
Chinook (yr-1)	0.72	0.51	1.40	0.18	0.11
Chin + coho	0.68	0.39	1.76	0.10	0.16
(Chin + coho) (yr-1)	0.52	0.39	1.34	0.20	0.10

Notes: CIB, Cook Inlet belugas; SE, standard error. Time-lagged series of each species were considered separately; then, plausible combinations of the more significant fits were considered for a projection model. Salmon counts were multiplied by average weight and by energy density (Chinook = 10.9 kg/fish × 1642 kcal/kg, coho = 3.6 kg/fish × 1366 kcal/kg); units were in 10^8 kcal.

year of birth and Chinook in the year prior to a beluga birth. The contraction of the range of the CIB population to the area surrounding the mouth of the Susitna River during the timing of these runs (Shelden et al. 2017) suggests that the population is likely dependent on the Chinook run, and to a lesser degree, the coho run, which has less than one-quarter of the energy content of the Chinook run, as primary food resources during the summer. We suggest no compensatory prey sources of sufficient quantity nor quality substitute for Chinook salmon declines and the accompanying nutritional stress (Ford et al.

2010). Nutritional quality is especially critical for the reproductive health in marine mammals (Malinowski and Herzing 2015), and in most mammals, metabolic and subsequent nutritional demands (i.e., calories, proteins, lipids, moisture) tend to increase gradually throughout pregnancy and into lactation (Robinson 1986), such that lactation is often considered the most costly