Modeling the impacts of a changing and disturbed environment on an endangered beluga whale population

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Abstract

Climate change and disturbance from human activities are key threats facing many wildlife populations worldwide. The ability to quantify the effects of such threats on individual health and population dynamics is critical for effective management and conservation. We used Stochastic Dynamic Programming (SDP), a method for implementing state-dependent life history theory, to explore the impacts of changes in prey availability and anthropogenic disturbance on survival and reproductive success of Cook Inlet belugas (*Delphinapterus leucas*, CIB), an endangered and isolated population in decline. We predicted behavioral decisions (whether to forage, travel to a new location, or rest) of pregnant CIBs within a spatially and seasonally dynamic prey landscape. We used those decisions to explore time-activity budgets and spatial use under a variety of hypothetical environmental scenarios and estimate the resulting impacts on body condition and vital rates. In all scenarios, foraging activity was highest during summer to capitalize on abundant prey, which in the model was assumed to be eulachon (*Thaleichthys pacificus*) and salmonids (*Oncorhynchus* spp.). This resulted in large increases in blubber reserves that pregnant CIBs relied on during October to April when prey was assumed to be less abundant. Prey availability outside of summer months was still critical, as it either exacerbated or buffered against reductions in prey availability during summer months. Spatial predictions of habitat use indicated that pregnant CIBs should forage in areas used historically that now appear to be abandoned, suggesting that prey availability alone is unlikely to explain the recent range contraction of CIBs to upper Cook Inlet. Reductions in prey availability from late spring to early fall adversely affected vital rates, but intermittent disturbances that resulted in lost foraging opportunities, such as those caused by anthropogenic activities during the ice-free season, had little impact on body condition or vital rates if prey were abundant during the summer and early fall. Accurate assessment of the effects of anthropogenic disturbance on CIBs requires robust data on both disturbances and year-round prey availability, as intermittent disturbances adversely affected survival and reproductive success when they occurred in environments with reduced prey availability. Our model represents an initial effort to fill a critical information gap for informing CIB management decisions, providing insights into conditions under which reductions in vital rates might be expected and highlighting key data needed to increase the applicability of the model to this endangered population.

1. Introduction

Rapid climate change and direct alteration of environments from human activities have led to concerns about adverse effects on wildlife populations. Climate-related changes can have wide-ranging effects on wildlife energy budgets, trophic interactions, habitat use, disease prevalence, and life history traits (Burek et al., 2008; Descamps et al., 2019; Isaac, 2009). These effects may have positive or negative impacts on vital rates and population dynamics, depending on factors such as life history strategies, thermal tolerances, and behavioral plasticity (Descamps et al., 2017; Orgeret et al., 2022; Sanderson and Alexander, 2020). Human activities, such as urbanization, resource exploration and extraction, pollution, noise, ecotourism, and fishing (Avila et al., 2018; Williams et al., 2015), may exacerbate or interact with effects of climate change to influence population dynamics (Williams et al., 2022). The ability to quantify how environmental and human-associated perturbations affect populations at multiple timescales is critical for effective management and conservation, particularly for populations with life history traits that inherently increase their extinction risk, such as a restricted geographic range, geographic isolation, low population density, low productivity and extended maternal care, and large body size (Davidson et al., 2012, 2009).

The resident beluga whale (*Delphinapterus leucas*) population in Cook Inlet, a tidally dynamic estuary in the Gulf of Alaska, is geographically, reproductively, and demographically isolated from other beluga populations (Laidre et al., 2000; O'Corry-Crowe et al., 2018). In addition to being listed as 'endangered' under the U.S. Endangered Species Act, NOAA Fisheries has designated Cook Inlet belugas (CIBs) as one of nine 'Species in the Spotlight', an initiative that brings attention to and helps mobilize resources to recover species 'most highly at risk of extinction'. As of 2018, the CIB population size was estimated at 279 individuals (CV = 0.061, 95% probability interval of 250 to 317) with an annual rate of decline of 2.3% (Shelden and Wade, 2019). Hunting by Alaska Natives was originally thought to be a primary factor for the decline, but the CIB population failed to recover after hunting restrictions were enacted in 1999. Hypotheses for the lack of recovery include insufficient prey availability, noise pollution, habitat loss, loss of cultural information and social cohesion, and stranding events, some of which may be exacerbated by cumulative effects and climate change (CIB Recovery Plan; National Marine Fisheries Service, 2016, Shelden et al., 2021). Human influences are of particular concern given

