



Assessing cetacean populations using integrated population models: an example with Cook Inlet beluga whales

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Abstract. Effective conservation and management of animal populations requires knowledge of abundance and trends. For many species, these quantities are estimated using systematic visual surveys. Additional individual-level data are available for some species. Integrated population modeling (IPM) offers a mechanism for leveraging these data sets into a single estimation framework. IPMs that incorporate both population- and individual-level data have previously been developed for birds, but have rarely been applied to cetaceans. Here, we explore how IPMs can be used to improve the assessment of cetacean populations. We combined three types of data that are typically available for cetaceans of conservation concern: population-level visual survey data, individual-level capture–recapture data, and data on anthropogenic mortality. We used this IPM to estimate the population dynamics of the Cook Inlet population of beluga whales (CIBW; *Delphinapterus leucas*) as a case study. Our state-space IPM included a population process model and three observational submodels: (1) a group detection model to describe group size estimates from aerial survey data; (2) a capture–recapture model to describe individual photographic capture–recapture data; and (3) a Poisson regression model to describe historical hunting data. The IPM produces biologically plausible estimates of population trajectories consistent with all three data sets. The estimated population growth rate since 2000 is less than expected for a recovering population. The estimated juvenile/adult survival rate is also low compared to other cetacean populations, indicating that low survival may be impeding recovery. This work demonstrates the value of integrating various data sources to assess cetacean populations and serves as an example of how multiple, imperfect data sets can be combined to improve our understanding of a population of interest. The model framework is applicable to other cetacean populations and to other taxa for which similar data types are available.

Key words: Bayesian statistics; beluga whales; cetaceans; integrated modeling; population dynamics; state-space models.

INTRODUCTION

Population abundance and trend are monitored to identify species of conservation concern, evaluate the success of management actions, and calculate allowable removal limits or estimate the population-level effects of incidental take. However, it is rarely possible to count all individuals within a population, so statistical methods for estimating population size have been developed

(Seber 1982). Visual surveys and capture–recapture methods are commonly used to estimate abundance and trend (Buckland et al. 2000).

Traditionally, different data sources are analyzed independently. However, combining multiple data sets for a single population into an integrated population model (IPM) may improve the precision of abundance estimates and enable estimation of life-history parameters that cannot be estimated reliably using the data sets independently (Besbeas et al. 2002, Schaub et al. 2007). IPMs can also be used to explore potential population trajectories and extinction risk (Mosnier et al. 2015), ultimately improving conservation and management efforts (Zipkin and Saunders 2018). IPMs have been applied to a variety of taxa (see Schaub and Abadi 2010 for a review of case studies) and a few have been developed for marine mammals, including spotted dolphins

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(*Stenella attenuata*; Hoyle and Maunder 2004), harbor porpoise (*Phocoena phocoena*; Moore and Read 2008), gray whales (*Eschrichtius robustus*; Punt and Wade 2012), and beluga whales (*Delphinapterus leucas*; Mosnier et al. 2015).

Some IPMs combine population- and individual-level data. To date, IPMs with individual-based data have primarily been applied to bird species for which extensive capture–recapture and count data are available (Ahrestani et al. 2017). Similar modeling frameworks, termed statistical catch-at-age analysis, have been used in fisheries research with various types of data (Fournier and Archibald 1982, Methot and Wetzel 2013, Nielsen and Berg 2014). IPMs can also incorporate data on anthropogenic mortality (Lee et al. 2015).

Our objective was to develop a model framework to improve cetacean population assessments by combining three types of data typically available for cetaceans of conservation concern in an IPM. Our generic model framework comprises a state-space model, based on a population dynamics model that represents the true state of the population, linked to observational submodels that describe how the true state is represented in observed data. IPMs can be used to link any number of submodels associated with different data sets, where submodels are linked to each other and to the main population model via shared parameters. Our state-space IPM combines three observational submodels that are linked to the underlying population process model: (1) a beta-binomial group detection model to describe total group size estimates from visual survey data; (2) a capture–recapture model to describe individual photographic capture–recapture data; (3) a Poisson regression model to describe historical data on anthropogenic mortality. Our IPM thus combines population- and individual-level data. Some population parameters are shared between the population model and multiple submodels, and therefore parameter estimation is informed by multiple data sets. Each observational submodel links the observed data to the state using a likelihood function. We used a Bayesian approach to fully account for uncertainty.

As a case study, we applied this model framework to an endangered population of beluga whales in Cook Inlet, Alaska. Beluga whales are long-lived, mature relatively late in life, and produce few offspring. Cook Inlet beluga whales (CIBW) are geographically and genetically isolated and found only in Cook Inlet (Laidre et al. 2000). CIBW declined in the late 20th century due to unsustainable levels of hunting and were designated as depleted under the Marine Mammal Protection Act (MMPA) in 2000 (National Oceanic and Atmospheric Administration 2000). The Alaska Native subsistence hunt has been regulated based on a co-management agreement since 1999, with very few (fewer than five) animals killed after 2000 and no documented killing of CIBW since 2005. Aerial survey data did not provide clear evidence of a return to population growth during

the early 2000s, and the CIBW was listed as an endangered Distinct Population Segment under the U.S. Endangered Species Act in 2008 (National Oceanic and Atmospheric Administration 2008).

In summer, CIBW aggregate in groups of tens to hundreds of animals in the northern part of Cook Inlet near Anchorage, Alaska (Shelden et al. 2015), where they can be studied. Estimates of CIBW abundance are based on strategic aerial surveys, conducted annually or biennially since 1994 (Hobbs et al. 2015a). The aim of these surveys is to detect and count all individuals in the population. However, some groups are likely not detected by the survey, and accurate group size estimation is challenging (Boyd et al. 2019). The resulting abundance estimates exhibit considerable interannual variation, exceeding biologically plausible rates of increase in some years. Photographic capture–recapture surveys have been conducted since 2005 (McGuire et al. 2018), but were not designed to estimate abundance. It is unclear what proportion of CIBWs are identifiable, and it is therefore difficult to use these data to estimate population size (Kaplan et al. 2009). Estimates of the minimum number of animals killed during dedicated hunts by Alaska Natives were collected through voluntary interviews of hunters between 1960 and 2005 (Mahoney and Shelden 2000, Hobbs et al. 2015b). However, data were not collected from all households or in all years and so represent an incomplete record.

We investigated whether combining these three imperfect data sets into a single IPM could improve CIBW population assessment by estimating population parameters of interest, including fecundity and survival rates, while also producing more biologically plausible estimates of the population's trajectory.