state of mammalian reproduction (Clutton-Brock 1991). Thus, this is a plausible mechanism of the reduced birth rate and lack of recovery. Furthermore, simulation results indicate that doubling the salmon abundance would be sufficient to allow recovery of the population regardless of impacts from other threats.

Demographic CIB data immediately prior to and during their population decline have been limited and largely inferential (NOAA, *unpublished data*). Very few studies have been conducted on beluga health to investigate how food limitation may influence their decline (Quakenbush et al. 2015). A range of other health threats including harvest, predation from killer whales, pollution, disease, and fishery interactions has been investigated (Mahoney and Shelden 2000, Moore et al. 2000, Shelden et al. 2003, Hobbs et al. 2015c). These studies generally indicate these threats are associated with lower survival or fecundity, but the challenge remains to quantify their impacts and determine their relative role in CIB population decline. Increasing populations, such as the Bristol Bay stock, experience
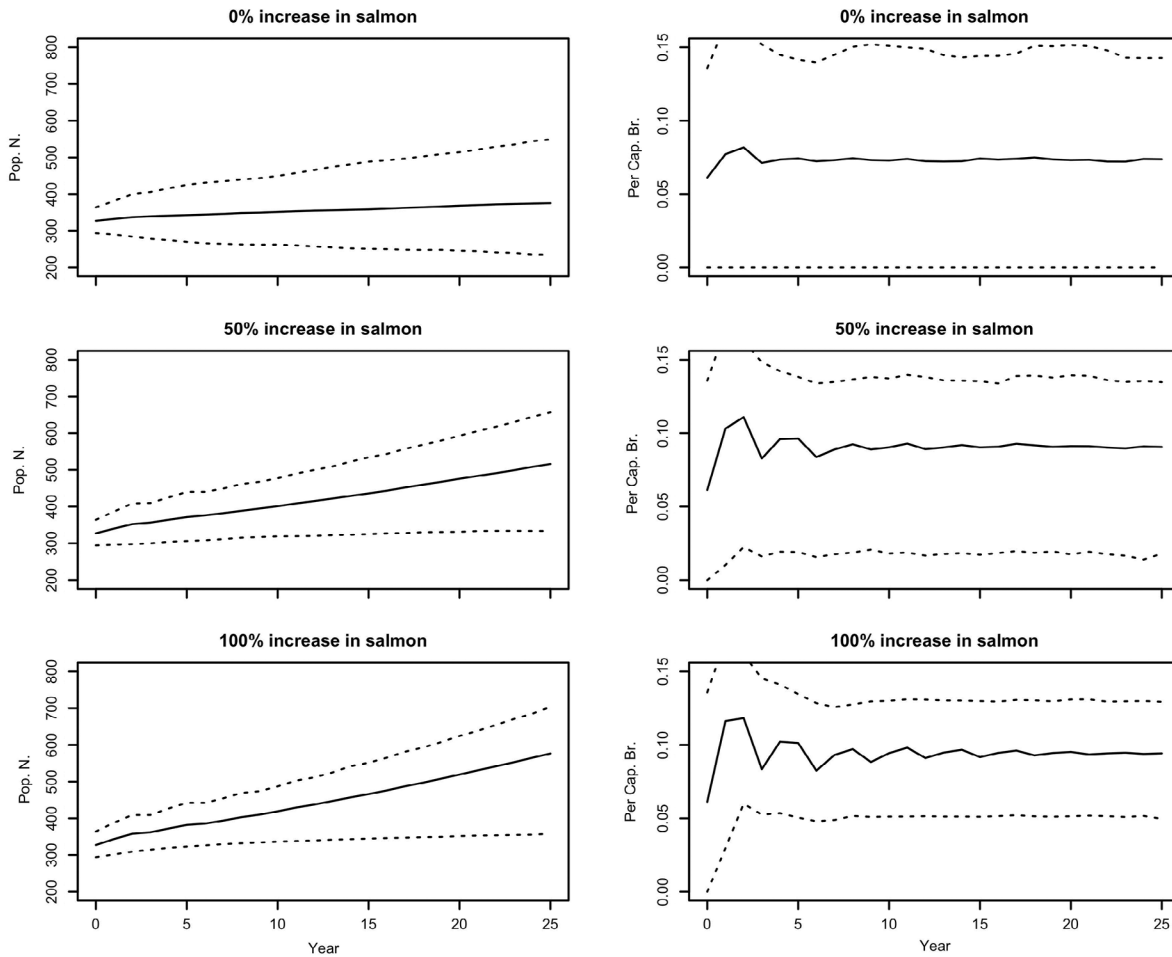
Fig. 4. Trajectories of population size (left) and per capita births (right) over the 25 yr following an increase in the average of salmon counts on the Deshka River. The solid line is the median population size trajectory, and the lower and upper dashed lines represent the 2.5% and 97.5% quantiles, respectively, of the range of trajectories.