the proximity of belugas to Anchorage, which lies at the northern end of Cook Inlet and is home to roughly 40% of Alaska's population (https://live.laborstats.alaska.gov/cen/2020-census-data.html). The decline in CIB population size coincided with a summer range contraction from >7000 km^2 to <3000 km^2 that concentrated the population in upper Cook Inlet where there is a high degree of human disturbance (Rugh et al., 2010), particularly from noise pollution. Sources of noise pollution include vessel traffic, aircraft traffic, pile driving, sub-bottom profiling, dredging, oil and gas drilling, seismic surveys, and military activities (Castellote et al., 2019).

Many beluga populations are experiencing changes in sea ice dynamics and prey community composition, resulting in diet shifts, changes in habitat use, and in some cases reductions in body condition (Choy et al., 2020; Hauser, 2016; Heide-Jørgensen et al., 2010; Vacquié-Garcia et al., 2018; Yurkowski et al., 2017). The diet of belugas is typically diverse but it is often dominated by just a few species at any given time (Choy et al., 2020; Loseto et al., 2009; Marcoux et al., 2012; Quakenbush et al., 2015). Anadromous fish are key prey species for CIBs from spring to fall (Castellote et al., 2021; Huntington, 2000; Quakenbush et al., 2015), including eulachon (*Thaleichthys pacificus*), and coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and chum (*O. keta*) salmon. Sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*) were not found in the limited number of stomachs with prey (n = 18) collected from CIBs between March - November of 2002 - 2012, but they are eaten by belugas in other areas of Alaska and traditional ecological knowledge indicated CIBs followed sockeye salmon up the Kenai River (Huntington, 2000; Quakenbush et al., 2015). Many key species are also commercially, recreationally, and individually (subsistence) fished in Cook Inlet, with some species likely to be affected by recent and future warming temperatures (Kovach et al., 2015; Schoen et al., 2017; von Biela et al., 2022). While no empirical data on prey consumption of CIBs exist, it is generally believed that intensive foraging occurs during the spring and summer on salmonids and other anadromous fish based on acoustic data and traditional ecological knowledge (Castellote et al., 2020; Huntington, 2000). Prey preferences, particularly during the fall to spring period, are not well known, but non-anadromous fish such as saffron cod (*Eleginus gracilis*) and flatfish, and invertebrates have been found in stomachs of CIBs (Quakenbush et al., 2015).

Despite an increase in research efforts in the last decade, many information gaps in the ecology of CIBs remain, limiting effective management of this population. That lack of information is due, at least in part, to environmental conditions such as winter ice cover, turbid waters, and extreme tidal range that make it difficult to conduct field research. Only recently have there been limited efforts to understand how prey availability and human activities, considered separately or together, might influence CIB population dynamics. Norman et al. (2020) found that per-capita birth rate of CIBs was related to prey abundance in a known hotspot of beluga use (Goetz et al., 2012a), although the analysis was limited to a single prey species and river tributary. The recent effort by Warlick (2022), who used an integrated population model (IPM) parameterized with data from a greater number of sites and prey species, identified positive relationships between an index of prey abundance and CIB fecundity rates and survival of older calves, providing the best evidence to date that prey availability may be one of the factors hindering population recovery. In this IPM analysis, proxies for anthropogenic stressors, including the human population size in Anchorage, hazardous spill volume, and shipping traffic, were not correlated with vital rates; however, the data available for these metrics may be too coarse to detect potential effects and further investigation is needed to better understand whether anthropogenic stressors are adversely affecting CIBs (Warlick, 2022).

The Population Consequences of Disturbance (PCoD) framework is one that conceptualizes how disturbances that occur at the individual level translate to changes in population dynamics through linkages between behavior, health, and vital rates (New et al., 2014; Wartzok and Tyack, 2008). Since its inception in 2005, PCoD models have been used to investigate the impacts of a variety of non-lethal anthropogenic and natural stressors on marine mammal populations, primarily using some metric of energy as the variable that links behavioral changes to vital rates (Keen et al., 2021; Pirotta et al., 2018a). Applications of this framework are still limited given most PCoD models require considerable data on a species' biology. In a preliminary implementation of this framework for CIBs, an expert elicitation workshop was held in 2016 to quantify relationships between disturbance and birth rate and calf survival, which were then used to understand the impact of a variety of hypothetical disturbance scenarios on these parameters (Tollit et al., 2016). While a useful first step, this effort was limited in its application to management decisions since it relied solely on opinion rather than empirical data. Not only is it