METHODS

Data collection

Aerial survey data.—Since 1994, aerial surveys for CIBW have been conducted annually or biennially in early June (Hobbs et al. 2015a). The survey design is strategic, depending on the observed distribution of beluga; consequently, the area covered by the survey is not consistent over time. During the survey, visual observers search for CIBW groups, but some groups may be outside the survey area and missed. Group sizes for CIBW are estimated by applying a series of correction factors for various types of availability and perception bias to video and observer count data. For further details on aerial survey equipment, protocols, and analysis of the resulting video data, see Hobbs et al. (2000, 2015a) and Boyd et al. (2019).

The survey design was changed in 2004, and estimation methods for the 1994–2003 and 2004–2016 surveys differ. For 1994–2003, a point estimation approach was used to estimate the sum of all total group sizes (the sum of all detected groups) in each of three survey sectors

covering the upper and lower Inlet over several days. Sector averages were summed and a small allowance for missed groups was added to determine the total group size estimates used in our analysis (Hobbs et al. 2000, 2015a). No beluga have been detected in the lower Inlet by the June aerial survey since 2001. For 2004–2016, a Bayesian approach was used to estimate total group sizes in the upper Inlet survey area on each of several days (Boyd et al. 2019). For these years, total group size estimates used in our analysis are based on posterior samples from the “best” survey day (i.e., the day with the highest mean total group size, when the largest proportion of the population was presumed to have been surveyed) and do not include an allowance for missed groups. We used the posterior mean estimated total group size with associated uncertainty as data in the IPM.

The survey is generally designed to coincide with low tide in the Susitna Delta, as tidal state may have a significant influence on sighting conditions. However, this was not possible in 2011, and likely led to a much lower proportion of the population being counted than in other years (Boyd et al. 2019). We therefore excluded the 2011 group size estimates from our analysis. No aerial surveys were conducted in 2013 or 2015.

Capture–recapture data.—Since 2005, a database of high-quality photographs has been maintained to enable capture–recapture studies of CIBW (McGuire et al. 2018). Photographs were taken from small boats or from shore. In post-processing, individuals were catalogued, and photographs compared to create capture histories for individual animals. McGuire and Stephens (2017) provide details on photo-ID survey methods and preliminary results. While beluga are mostly gray or white and lack a dorsal fin, they can acquire distinctive marks (usually scars) that allow them to be reliably identified in photographs. Most calves do not have identifiable marks, so we focused our analysis of photo-ID data on juvenile/adult survival only. It is unclear whether the entire adult population was available to be photographed; some individuals may not frequent areas of Cook Inlet that are accessible for photographic survey effort, or may not come close enough to the camera to ensure high-quality photographs that permit identification. A previous assessment (Kaplan et al., 2009) provides a detailed discussion of factors affecting probability of identification and found support for a spatially well-mixed population (unlike some beluga populations that form sex-segregated groups), such that the capture–recapture sampling effort was not thought to be biased. Linked right-side and left-side capture histories are not available for all individuals in the database, and more right-side than left-side capture histories were available between 2005 and 2016. Therefore, we used only the right-side capture histories collected between 2005 and 2016, which includes 386 uniquely identified individuals.

Hunt data.—Systematic data were not collected on the number of animals killed for most of the period that beluga were hunted in Cook Inlet. Mahoney and Sheldon (2000) compiled available sources of data on human-caused mortality of CIBW (principally due to hunting, but also as incidental catch in the salmon fishery). These data are from voluntary interviews of local hunters and fishers, and, in some years, include estimates of animals that were struck during the hunt but lost. These data are minima and incomplete estimates of anthropogenic mortality because data were not collected in all years or from all hunting and fishing households. Subsistence and commercial hunting occurred prior to 1950, but was inconsistently documented, and so is not included in our model.

Data analysis

We constructed an IPM, as outlined above, consisting of a population process model and three observational submodels (Fig. 1). At least one life-history parameter or derived quantity is shared between the population process model and each observational submodel. In the following sections, we provide more detail about each component of the IPM.

Population process model

In the IPM, CIBW population dynamics are described using an age-structured Leslie matrix model (Leslie 1945, 1948, Caswell 2001). This model component is broadly applicable to small, discrete cetacean populations. We assume that the CIBW population is closed to emigration and immigration because CIBW are geographically isolated (Laidre et al. 2000). The population is represented by the matrix \mathbf{N} , which has rows for each year y and columns for each age class x . The population is structured based on our understanding of beluga life history so that individuals progress from neonates/young-of-the-year (YOTY, age 0, with survival S_0) to calves (ages 1–4, with survival S_1) to juveniles (ages 5–8, with survival S_2) to adults (ages 9+, with survival S_2). We assume that the population has an even sex ratio across age classes and that male survival is equal to female survival.

In the model, only adult animals reproduce because the estimated age at first reproduction for beluga is 9+ years (Burns and Seaman 1986, Robeck et al. 2005, Suydam 2009) and fecundity is expressed relative to the total number of mature animals. Fecundity is assumed to be density dependent (Pella-Tomlinson type; Pella and Tomlinson 1969, Brandon et al. 2007). Realized fecundity in each year f_y is a function of fecundity at unexploited equilibrium f_0 , maximum fecundity f_{\max} , the population size of non-YOTY animals in year y , $\mathbf{N}_{y,1+}$, relative to carrying capacity K , and the Pella-Tomlinson shape parameter P