similar threats, but appear to thrive (Lowry et al. 2008).

An age-structured population model allowed a separate analysis of the responses of survival and fecundity to decreased salmon intake in a simulated CIB population. Demographic parameters from a healthy beluga population in Bristol Bay were modified to create ranges for the survival and fecundity and subsequently used to quantify differences in the CIB population. Decreased energy intake from reduced salmon runs correlated with reduced per capita calving as observed from aerial surveys. The noticeable association between changes in Chinook and coho salmon abundance and birth rate of CIB suggests that prey limitation is an important factor in recent population declines. While low salmon abundance may indeed reduce survival rates, the simulations indicated that the change in birth effect alone would be sufficient to allow recovery.

Survival as estimated by carcass counts was not correlated with salmon abundance. This suggests that the carcass discovery process rather than survival was influenced by the size of the run and the survival influence was not considered further (cf Williams et al. 2011). Location of a beluga carcass and cause of death can impact whether or not a carcass is discovered. The positive correlation between CIB yearly carcass counts and Chinook salmon abundance was more likely a reflection of the
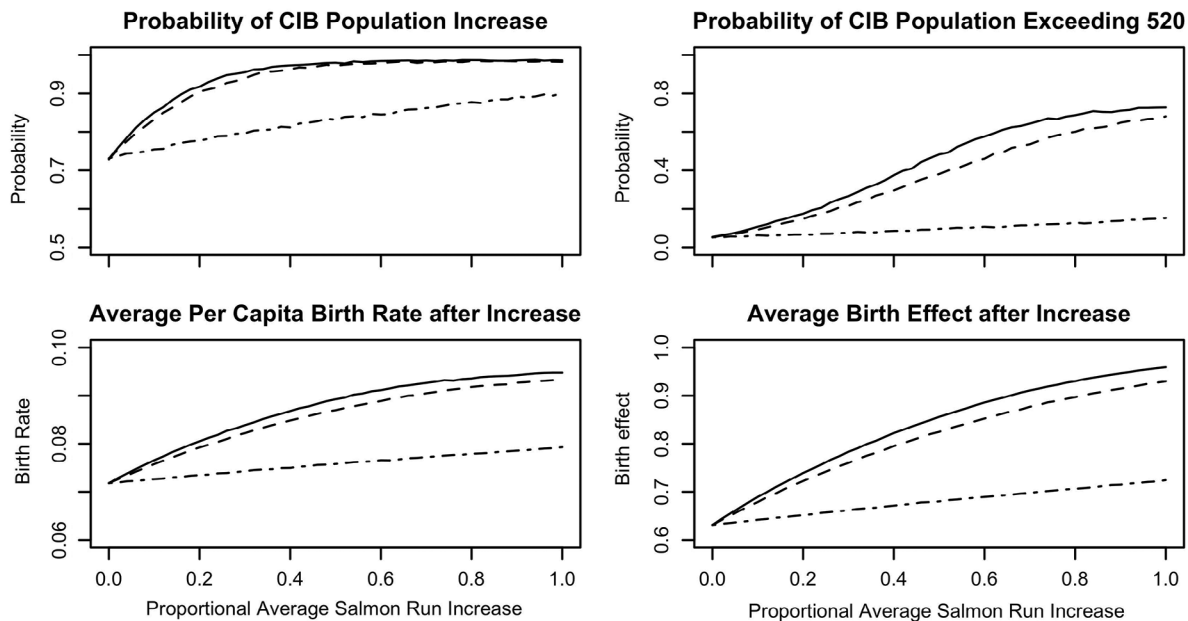
Fig. 5. Summary results from simulations with various increases in the size of the Deshka salmon counts over 25 yr for both Chinook and coho salmon, increased by the same proportion (solid line), Chinook only increased (dashed line), and coho only increased (dot-dash line). All results are for the 25 yr following the change in the mean salmon run sizes.

greater likelihood of discovering a beluga carcass due to more numerous beluga feeding in the Susitna River delta during years of larger salmon runs, rather than a true increase in probability of death.

Examination of the annual growth isopleths indicates that percentage change in survival had more of an impact on population growth compared to changes in fecundity. Therefore, for a long-lived species like beluga whales, selection has favored preserving the life of a reproductive female over an individual fetus. The present study models the potential impact of decreased salmon intake on CIB population recovery, through the relative impacts on a population and per capita calving. While the ultimate cause(s) of the CIB decline cannot be confirmed, understanding the proximate changes in survivorship and fecundity may help estimate the importance of these ecologic drivers, as well as aid in prioritizing research funds and management actions (Morris et al. 2002).

The models in this study reveal that a relatively small increase in salmon available to CIB would elicit a population increase. Further, this change in the nutritional environment would diminish the time necessary to change its population status from downlisted to threatened under different scenarios of increased energy intake (NMFS 2016). For example, from models presented here, if Chinook and coho runs doubled over the next 25 yr, growth rates would be predicted to increase to near the maximum in this model from the current -0.04%. This would result in the population recovering to the downlisting size of 520 individuals 95% of the time. Obviously, these models do not provide the mechanisms in which to increase the food availability but may afford managers with the magnitude of the changes required for CIB recovery. Our modeling approach also provides a method in which to monitor population recovery progress without waiting 10 yr for the population to show a change in trajectory. Using the age-structured model, a doubling of per capita calving is predicted if the salmon runs are doubled (Fig. 5). We surmise changes in calving success can be detected with just a few years of monitoring data derived from aerial and photo-identification studies (cf. Hobbs et al. 2015b).