difficult to validate output but it did not account for potential interactions between disturbance and environmental conditions. The ability to assess such interactions is necessary because the cumulative impacts of multiple stressors is identified in the NOAA Fisheries CIB recovery plan – a document that describes the research management actions necessary to support species recovery – as a threat of high relative concern (National Marine Fisheries Service, 2016). The cumulative impacts of multiple stressors is a growing concern for many wildlife populations (National Academies of Science, Engineering, and Medicine 2017; Orr et al., 2020), and simultaneous mitigation of anthropogenic stressors (noise, pollution) and prey availability through fisheries management actions has been identified as the most likely mechanism for reversing the population decline of the endangered beluga population in St. Lawrence Estuary, Canada (Williams et al., 2021).

To address the gaps in our understanding of the impacts of prey availability and disturbance on CIB survival and reproductive success, we developed a model to predict the movement and foraging decisions of pregnant CIBs in a spatially and temporally dynamic environment using stochastic dynamic programming (SDP). Stochastic dynamic programming, a term referring to both the model itself and the mathematical method for solving the model (Clark and Mangel, 2000; Houston et al., 1988), is a way to implement state-dependent life history theory, or the strategic decisions an animal should make over its lifetime (or a part of it) based on their intrinsic state and external conditions (McNamara and Houston, 1996). We used these decisions to predict the effects of a variety of informed environmental and anthropogenic disturbance scenarios on female condition, survival, and reproductive success, focusing on pregnant females not only because of increasing evidence suggesting fecundity may be depressed (Himes Boor et al., 2023; Warlick, 2022), but also because the dynamics are simpler to model and parameterize than for other reproductive stages. This effort should be considered an initial step in a larger effort to develop a full PCoD model for CIBs that can be used to predict the effects of different management actions on the population. As such, we focus much of our discussion on general patterns and highlight specific data needs that would help refine model parameterization and increase the utility of the model for making predictions about CIBs.

2. Methods

2.1. Model overview

Stochastic dynamic programming (SDP) models can be used to predict how an individual should behave, assuming they act in a way that maximizes some expected future reward and that this reward varies depending on the state of the animal. For example, we expect that an individual in poor body condition (the state) might undertake a risky foraging strategy (the behavior) in their attempt to survive (the reward), as they are balancing the tradeoffs associated with predation and starvation. Similarly, we might expect such decisions to vary depending on how far the animal is from some endpoint or time horizon, such as the end of their natural lifespan. Once predictions are made for all possible combinations of state variables at each time step of the model (referred to here as the backward iteration), predictions can be used to understand the sequence of behaviors that emerge within a population (referred to here as the forward simulation).

For this model, we determined whether a pregnant beluga whale should choose to forage, travel, or rest (the behavior) depending on three intrinsic state variables (pregnant female blubber mass, fetal blubber mass, pregnant female stomach fullness), and two extrinsic state variables (location, tidal phase) from the first day of pregnancy to birth (the time horizon), assuming she is attempting to maximize her expected future reproductive success (the reward), based here on the sum of her own survival probability and that of her fetus once it is born (referred to here as calf survival). The following sections provide further detail on each of these model components, including the specific values and bounds of state variables and the state dynamics (how state variables change under each behavior), and the derivation of fitness using the SDP equations. The state dynamics section primarily focuses on how pregnant female and fetal blubber mass change due to the energy costs and gains associated with behavior (in essence a bioenergetic model). A simplified schematic of the model is shown in Fig. 1, including where the bioenergetic model is integrated into the backward iteration and forward simulation. As the model is focused on a single gestation event, we chose parameter values based on an adult CIB female at asymptotic length (383 cm, Vos et al., 2020). R versions 4.0 - 4.2 were used to run the model and all associated analyses (R Core Team, 2022).

2.2 Time horizon and time steps

The model was run from CIB conception (assumed to be April 16th) to birth (T, assumed to be August 4th in the year following conception), lasting a total of 475 days (Robeck et al., 2015). The date of birth was based on estimates from fetal and calf morphology (Shelden et al., 2020) and timing of neonate observations (McGuire et al., 2020b). The date of conception was then assumed to occur 475 days prior. Neonates have been observed as early as July and as late as October in Cook Inlet (McGuire et al., 2020b), but for model simplicity we assume fixed times for conception and birth. It is possible to allow a range of conception and birth times but it would require a different model structure and is outside the scope of this initial model.