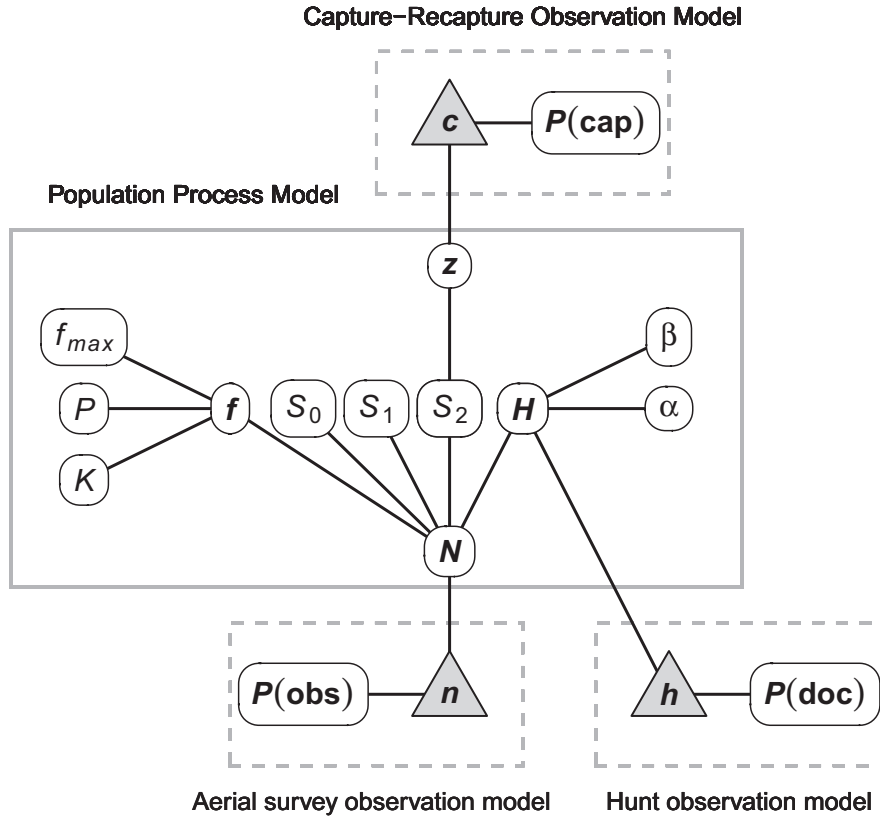


FIG. 1. Schematic of state-space model structure showing linkages between the population process model (within solid gray rectangle) and each observational submodel (within dashed gray rectangles). Data are indicated by gray triangles, while parameters and derived quantities to be estimated by the model are shown in white rounded rectangles. Black lines indicate dependencies between parameters and data. Parameters are defined in *Methods: Population Process Model and Observation models*.

$$f_y = f_0 + (f_{max} - f_0) \times \left(1 - \left(\frac{N_{y,1+}}{K} \right)^P \right) \quad (1)$$

The parameters f_{max} and K are estimated. The value of f_0 is calculated according to the characteristic equation of the Leslie matrix under equilibrium conditions, when $N_y = K$ (Breiwick et al. 1984, Brandon et al. 2007)

$$f_0 = \frac{1 - S_2}{S_1^{(a_t)} \times S_2^{(a_m - a_t)} \times \left(1 - S_2^{(a_{max} - a_m - 1)} \right)} \quad (2)$$

The pre-defined coefficients a_t , a_m , and a_{max} denote the age of transition from calf to juvenile, the age of transition from juvenile to adult, and the maximum age, respectively. The value of the Pella-Tomlinson parameter P controls how fecundity changes as the population approaches carrying capacity.

Reproduction, hunting, and natural mortality are assumed to occur instantaneously and sequentially in the model. The aerial survey is presumed to occur post-breeding and pre-mortality. Based on observed ages and

sexes of hunted animals (Vos et al. 2019), only reproductively mature individuals are susceptible to the hunt in the model, and both males and females are susceptible.

In any year $y + 1$, the number of YOTY produced, $N_{y+1,0}$, is a binomial function of the number of reproductively mature individuals that survived from the previous year $N_{y,9*} = \text{Bin}(N_{y,x} - H_y, S_2)$ and realized fecundity f_y

$$N_{y+1,0} = \text{Bin}(N_{y,9*}, f_y) \quad (3)$$

Beluga calves depend on their mothers for at least the first year of life (Suydam 2009, McGuire and Stephens 2017), so the survival of YOTY to age 1 is reduced in proportion to the number of mature individuals killed in the hunt H_y . The number of age 1 calves $N_{y+1,1}$ is therefore a binomial function of YOTY survival S_0 multiplied by the realized survival of mothers $S_{y,2} = (N_{y,9*}) / (N_{y,9})$ and the number of YOTY produced in the previous year $N_{y,0}$

$$N_{y+1,1} = \text{Bin}(N_{y,0}, S_{y,2} \times S_0) \quad (4)$$

We apply a calf survival rate S_1 for calves aged 2–4 (Eq. 5) and assume that juveniles aged 5–8 survive at the

same rate as adults, S_2 (Eq. 6)

$$N_{y+1,x} = \text{Bin}(N_{y,x-1}, S_1) \quad \text{for } 2 \leq x < 5 \quad (5)$$

$$N_{y+1,x} = \text{Bin}(N_{y,x-1}, S_2) \quad \text{for } 5 \leq x < 9 \quad (6)$$

The number of reproductively mature individuals, ages 9+, is a function of juvenile/adult survival S_2 , the number of animals recruited from the previous age class, $N_{y,8}$, the number of animals already in the mature age class, $N_{y,9}$, and the number of animals killed in the hunt, H_y . While survival is estimated as a probability, the hunt is expressed as an absolute number of animals killed in each year

$$N_{y+1,9} = \text{Bin}(N_{y,9} - H_y, S_2) + \text{Bin}(N_{y,8}, S_2) \quad (7)$$

Observation models

Aerial survey observation model.—We use an observational model to describe how the true underlying population N is observed by aerial surveys. This submodel is specific to the CIBW aerial survey data and would need to be adapted for other survey data sets.

The mean and variance of the number of animals counted are estimated from the best day of aerial survey data (Boyd et al. 2019) and are treated as data in the IPM. We assume that the mean number of animals counted in each year, \bar{n}_y , is normally distributed with mean equal to the number of animals observed n_y and sample standard deviation $\bar{\sigma}_y$ (Eq. 8)

$$\bar{n}_y \sim \text{Norm}(n_y, (\bar{\sigma}_y)^2) \quad (8)$$

The likelihood of the number of animals observed, n_y , is included as a binomial distribution with N_y trials (the true number of post-breeding, pre-mortality individuals in the population, including YOTY and calves, in year y) and probability of observation $P(\text{obs})_y$,

$$n_y \sim \text{Bin}(N_y, P(\text{obs})_y) \quad (9)$$

The probability of detecting beluga, and the resulting group size estimates, are not consistent over the period from 1994 to 2016 due to interannual variation in survey conditions, data collection, and analysis techniques. Therefore, we allowed the probability of observation to vary among years. Individual beluga whales are not detected independently by the aerial survey. Rather, groups of animals are detected, and applying a binomial group detection process could lead to overestimates of population size. This issue can be addressed by using a beta-binomial mixture model (Martin et al. 2011). To determine a plausible prior for the probability of observing CIBW, we assumed that the true number of CIBW does not change over the course of multiple aerial survey days

within each year, whereas the fraction of the population that is observed may vary. We then used the observed between-day variation in the median number of animals counted by the survey as a proxy for between-year variation in the proportion of the population detected by the survey (see Appendix S1 for details). We resampled from these data to generate a distribution of the possible proportion of the population observed on the best survey day in each year and then estimated the parameters of a beta distribution from the distribution of proportions. The resulting beta distribution was used as an informative prior for the proportion of the population observed by the aerial survey each year $\mathbf{P}(\text{obs})_y$

$$\mathbf{P}(\text{obs})_y \sim \text{Beta}(\alpha = 15.35, \beta = 1.51) \quad (10)$$

We considered using total group size estimates for all survey days together with an N-mixture model to account for the within- and between-year variation in the observed total group size estimates. However, we would need to allow $\mathbf{P}(\text{obs})$ to vary across days and years, since the aerial survey does not necessarily observe the same fraction of the population on each survey day. This structure would increase model complexity without adding any additional information to the analysis.