A limitation of these models is incorporating incomplete CIB demographic data and assuming that the Bristol Bay beluga demographic parameters are representative under optimal ecological conditions, and that the assumptions regarding the current age structure approximate the actual population. While the stable age distribution is a convenient assumption, we modified the age structure to account for the loss of approximately 60% of the adult population in just a few years prior to 1999. This left a deficit in age classes 28 yr and older (i.e., the generation length or the average at giving birth for adult females). Over the 25 yr of the simulation, this deficit ages out of the population and the per capita birth rate increases even without an increase in salmon abundance, accounting for the 70% chance of increase with no change. Additionally, available data on demographic response of CIB to changes in salmon abundance do not include a range of population sizes and environmental conditions, which limits the ability of the model to accurately capture the response to the complete range of interannual environmental variability or to account for density-dependent demographic rates (Bierzychudek 1999). Over longer temporal scales of years, density-dependent responses would affect population growth and the relative impact of increasing the size of salmon runs. The projection model does not include a density-dependent effect; however, the population is assumed to be below its carrying capacity of 1300 beluga whales. This modeling effort is based on current CIB demographic data, and thus, while we predict that an increase in salmon availability results in a population increase, we must include the caveat that model predictions will be less reliable as the population increases to the 520 whale minimum which is one of the criteria to downlist to threatened status.

In this study, the models revealed the partial or relative contribution of a threat (i.e., decreased energy intake) on a target population in its current state. The age-structured model framework can model additional external threats and provides a mechanism to consider multiple environmental or anthropogenic threats within the same model. As additional data on health threats and their relative influence on CIB or other cetaceans become available, the model used in this study can be improved to assess the interaction of multiple threats as a function of age class. Results from this study will provide researchers with insights to develop additional studies that address the low birth rates of the CIB, and to fisheries resource managers, some guidance on the degree of increase in salmon escapement.

ACKNOWLEDGMENTS

LITERATURE CITED

Alaska Department of Fish and Game (ADFG). 2018. Fish Counts. https://www.adfg.alaska.gov/sf/Fish Counts/

Bell, D. A., R. P. Kovach, S. C. Vulstek, J. E. Joyce, and D. A. Tallmon. 2017. Climate-induced trends in predator-prey synchrony differ across life-history stages of an anadromous salmonid. Canadian Journal of Fisheries and Aquatic Sciences 74:1431–1438.

Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9:1278–1287.

Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. A review of size trends among North Pacific salmon (Oncorhynchus spp.). Canadian Journal of Fisheries and Aquatic Sciences 53:455–465.

Burns, J. J., and G. A. Seaman. 1986. Investigations of belukha whales in coastal waters of western and northern Alaska. II. Biology and ecology. OCSEAP Final Report 56. ADFG, Minerals Management Service. https://www.boem.gov/ESPIS/0/81.pdf

Cárdenas-Alayza, S. 2012. Prey abundance and population dynamics of South American fur seals (Arctocephalus australis) in Peru. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Clutton-Brock, T. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey, USA.

Durant, J. M., D. Ø. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch

between predator requirements and resource availability. Climate Research 33:271–283.

Ford, J. K. B., G. M. Ellis, P. F. Olesiuk, and K. C. Balcomb. 2010. Linking killer whale survival and prey abundance: Food limitations in the oceans' apex predator? Biology Letters 6:139–142.

Goren, A. D., P. F. Brodie, S. Spotte, G. C. Ray, H. W. Kaufman, A. J. Gwinnett, J. J. Sciubba, and J. D. Buck. 1987. Growth layer groups (GLGs) in the teeth of an adult belukha whale (*Delphinapterus leucas*) of known age: evidence for two annual layers. Marine Mammal Science 3:14–21.

Heligman, M. A., and J. H. Pollard. 1980. The age pattern of mortality. Journal of the Institute of Actuaries 107:49–80.

Hobbs, R. C., K. E. W. Shelden, D. J. Rugh, C. L. Sims, and J. M. Waite. 2015a. Estimated abundance and trend in aerial counts of beluga whales, *Delphinapterus leucas*, in Cook Inlet, Alaska, 1994–2012. Marine Fisheries Review 77:11–31.

Hobbs, R. C., C. L. Sims, K. E. W. Shelden, L. Vate Brattström, and D. J. Rugh. 2015b. Annual calf indices for beluga whales, *Delphinapterus leucas*, in Cook Inlet, Alaska, 2006–12. Marine Fisheries Review 77:40–58.