The backward iteration, which identifies the optimal behavioral decision for all combinations of state variables, was assessed at a time step of 1 day, although the physiological dynamics were assessed at a 6-hour time step since this was the time step used in the forward simulation to approximately match the length of a tidal phase. Thus, the backward iteration output for a given combination of state variables represented the optimal behavioral decision for a 6-hour period for each day. This approach assumes that the future expected fitness of each behavior and thus the optimal behavioral decision does not vary within a single day, which helped to reduce computational time for the backward iteration while maintaining higher temporal resolution in the forward simulation.
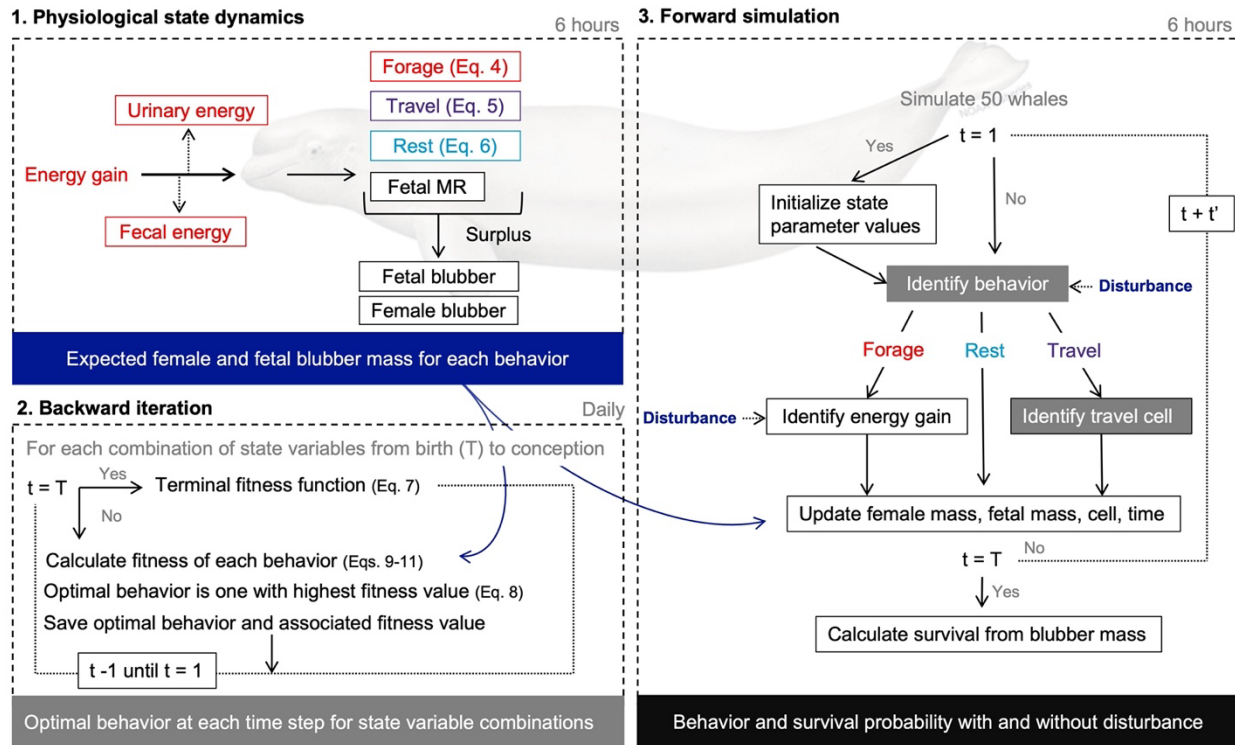
Figure 1. Conceptual diagram of the primary components of the SDP model, showing the general steps and main output of each component and how the three components relate to each other. (1) The balance between energy gain and energy costs dictates how maternal and fetal reserves (blubber mass) change from one 6-hour time step to the next for each behavior. Colored text corresponds to costs associated with specific behaviors (forage, travel, rest), whereas black text corresponds to costs experienced for all behaviors. Fetal MR refers to the minimum cost a female must invest in the fetus, covering the heat increment of gestation and growth of structural tissue. Any surplus energy was allocated to maternal and fetal blubber, the amount of which varied depending on the state variables, with fetal reserve values derived from a separate SDP model. As indicated by the arrows, dynamics in (1) were used in the backward iteration to estimate the future expected fitness associated with each behavioral choice for each day of gestation (2), and in the forward simulation to calculate blubber mass changes of 50 simulated whales during gestation (3), where behavioral decisions at each 6-hour time step are dictated by the output of the backward iteration. In (2), we only show the derivation of the optimal behavioral choice (and not the suboptimal choice) for simplicity. In (3), the gray boxes indicate at what step the output of the backward iteration is integrated, and the blue text shows the two parts of the model affected by the simulated disturbance scenarios.