Capture–recapture observation model.—Following Kéry and Schaub (2012), we use a Cormack–Jolly–Seber capture–recapture model to inform the estimate of estimate of S_2 from the photo-ID data. This submodel is broadly applicable to individual capture–recapture data. The true, underlying state sequence $\mathbf{z}_{i,y}$ describes whether each individual i in the marked portion of the population of juvenile and adult (ages 5+) individuals is alive or dead in each year y . The probability of an individual i surviving from time y to time $y + 1$ is described as a Bernoulli process with probability S_2

$$\mathbf{z}_{i,y+1} | \mathbf{z}_{i,y} \sim \text{Bern}(\mathbf{z}_{i,y} \times S_2) \quad (11)$$

This true state is not necessarily observed; the observed capture histories are an incomplete version of the true state \mathbf{z} . The observed capture histories $\mathbf{c}_{i,y}$ depend on the underlying state \mathbf{z} and the probability of capture in year y ($\mathbf{P}(\text{cap})_y$)

$$\mathbf{c}_{i,y} | \mathbf{z}_{i,y} \sim \text{Bern}(\mathbf{z}_{i,y} \times \mathbf{P}(\text{cap})_y) \quad (12)$$

We assume that natural juvenile/adult survival (S_2) is constant over time, and the same for identified and unidentified individuals. Photographic survey effort was not spatially or temporally constant over years, and other differences in methods (such as the approach distance allowed by the research permit) may have affected

the probability of individual identification. Consequently, we allowed $\mathbf{P}(\text{cap})_y$ to vary among years.

Hunt observation model.—An observational model is used to describe the hunt documentation processes because only some of the true number of animals killed were documented. This submodel is broadly applicable to data sets on anthropogenic mortality characterized by underreporting. Based on historical accounts of Alaska Native migration to Anchorage and the observed number of animals killed, it is likely that there was an exponential increase in the number of beluga killed per year between 1950 and 1999 (Mahoney and Shelden 2000). The number of beluga killed increased because of an increase in human hunting effort, not because of an increase in the beluga population. The true hunt is therefore a function of year only and is independent of the population size; it is modeled as an absolute number rather than a rate. The true, unobserved number of animals killed in each year (\mathbf{H}_y) is modeled as a Poisson process with expected value given by an underlying exponential growth function

$$\mathbf{H}_y \sim \text{Pois}(e^{\alpha+\beta y}) \quad (13)$$

The likelihood of the observed hunt \mathbf{h}_y is assumed to be a binomial process with \mathbf{H}_y trials and probability of documentation in each year $\mathbf{P}(\text{doc})_y$,

$$\mathbf{h}_y \sim \text{Bin}(\mathbf{H}_y, \mathbf{P}(\text{doc})_y) \quad (14)$$

Years in which no animals were reported as killed are not included in the likelihood, as there were no observed data. In years when multiple, potentially conflicting reports of the number of animals killed were available, we used the lowest reported number of animals killed in each year as data in the model and did not include reports of animals that were struck and lost. This ensures that the model assumption that the observed hunt was less than or equal to the true hunt is respected, and may lead to an overestimate of underreporting, but should not influence estimates of true hunt or of population size. Hunt numbers after 1998, when co-management was in place, are assumed to have been reported perfectly, and are included as data in the model.

Integrated model.—We combined the population process model and aerial survey, capture–recapture, and hunt observation submodels into a single IPM (Fig. 1). The true number of animals alive in each year \mathbf{N}_y is a derived quantity in the population process model and a parameter in the aerial survey observation model. The unobserved, true number of animals killed in each year \mathbf{H}_y is a parameter in both the hunt observation model and the population model. Juvenile/adult survival S_2 is a parameter in both the capture–recapture model and the

population model. These shared parameters provide links between the three submodels to form an integrated whole, such that estimation of all parameters is informed by multiple data sets. The model code is provided in Data S1: JacobsonEtAl_IPMCode.R.

Trend estimation

To calculate the trend in the population over the last 10 yr of the time series, we summed all age classes in each year from 2006 to 2016 for each posterior draw to calculate total estimated population size, then calculated the year-to-year change $\mathbf{N}_{y+1}/\mathbf{N}_y$. We then used the geometric mean to average estimates of year-to-year change for each of the posterior draws (Caswell 2001) resulting in a posterior estimate of 10-yr population trend.

Implementation

Priors for life-history parameters were constrained by biologically plausible limits, with upper and lower bounds taken from the literature review provided in Hobbs et al. (2015b) when available. Survival was constrained so that YOTY survival (S_0) is less than calf survival (S_1), which is less than juvenile/adult survival (S_2). The prior for YOTY survival was uniform between 0.7 and the value of calf survival, the prior for calf survival was uniform between 0.8 and juvenile/adult survival, and the prior for juvenile/adult survival was uniform between 0.9 and 1. The lower limits of 0.7, 0.8, and 0.9 were chosen based on lowest reported survival rates for YOTY, calves, and juveniles/adults (Hobbs et al. 2015b).

The prior for maximum fecundity was constructed with a truncated beta distribution to ensure that $f_{\text{max}} > f_0$. Previous publications have reported inter-birth intervals of 2–3 yr for beluga whales (Taylor et al. 2007b, Hobbs et al. 2015b). Based on this information, the mean of the prior was set to 0.21, which corresponds to an inter-birth interval of 2.5 yr. The upper limit of the prior for maximum fecundity was set to 0.5 as this is the highest biologically feasible fecundity in a population with an even sex ratio, corresponding to 1-yr inter-birth intervals. The lower limit was set to 0.125, corresponding to 4-yr inter-birth intervals.