Hobbs, R. C., P. R. Wade, and K. E. W. Shelden. 2015c. Viability of a small, geographically-isolated population of beluga whale, *Delphinapterus leucas*: effects of hunting, predation, and mortality events in Cook Inlet, Alaska. Marine Fisheries Review 77:59–88.

King, S. L., R. S. Schick, C. Donovan, C. G. Booth, M. Burgman, L. Thomas, and J. Harwood. 2015. An interim framework for assessing the population consequences of disturbance. Methods in Ecology and Evolution 6:1150–1158.

Leslie, P. H. 1945. The use of matrices in certain population mathematics. Biometrika 33:183–212.

Lowry, L., K. J. Frost, A. Zerbini, D. DeMaster, and R. R. Reeves. 2008. Trend in aerial counts of beluga or white whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, 1993–2005. Journal of Cetacean Research and Management 10:201–207.

Mahoney, B. A., and K. E. W. Shelden. 2000. Harvest history of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. Marine Fisheries Review 62:124–133.

Malinowski, C. R., and D. L. Herzing. 2015. Prey use and nutritional differences between reproductive states and age classes in Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas. Marine Mammal Science 31:1471–1493.

Matthews, C. J. D., and S. H. Ferguson. 2014. Validation of dentine deposition rates in beluga whales by interspecies cross dating of temporal δ^{13}C trends in teeth. NAMMCO Scientific Publications 10:8.

McGuire, T., and A. Stephens. 2017. Photo-identification of Beluga Whales in Cook Inlet, Alaska: summary and synthesis of 2005–2015 data. Report prepared by LGL Alaska Research Associates, National Marine Fisheries Service, Alaska Region, Anchorage, Alaska, USA.

Moore, S. E., K. E. W. Shelden, L. K. Litzky, B. A. Mahoney, and D. J. Rugh. 2000. Beluga, *Delphinapterus leucas*, habitat associations in Cook Inlet, Alaska. Marine Fisheries Review 62:60–80.

Morris, W. F., P. L. Bloch, B. R. Hudgens, L. C. Moyle, and J. R. Stinchcombe. 2002. The use of population viability analysis in endangered species recovery planning: past trends and recommendations for future improvement. Ecological Applications 12:708–712.

Muto, M. M., et al. 2017. Alaska marine mammal stock assessments, 2017. NOAA Technical Memorandum NMFS-AFSC-378. U.S. Department of Commerce. https://www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-378.pdf

National Marine Fisheries Service. 2015. Species in the spotlight initiative. Silver Spring, Maryland, USA. http://www.nmfs.noaa.gov/stories/2015/05/05_14_15species_in_the_spotlight.html

National Marine Fisheries Service. 2016. Recovery plan for the Cook Inlet beluga whale (Delphinapterus leucas). National Marine Fisheries Service, Alaska Region, Protected Resources Division, Juneau, Alaska, USA. https://alaskafisheries.noaa.gov/pr/cib-recovery-plan

Norman, S. A., R. C. Hobbs, C. E. C. Goertz, K. A. Burek-Huntington, W. A. Smith, and L. A. Beckett. 2015. Potential natural and anthropogenic impediments to the conservation and recovery of Cook Inlet beluga whales, *Delphinapterus leucas*. Marine Fisheries Review 77:89–105.

O'Neill, S. M., G. M. Ylitalo, and J. E. West. 2014. Energy content of Pacific salmon as prey of northern and southern resident killer whales. Endangered Species Research 25:265–281.

Pascariu, M. D. 2018. MortalityLaws: parametric Mortality Models, Life Tables and HMD. R package version 1.5.0. https://github.com/mpascariu/MortalityLaws

Quakenbush, L. T., R. S. Suydam RS, A. L. Bryan, L. F. Lowry, K. J. Frost, and B. A. Mahoney. 2015. Diet of beluga whales, *Delphinapterus leucas*, in Alaska from stomach contents, March–November. Marine Fisheries Review 77:70–84.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, F. L., A. A. Hohn, and C. H. Lockyer. 2018. A review of age estimation methods in marine

mammals with special reference to monodontids. NAMMCO Scientific Publications 10:5.