2.3. State variables

We used blubber mass, $X(t)$ at time t with a particular value denoted by x, as the metric to describe a female's energy reserves. Blubber mass was bounded by a critical (x_{crit}) and upper limit (x_{max}). Mortality was assumed to occur when blubber mass was below x_{crit}. We assumed that x_{crit} and x_{max} occurred at 80 kg and 543 kg, or when blubber mass was 12% or 45% of estimated body mass, respectively (Appendix A). Behavioral decisions were assessed at 10 kg intervals between x_{crit} and x_{max}. This interval was chosen to balance computational efficiency with discriminatory ability given the total range of blubber mass and daily fluctuations in blubber masses.

We used fetal blubber mass, $X_f(t)$ at time t with a particular value denoted by x_f, to describe the energy reserves of the fetus. As above, this variable was bounded by x_{fcrit}, which was assumed to be 0 kg based on the findings that an aborted fetus had essentially no blubber layer (Burek-Huntington et al., 2015). The upper bound, x_{fmax}, was set at 60% of estimated body mass at any given time and thus increased exponentially as the fetus grew (Appendix A). Behavioral decisions were assessed at 74 discrete fetal blubber masses, from 0 kg to 52 kg. Intervals were not constant because fetal growth is exponential and blubber masses are very small during early gestation. At very small blubber masses we assessed behavioral choices at fetal blubber masses that differed by 0.0001 kg - 0.1 kg, with increments of <0.01 when blubber masses were <0.01 kg, increments of 0.01 kg when blubber masses were between 0.01 and 0.1, and increments of 0.1 when blubber masses were between 0.1 and 1.0 kg. From 1 kg in blubber mass onwards we used increments of 1 kg.

Stomach fullness, $S(t)$ at time t with a particular value s, described the proportion of prey intake relative to the maximum that could be consumed per time step, thus influencing the amount of prey that could be consumed. The maximum amount of prey that could be consumed per time step was based on estimates of forestomach capacity and clearance rate (see section *2.4. Physiological parameters*). Since these estimates resulted in a forestomach that could be filled and cleared within a single time step, this state variable essentially represented the proportion of

the forestomach that was full, with a value of 1.0 being full and a value of 0.5 being empty. Behaviors were assessed in 0.1 increments ranging from 0.5 to 1.0.