The prior for the Pella-Tomlinson shape parameter was a normal distribution with $\mu = 3$ and $\sigma^2 = 2.2$, based on previous studies of marine mammal populations (Jeffries et al. 2003, Romero et al. 2017). This range of P values corresponds to left-skewed surplus-production models, where productivity is maximized at $>50\%$ of K . The prior for carrying capacity was uniform between 750 and 2,000 based on historical reports (Shelden et al. 2015).

The informative prior used for the probability of observing groups of CIBW in each year of the aerial survey $\mathbf{P}(\text{obs})_y$ is described in Appendix S1. The prior for the probability of capturing individuals during each year of the photographic capture–recapture survey $\mathbf{P}(\text{cap})_y$

was uniform between 0 and 1. The prior for the probability of documenting animals killed in each year of the hunt $\mathbf{P}(\mathbf{cap})_y$ was uniform between 0.1 and 1. The priors for the coefficients of the exponential function that describes the true hunt, $\alpha \sim N(0, 1)$ and $\beta \sim N(0, 0.2)$, were chosen so that in early years the resulting prior for true hunt was 0–20 animals per year and in later years up to 80 animals per year.

Life-history parameters were assumed to be constant over the timespan covered by the model and were assumed to be the same between sexes. The population model was initialized in 1900 with a distribution amongst age classes according to initial values of S_0, S_1, S_2, f_{\max} , and K . We fit the model using the package jagsUI (Kellner 2016) within the statistical software R (v. 3.5.2; R Core Team 2018). We ran a Markov Chain Monte Carlo algorithm in parallel with four chains, 1,000,000 iterations, an adaptation phase of 10,000 iterations, a burn-in period of 750,000 iterations, and 100-fold thinning. We visually inspected trace plots of model parameters and used the Gelman-Rubin diagnostic (Gelman and Rubin 1992) to test for convergence. Model fit was evaluated using posterior predictive checks (Gelman et al., 2004) for estimated mean population size, \bar{n}_y , and observed number of animals killed, \mathbf{h}_y .

RESULTS

All model parameters converged, as indicated by visual characteristics of trace plots and by Gelman-Rubin statistics (potential scale reduction factor < 1.02 for all key model parameters except K , for which PSRF = 1.09). Results for key model parameters are included in Table 1. The model estimated a median carrying capacity of 1,664 (95% CI 1,205–1,985) individuals, a median maximum fecundity of 0.23 (95% CI 0.16–0.33) and a realized annual fecundity of 0.16–0.22 (Appendix S2: Table S1). Median survival was estimated to be 0.80 (95% CI 0.71–0.91) for YOTY, 0.91 (95% CI 0.85–0.93) for calves, and 0.93 (95% CI 0.93–0.94) for juveniles/adults. The median 10-yr population trend from 2006 to 2016, when no hunting occurred, was marginally positive at 0.8% per year. (95% CI –0.5% to

TABLE 1. Key parameters, their priors, posterior medians, and 95% CIs.

Parameter	Prior	Median	LCI	UCI
S_0	$U(0.7, S_1)$	0.80	0.71	0.90
S_1	$U(0.8, S_2)$	0.90	0.85	0.93
S_2	$U(0.9, 1)$	0.93	0.93	0.94
f_{\max}	Beta [0.125, 0.5]†	0.23	0.16	0.33
K	$U(750, 2,000)$	1,664	1,205	1,985
N_{2016}	NA	439	388	507

†The prior for f_{\max} was a truncated, scaled beta distribution in the interval [0.125–0.5]. See Data S1: JacobsonEtAl_IPMCode.R for details.

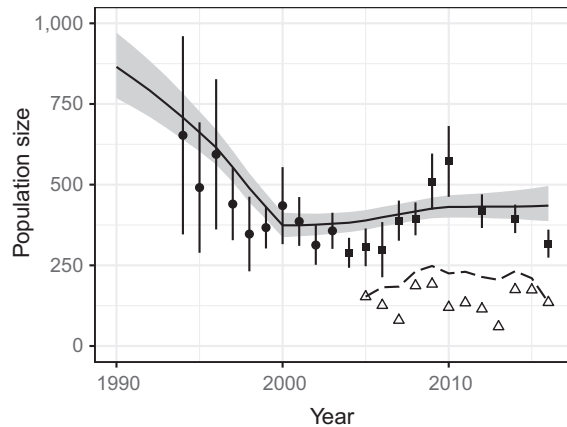


FIG. 2. Cook Inlet beluga whales mean total group size estimates from aerial surveys (black dots and black squares) and number of animals identified in photographs (open triangles) for each year. Because not all belugas are detected by the aerial survey in all years (Appendix S2: Table S1), the model estimate of true population size is generally higher than the group size estimates from the aerial surveys. The minimum number of animals known to be alive from individual photographic capture-recapture histories is shown as a dashed line. The 95% credibility interval of the posterior annual population size estimates from the IPM is shown in gray with the median as a black line.

2.1%; Fig. 2; Appendix S2: Fig. S1), though interannual changes in the population trajectory were sometimes negative (Fig. 2). The median estimate of population size in 2016 N_{2016} was 439 (95% CI 388–507; Fig. 2).

The aerial survey estimates represent a median of 91% (range 85–95%) of the median estimated true population size for 1994–2003 and 93% (range 77–97%) for 2004–2016 (Appendix S2: Table S1). In years when photo-ID data were collected, the number of individual animals identified per year ranged from 60 to 192, corresponding to a median of 31% (range 14–45%) of the median estimated population size (including YOTY and calves). The model estimated that a median of 50% (range among years of 26–74%) of the identifiable (marked) portion of the population was photographed in years when photo-identification data were collected (Appendix S2: Table S1).

The model estimated a median posterior total of 863 animals killed between 1950 and 2005 (95% CI 496–1394). The model-predicted true number of animals killed per year ranged from 0 to 55, corresponding to 10.7% of the estimated population size in the year with the highest number (and proportion) of animals killed. The posterior median proportion of the hunt that was documented ranged from 0.19 to 0.93 in years when data were collected. As expected from Eqs. 13 and 14, the estimated true number of animals killed is always higher than the reported number of animals killed (Fig. 3). Posterior predictive checks of the number of animals reported as killed are shown in Appendix S2: Fig. S2.