Robinson, J. 1986. Changes in body composition during pregnancy and lactation. Proceedings of the Nutrition Society 45:71–80.

Saavedra, C., G. J. Pierce, J. Gago, D. Jusufovski, Á. Cabrero, S. Cerviño, A. López, J. A. Martínez-Cedeira, and M. B. Santos. 2017. Factors driving patterns and trends in strandings of small cetaceans. Marine Biology 164:165.

Sergeant, D. E. 1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. Journal of the Fisheries Research Board of Canada 30:1065–1090.

Sharrow, D. J. 2013. Modeling the age pattern of human mortality: mathematical and tabular representations of the risk of death. Dissertation. University of Washington, Seattle, Washington, USA.

Shelden, K. E. W., J. J. Burns, T. L. McGuire, K. A. Burek-Huntington, D. J. Vos, C. E. C. Goertz, G. O'Corry-Crowe, and B. A. Mahoney. 2019. Reproductive status of female beluga whales from the endangered Cook Inlet population. Marine Mammal Science. https://doi.org/10.1111/mms.12648

Shelden, K. E. W., R. C. Hobbs, C. L. Sims, L. Vate Brattström, J. A. Mocklin, C. Boyd, and B. A. Mahoney. 2017. Aerial surveys of beluga whales (Delphinapterus leucas) in Cook Inlet, Alaska, June 2016. Processed Report AFSC 2017-09. NOAA, Seattle, Washington, USA. https://www.afsc.noaa.gov/Publications/ProcRpt/PR2017-09.pdf

Shelden, K. E. W., D. J. Rugh, B. A. Mahoney, and M. E. Dahlheim. 2003. Killer whale predation on belugas in Cook Inlet, Alaska: implications for a depleted population. Marine Mammal Science 19:529–544.

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proceedings of the National Academy of Sciences USA 108:7075–7080.

Sidorovich, V. E. 2006. Relationship between prey availability and population dynamics of the Eurasian lynx and its diet in northern Belarus. Acta Theriologica 51:265–274.

Stewart, R. E. A., S. E. Campana, C. M. Jones, and B. E. Stewart. 2006. Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. Canadian Journal of Zoology 84:1840–1852.

Suydam, R. S. 2009. Age, growth, reproduction, and movements of beluga whales (Delphinapterus leucas) from the eastern Chukchi Sea. Dissertation. University of Washington, Seattle, Washington, USA.

Tollit, D. J., J. Harwood, C. G. Booth, L. Thomas, L. New, and J. D. Wood. 2016. Cook Inlet beluga whale PCoD expert elicitation workshop report SMRUC-NA-NOAA0915. SMRU Consulting North America. http://www.smruconsulting.com/publications/

van Groenendael, J., H. de Kroon, and H. Caswell. 1988. Projection matrices in population biology. Trends in Ecology and Evolution 3:264–269.

Vos, D. J., K. E. W. Shelden, N. A. Friday, and B. A. Mahoney. 2019. Age and growth analyses for the endangered belugas in Cook Inlet, Alaska. Marine Mammal Science. https://doi.org/10.1111/mms.12630

Ward, E. J., E. E. Holmes, and K. C. Balcomb. 2009. Quantifying the effects of prey abundance on killer whale reproduction. Journal of Applied Ecology 46:632–640.

Waugh, D. A., R. S. Suydam, J. D. Ortiz, and J. G. M. Thewissen. 2018. Validation of growth layer group (GLG) depositional rate using daily incremental growth lines in the dentin of beluga (*Delphinapterus leucas* (Pallas, 1776)) teeth. PLOS ONE 13:e0190498.

Wells, B. K., J. A. Santora, J. C. Field, R. B. MacFarlane, B. B. Marinovic, and W. J. Sydeman. 2012. Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Marine Ecology Progress Series 457:125–137.

Williams, R., S. Gero, L. Bejder, J. Calambokidis, S. D. Kraus, D. Lusseau, A. J. Read, and J. Robbins. 2011. Underestimating the damage: interpreting cetacean carcass recoveries in the context of the *Deepwater Horizon/*BP incident. Conservation Letters 4:228–233.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2955/full