Location (hereafter referred to as cell), $C(t)$ at time t with a particular value c, was one of 27 discretized cells in Cook Inlet (Fig 2). Cell boundaries were delineated based on CIB distribution and on available prey data. Average travel distances between each cell were calculated based on cell midpoints. Cells differed in the amount of energy gained from foraging at any given time (see section *2.5. State dynamics*). When referencing cells in the **Results** and **Discussion**, we provide not only the number but also the general geographic area represented by the cell, such as Knik Arm and the Susitna Delta.
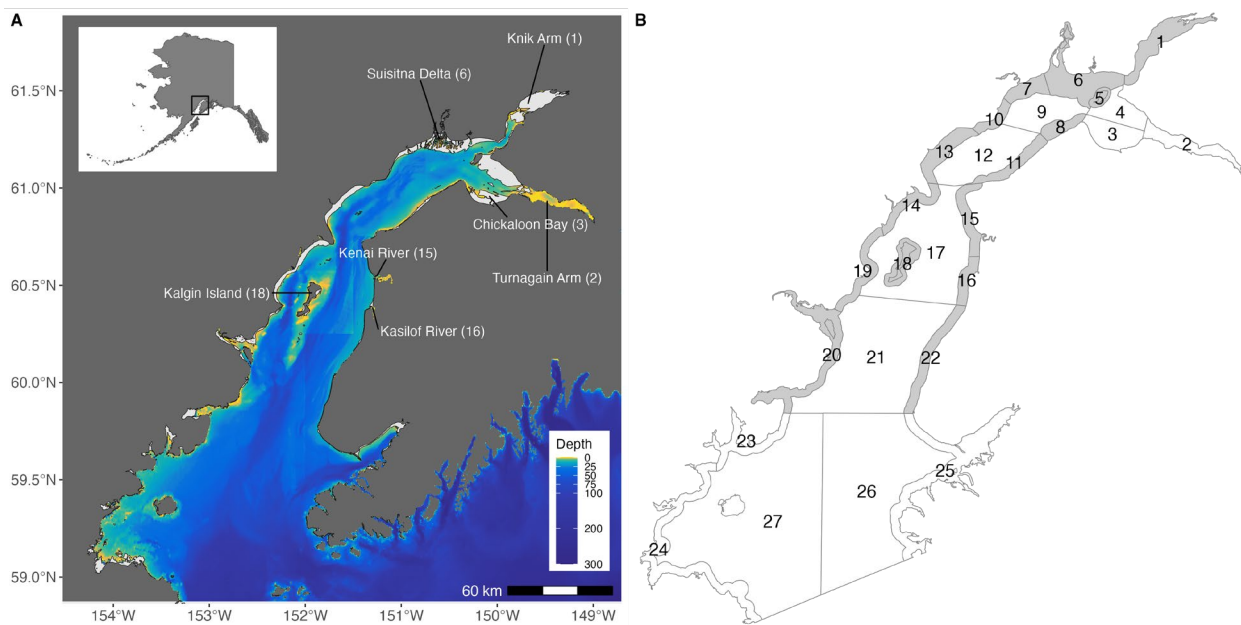
Figure 2. A. Key locations within Cook Inlet, with the corresponding model cell from B shown in parentheses. Colors represent bathymetry, with tidal mudflats denoted by light gray areas. Inset map shows the location of Cook Inlet within Alaska. B. Delineation of Cook Inlet into 27 unique cells used in the model. Gray cells represent cells with salmonid escapement or harvest data, whereas white cells represent those with no salmonid data. Cells 2 and 6 were also assumed to have eulachon runs.

Tidal phase, $P(t)$ at time t with a particular value p, was included given the large tidal flux throughout the estuary, which is known to influence beluga movement and behavior. This state variable had two phases, one which encompassed high tide and the upper portions of the rising and falling tide (above slack), and one that encompassed low tide and the lower portions of the rising and falling tide (below slack). We split the tidal cycle around slack tide, instead of having it encompass solely the rising or falling tide, based on observations of beluga behavior and the assumption that water levels must reach some critical threshold to allow access to mud flats or river entrances, which are exposed at low tide (Huntington, 2000). Tidal activity strongly influences CIB movements in portions of their habitat, but the relationship between tidal height and behavior is not uniform throughout Cook Inlet (Ezer et al., 2008; Shelden et al., 2015; Small et al., 2017). For example, in some areas low tidal heights may make habitat inaccessible, whereas in others foraging is observed around river mouths at low tide. More research is needed to properly parameterize inlet-wide and year-round influence of tides on CIB movement behavior and energetics. As such, its inclusion here as a state variable is largely a placeholder to show how it could be included in future efforts.

2.4. Physiological parameters

The dynamics of female and fetal blubber mass depended on how much energy a female beluga expended, how much energy she gained from foraging (if any), and the energy density of blubber. Energy costs incurred by the female included her own maintenance, locomotion, pregnancy, digestion, and urine production, assuming that any thermoregulatory costs were negligible. We separated the energy costs of pregnancy into two categories: 1) the minimum cost a female must invest in the fetus, which we assumed to include metabolic costs and energy stored in non-blubber tissues, and 2) additional energy that was allocated to fetal blubber reserves. A complete list of parameter notation and values can be found in Table 1. Specific references in text to the model parameters are italicized while general references are not. Below we describe how each parameter was determined, while the specific equations describing the dynamics of female and fetal blubber mass are found in section *2.5. State dynamics*.