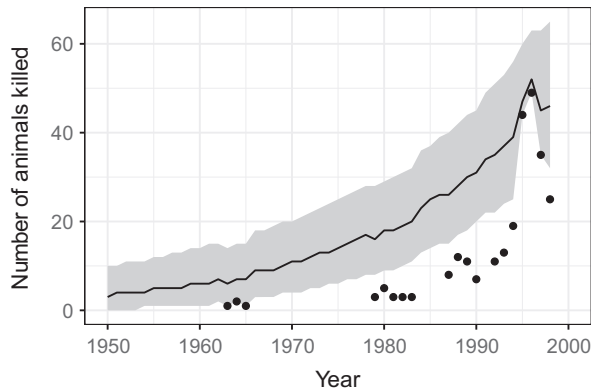


FIG. 3. Number of beluga reported as killed (black dots) in each year that hunt was documented between 1950 and 1998. The black line is the median posterior estimate of true hunt with 95% credibility intervals shown in gray. The reported number of animals killed is a function of both the true number of animals killed and the proportion of the hunt that was documented (Eq. 10, Fig. 1) and so is necessarily less than or equal to the estimated true number of animals killed.

DISCUSSION

The abundance and trend of cetacean populations is often difficult to assess using traditional methods due to insufficient survey data (Taylor et al. 2007a). The case study presented here shows how cetacean population assessment can be improved by combining three types of data typically available for cetaceans of conservation concern into an IPM. The model produced biologically plausible estimates of the population trajectory and life-history parameters consistent with all three data sets. We used a state-space model structure with a central population process model and three observational submodels. This model is necessarily a simplified representation of reality. In particular, the model assumes that life-history parameters do not vary over time. Nevertheless, we believe it is a useful tool for understanding the life history and population status of CIBW as we will discuss.

The model estimates a steeply declining population under unsustainable hunting pressure until the moratorium at the end of the 1990s, followed by a gradually increasing population until approximately 2010, when the population growth rate slowed (Fig. 2). The estimated population trajectory is similar to that indicated by aerial survey total group size estimates, but exhibits less interannual variation, and estimated interannual variation falls within biologically plausible constraints. These constraints are informed by the population model structure (Eqs. 3–7), combined with priors on fecundity parameters and estimates of survival rates based on the capture–recapture data. The precision of the IPM estimates of population size is due in part to the structural constraints of the model and may be overestimated

(Abadi et al. 2010), especially if life-history parameters varied over time.

For most years, the IPM-estimated abundance is slightly higher than the total group size estimates from the aerial survey (Fig. 2). This reflects the assumption that the aerial survey total group size estimates are generally lower than the true population size because the aerial survey estimates include a minimal or no allowance for missed groups (Hobbs et al. 2000, 2015a, Boyd et al. 2019), but could be higher if group sizes are overestimated (e.g., in 2009 and 2010).

The aerial survey data alone do not provide enough information to estimate the proportion of the population that is missed by the surveys. Previously, it was unclear whether increases and decreases in total group size estimates were due to observation error (e.g., interannual differences in the proportion of the population that was counted, or measurement error in the counting process) or to true changes in the population over time. However, the IPM is able to partition the variation in group size estimates into biologically plausible variation in population size and observation error. Variability in the estimated proportion of the population missed in aerial surveys likely reflects variation in the distribution and behavior of CIBW (e.g., in response to variations in prey availability and tidal state) and the non-systematic nature of the aerial survey design (Boyd et al. 2019). The model estimates that 3–23% of the population is missed by the aerial surveys depending on the year (Appendix S2: Table S1).

The IPM abundance estimates represent the minimum population sizes that are consistent with the model structure and assumptions and the three observed data sets. To investigate the sensitivity of our results to the prior for the proportion of the population observed by the aerial survey in each year, we explored two alternate parameterizations of the aerial survey observation model (Appendix S3). This analysis indicated that the estimated population trajectory is relatively insensitive to changes in assumptions about missed groups, while estimated abundance is more sensitive. As expected, abundance estimates are generally lower if it is assumed that no groups are missed, and higher if the prior suggests a higher proportion is missed.

The median estimated population trend of 0.8% per year over the past 10 yr is much lower than would be expected for a recovering population that is well below carrying capacity. The maximum growth rate for cetaceans is generally considered to be 4% per year (Wade 1998). The population of beluga whales in Bristol Bay, Alaska is thought to have increased at a rate of nearly 5% per year between 1993 and 2005 (Lowry et al. 2008). However, coastal cetacean populations in general have shown greater declines and slower recoveries than non-coastal cetacean populations (Magera et al. 2013), and other populations of beluga whales have also failed to recover from exploitation (e.g., the St Lawrence Estuary

population; Mosnier et al. 2015) possibly due to disruption of social systems by hunting (Wade et al., 2012).

It is unclear whether the apparent decreasing trend in aerial survey group size estimates between 2010 and 2016 is real or reflects a decrease in the proportion of groups that are counted by the aerial survey. The IPM indicates that this could be attributable to either unusually poor survival or recruitment or to unusually high observation error. However, if this trend continues, then both explanations would become increasingly unlikely and the model framework may need to be extended to allow for a change in life-history parameters consistent with the apparent decline.

The IPM estimates that realized fecundity approached maximum fecundity (posterior median = 0.23) as the population declined and has been close to estimated maximum fecundity since the early 1990s (median range = 0.21–0.22). In the population model formulation, fecundity is expressed relative to the number of reproductively mature individuals in the population. Therefore, a maximum fecundity of 0.25 would correspond to an inter-birth interval (IBI) of 2 yr. These results imply that currently, most females give birth every other year, which is higher than expected based on visual observations of mother–calf pairs (McGuire and Stephens 2017) and published estimates (e.g., IBI = 2.88; Taylor et al. 2007b). However, the model estimates of realized fecundity and YOTY survival are confounded, so it is possible that the true realized fecundity is less and the true YOTY survival is greater than the model estimates. Future estimates could be improved through additional data on fecundity (e.g., an annual index of the proportion of calves in the population, c.f. Mosnier et al. 2015).

Estimates of YOTY and calf survival were imprecise, due to a lack of pertinent information for these age classes (Table 1, Appendix S2: Fig. S3). In contrast, the estimate of juvenile/adult survival was well-identified (posterior median = 0.93, 95% CI 0.93–0.94, Appendix S2: Fig. S3). This estimate is informed primarily by the capture–recapture data, which were collected post-2005, and may not be representative of historical juvenile/adult survival. This estimate is lower than has typically been reported for cetaceans (e.g., 0.95; Taylor et al. 2007b), but is comparable to reports for other populations of beluga whales that have experienced a decline due to anthropogenic mortality (Mosnier et al. 2015, Hobbs et al. 2015b). This suggests that low juvenile/adult survival may be impeding population recovery (Wade et al. 2012). Alternatively, it is possible that this result is biased due to individual heterogeneity in capture probability that we were not able to account for given the design of the photo-identification study (Abadi et al. 2013). This question merits investigation in future studies.

The model estimates that in years when photographic capture–recapture data were collected, 26–74% of the identifiable (marked) proportion of the population was

identified (Appendix S2: Table S1). The variability in the percentage identified reflects variation in the number of photographic survey days and number of quality photographs from year to year.

As expected, the model infers considerable interannual variation in the proportion of the hunt that was documented (range = 0.19–0.93, Appendix S2: Table S1). As in Monnahan et al. (2014), data on anthropogenic mortality, while sporadically collected, provide a crucial anchor point for the model estimates of current and historical population size, as the population size must have been large enough to allow for the documented take. Without the hunt data, more parameters of the model would be unidentifiable. Anthropogenic mortality prior to 1950 was not included in the model, even though some hunting occurred, because hunting data were inconsistently reported (Mahoney and Shelden 2000; B. Mahoney, *personal communication*). If there was a large amount of anthropogenic mortality prior to 1950, we would expect carrying capacity to be underestimated or the number killed post-1950 to be overestimated.

We did not include stranding data in the IPM because it is possible that some animals stranded as a result of hunting (i.e., were struck and lost, then documented as stranded) and it would be difficult to partition documented strandings into natural and anthropogenic mortality in our population model structure. However, this means that we can use stranding data as an independent data set to evaluate IPM estimates of mortality. We compared our estimates of annual mortality to documented numbers of dead stranded animals (Vos and Shelden 2005, Burek-Huntington et al. 2015) and found that estimated mortality was always greater than observed mortality. Documented strandings represent 0–55% of estimated combined natural and anthropogenic mortality.

For some model parameters, posterior distributions appeared to be constrained by the priors. For example, the posterior distribution of YOTY survival approaches the lower limit of the prior (Appendix S2: Fig. S3) and the posterior distribution of carrying capacity approaches the upper limit of the prior (Appendix S2: Fig. S4). Several parameters estimated by the model were correlated due to the structure of the population model and the nature of the available data. Juvenile/adult survival and maximum fecundity and carrying capacity and maximum fecundity were negatively correlated. Additionally, several parameters were non-identifiable due to the limited data available to inform the life-history parameter estimates. Importantly, we cannot adequately discriminate between values of fecundity and YOTY survival.

We used a model framework consisting of a state-space IPM with a population process model and three observation submodels estimated using Bayesian methods. This framework was designed to be generic and broadly applicable to cetaceans of conservation concern and other taxa for which similar data types are available.

Our model framework differs from some other implementations of IPMs (Mosnier et al. 2015) in that it incorporates individual-level capture–recapture data, population-level abundance estimates, and population-level data on anthropogenic mortality.

The Leslie population model is the foundational component of our model framework. It could be restructured to be as simple or as complex as needed, depending on available information. For example, the model shown here could be expanded to include more life stages, including pregnancy and lactation (Cooke et al. 2013). Additional observational submodels could be incorporated, as long as some life-history parameters are shared among submodels (Kéry and Schaub 2012). In particular, the framework could be expanded to include stranding data, acoustic metrics of abundance, or genetic capture–recapture, if suitable data sets were available. The flexible and modular nature of the framework make it applicable to a diverse array of species for which varying qualities and quantities of data are available. As has been shown with other taxa, data sets do not need to overlap in time or space to be included in an IPM; this is a particularly valuable feature in the case of cetaceans, where long time series are rare.

While we have used the CIBW as a case study for the development of this model, these methods may be useful for studies of other small, discrete cetacean populations for which multiple data types exist, including insular false killer whales (*Pseudorca crassidens*) and Irrawaddy dolphins (*Orcaella brevirostris*). This IPM approach could be applied to other poorly understood and exploited marine taxa; for example, photographic capture–recapture and bycatch data are collected for some populations of manta rays (*Manta alfredi*). Each application will differ and it will be important to consider the idiosyncrasies of each population and data set and adapt the model framework and submodels as appropriate. We hope that the example provided here of how population assessments can be improved by combining multiple data sets within a single IPM will inspire more widespread use of this technique for a variety of taxa.

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LITERATURE CITED

- Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* 91:7–14.
- Abadi, F., A. Botha, and R. Altwegg. 2013. Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: Does it matter? *PLoS ONE* 8:e62636.
- Ahrestani, F. S., J. F. Saracco, J. R. Sauer, K. L. Pardieck, and J. A. Royle. 2017. An integrated population model for bird monitoring in North America. *Ecological Applications* 27:916–924.
- Besbeas, P., S. N. Freeman, B. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* 58:540–547.
- Boyd, C., R. C. Hobbs, A. E. Punt, K. E. Shelden, C. L. Sims, and P. R. Wade. 2019. Bayesian estimation of group sizes for a coastal cetacean using aerial survey data. *Marine Mammal Science* 9999:1–25.
- Brandon, J. R., J. M. Breiwick, A. E. Punt, and P. R. Wade. 2007. Constructing a coherent joint prior while respecting biological realism: application to marine mammal stock assessments. *ICES Journal of Marine Science* 64:1085–1100.
- Breiwick, J. M., L. L. Eberhardt, and H. W. Braham. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:484–496.
- Buckland, S. T., I. B. J. Goudie, and D. L. Borchers. 2000. Wildlife population assessment: past developments and future directions. *Biometrics* 56:1–12.
- Burek-Huntington, K. A., J. L. Dushane, C. E. Goertz, C. H. Romero, and S. A. Raverty. 2015. Morbidity and mortality in stranded Cook Inlet beluga whales *Delphinapterus leucas*. *Diseases of Aquatic Organisms* 114:45–60.
- Burns, J. J., and G. A. Seaman. 1986. Investigations of belukha whales in coastal waters of western and northern Alaska. II. Biology and ecology. US Department of Commerce, NOAA, OCSEAP Final Report 56:221–357.
- Caswell, H. 2001. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.
- Cooke, J. G., D. W. Weller, A. L. Bradford, A. o. Sychenko, A. M. Burdin, and R. L. Brownell Jr. 2013. Population assessment of the Sakhalin gray whale aggregation. 12pp. Paper SC/65A/BRG27 presented to the IWC Scientific Committee, Jeju, Korea, June 2013.
- Fournier, D., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1195–1207.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.

- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin 2004. Bayesian data analysis. Texts in statistical science series. CRC Press, Boca Raton, Florida, USA.
- Hobbs, R. C., J. M. Waite, and D. J. Rugh. 2000. Beluga, *Delphinapterus leucas*, group sizes in Cook Inlet, Alaska, based on observer counts and aerial video. *Marine Fisheries Review* 62:46–59.
- Hobbs, R. C., D. J. Rugh, C. L. Sims, J. M. Waite, and K. E. W. Shelden. 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., P. R. Wade, and K. E. W. Shelden. 2015b. 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.
- Hoyle, S. D., and M. N. Maunder. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. *Animal Biodiversity and Conservation* 27:247–266.
- Jeffries, S., H. Huber, J. Calambokidis, and J. Laake. 2003. Trends and status of harbor seals in Washington state: 1978–1999. *Journal of Wildlife Management* 67:207–218.
- Kaplan, C. C., T. L. McGuire, M. K. Bles, and S. W. Raborn. 2009. Photo-identification of beluga whales in Upper Cook Inlet, Alaska. Report prepared for National Fish and Wildlife Foundation, Chevron, and ConocoPhillips Alaska, Inc. LGL Alaska Research Associates, Anchorage, Alaska, USA.
- Kellner, K. 2016. jagsUI: A wrapper around rjags to streamline JAGS analyses. R package version 1.4.4. cran.r-project.org/web/packages/jagsUI/index.html
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS. Elsevier, Waltham, Massachusetts, USA.
- Laidre, K. L., K. E. W. Shelden, D. J. Rugh, and B. A. Mahoney. 2000. Beluga, *Delphinapterus leucas*, distribution and survey effort in the Gulf of Alaska. *Marine Fisheries Review* 62:27–36.
- Lee, A. M., E. M. Bjørkvoll, B. B. Hansen, S. D. Albon, A. Stien, B.-E. Sæther, S. Engen, V. Veiberg, L. E. Loe, and V. Grøtan. 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos* 124:806–816.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213.
- Lowry, L. F., 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.
- Magera, A. M., J. E. Mills Flemming, K. Kaschner, L. B. Christensen, and H. K. Lotze. 2013. Recovery trends in marine mammal populations. *PLoS ONE* 8:e77908, 1–12.
- 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.
- Martin, J., A. Royle, D. I. Mackenzie, H. H. Edwards, M. Kéry, and B. Gardner. 2011. Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Methods in Ecology and Evolution* 2:595–601.
- McGuire, T., and A. Stephens 2017. Photo-identification of beluga whales in Cook Inlet, Alaska: summary and synthesis of 2005–2015 data. Report for National Marine Fisheries Service, Alaska Region Anchorage, Alaska, USA
- McGuire, T., A. Stephens, S. Dufault, and J. McClung 2018. Photo-identification of Beluga Whales in Cook Inlet, Alaska: Inclusion of Previously Uncataloged Photographs from 2012–2014 Final report prepared by LGL Alaska Research Associates, Inc., Anchorage, AK, for National Marine Fisheries Service, Alaska Region. 93 p.
- Method, R. D. Jr., and C. R. Wetzel. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research* 142:86–99.
- Monnahan, C. C., T. A. Branch, and A. E. Punt. 2014. Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? *Marine Mammal Science* 31: 279–297.
- Moore, J. E., and A. J. Read. 2008. A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecological Applications* 18:1914–1931.
- Mosnier, A., T. Doniol-Valcroze, J. F. Gosselin, V. Lesage, L. N. Measures, and M. O. Hammill. 2015. Insights into processes of population decline using an integrated population model: the case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). *Ecological Modelling* 314:15–31.
- National Oceanic and Atmospheric Administration. 2000. Designating the Cook Inlet, Alaska, stock of beluga whale as depleted under the Marine Mammal Protection Act (MMPA). Federal Register 65:34590–34597.
- National Oceanic and Atmospheric Administration. 2008. Endangered and threatened species; endangered status for the Cook Inlet beluga whale. Federal Register 73:62919–62930.
- Nielsen, A., and C. W. Berg. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. *Fisheries Research* 158:96–101.
- Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock production model. *Bulletin of the Inter-American Tropical Tuna Commission* 13:421–496.
- Punt, A. E., and P. R. Wade. 2012. Population status of the eastern North Pacific stock of gray whales in 2009. *Journal of Cetacean Research and Management* 12:15–28.
- R Core Team. 2018.R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Robeck, T. R., S. L. Monfort, P. P. Calle, J. L. Dunn, E. Jensen, J. R. Boehm, S. Young, and S. T. Clark. 2005. Reproduction, growth and development in captive beluga (*Delphinapterus leucas*). *Zoo Biology* 24:29–49.
- Romero, M. A., M. F. Grandi, M. Koen-Alonso, G. Svendsen, M. Ocampo Reinaldo, N. A. García, S. L. Dans, R. González, and E. A. Crespo. 2017. Analysing the natural population growth of a large marine mammal after a depletive harvest. *Nature Publishing Group* 7:597–16.
- Schaub, M., and F. Abadi. 2010. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152:227–237.
- Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology* 21:945–955.
- Seber, G. 1982. The estimation of animal abundance. Edward Arnold, London, UK.
- Shelden, K. E. W., K. T. Goetz, D. J. Rugh, D. G. Calkins, B. A. Mahoney, and R. C. Hobbs. 2015. Spatio-temporal changes in beluga whale, *Delphinapterus leucas*, distribution: results from aerial surveys (1977–2014), opportunistic sightings (1975–2014), and satellite tagging (1999–2003) in Cook Inlet, Alaska. *Marine Fisheries Review* 77:1–31.
- 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.*
- Taylor, B. L., M. Martinez, T. Gerrodette, J. Barlow, and Y. N. Hrovat. 2007a. Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science* 23: 157–175.
- Taylor, B. L., S. J. Chivers, J. Larese, and W. F. Perrin. 2007b. Generation length and percent mature estimates for IUCN assessments of cetaceans. NOAA, NMFS, Southwest Fisheries Science Center Administrative Report LJ-07-01, 21 p., La Jolla, California, USA.
- Vos, D. J., and K. E. Shelden. 2005. Unusual mortality in the depleted Cook Inlet beluga (*Delphinapterus leucas*) population. *Northwestern Naturalist* 86:59–65.
- 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* 2019:1–12.
- Wade, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science* 14:1–37.
- Wade, P. R., R. R. Reeves, and S. L. Mesnick. 2012. Social and behavioural factors in cetacean responses to overexploitation: Are odontocetes less “resilient” than mysticetes? *Journal of Marine Biology* 2012:1–15.
- Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation* 217:240–250.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2114/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9zw3r229w>