Variability in parameter estimates, such as the physiological ones described below, can theoretically be incorporated into either the backward iteration or forward simulation. In practice

it can be challenging to implement in the backward and easier to incorporate into the forward simulation (see section *2.7. Forward simulation*), particularly for parameters where individuals with the same state variables may exhibit a range of potential values, such as is often the case with metabolic rates. As a result, incorporating individual variation in parameter estimates is typically focused on the forward simulation, excluding age- or size-specific variation or for parameters dealing with the prey landscape (e.g., McHuron et al., 2021; Pirotta et al., 2018b). Incorporation of variation into parameter estimates into just the forward simulation assumes that optimal behavioral decisions are not affected by such variation. In this model, we focused mainly on using point estimates given we often had very little, if any data, to inform these estimates, but variation could easily be incorporated into the forward simulation of future efforts.

Maintenance costs were taken from John (2020), who used respirometry measurements from three belugas in human care to estimate resting metabolic rate (RMR). We used non-mass specific values since fat is not believed to contribute notably to an individual's maintenance metabolic costs (Rea and Costa, 1992), and mass changes in this model only occurred through changes in blubber reserves that have a high lipid content. In support of this, differences in mean RMRs between belugas from John (2020) and a single adult male from Rosen and Trites (2013) were only 1% despite average mass differences of 180%, which were primarily due to excess blubber reserves.

Locomotion costs were estimated based on the cost of transport (COT) and the cost of surface swimming (COS), also derived from John (2020). Both of these costs include RMR in the measurement. We assumed that when foraging, whales spent 100% of the time step swimming (6 hours, h_{swim}), whereas for resting we assumed it was 17%. Since detailed time-activity budgets of belugas are largely unknown, these values were relatively arbitrarily chosen to produce the general pattern that resting was less energetically costly than the other two behaviors.

Minimum gestation costs ($E_{MGestation}$) included the heat increment of gestation and the energy stored in the fetus and associated tissues. Instead of assuming a fixed allocation of blubber reserves ($E_{BGestation}$), we modeled it using a separate SDP model to identify the optimal value for each day based on female blubber mass, fetal blubber mass, and energy gain (Appendix A).

This provided a mechanism for changes in maternal body condition to influence fetal growth (and hence, probability of survival), something that has been detected in other cetacean species (Christiansen et al., 2014; Smith, 2021). This was done in lieu of using researcher-assigned *a priori* rules about fetal energy allocation under poor maternal body condition. We took a conservative approach by assuming that females could not allocate more energy than what was expected based on fetal age (Appendix A), meaning that a female could not make up reductions at one point in time by over allocating at another time.

There are no available data for the heat increment of feeding (HIF, the metabolic cost of processing food), digestive efficiency (DEF, percent of ingested energy left after fecal energy losses), or urinary energy loss (UEL) for beluga whales. Existing HIF values for pinnipeds range from 4.3% to 19.4% of gross energy intake, with values that can be influenced by the proximate composition of prey (Rosen and Worthy, 2018). Feeding trials where animals were fed lipid-rich prey resulted in HIF values between 5.1% and 12.4%. We used a value of 10% for *HIF* (of gross energy intake) since much of the summer prey eaten by CIBs is relatively energy dense, particularly eulachon. For *DEF*, we used a value of 95% based on data from bottlenose dolphins (*Tursiops truncatus*) and pinnipeds (Reddy et al., 1994; Rosen and Worthy, 2018). Values of UEL in pinnipeds typically range from about 6.9% to 9.5% of digestive energy intake (after energy lost to feces). We assumed a value of 8%.

We used a value of 34.32 MJ kg^{-1} for the energy density of female blubber, $ED_{Blubber}$ (Kuhnlein et al., 2002), which assumes that blubber energy density is constant throughout the year. While this is unlikely to be true since seasonal changes in lipid content of blubber are common in cetaceans (Koopman, 2007), we did not have the data to resolve this further. The energy density of fetal blubber, $ED_{FetalBlubber}$, was based on the estimated protein and lipid composition of blubber given fetal age (Appendix A).

There were very few data available to characterize the prey landscape experienced by CIBs and estimate the energy gained from foraging, E_{Gain}. We primarily used data from salmonids, with some additional data from eulachon. Salmonids were the only prey for which we had any data to approximate abundance, sourced from spatially- and temporally explicit set-net harvest and

escapement data. These data were only available for 15 of the 27 cells and were extremely limited or absent from several of the cells located in the upper inlet where beluga presence is concentrated (Fig. 2). We provide a brief overview of our approach in the following paragraphs, with a more in-depth description of how the prey landscape was parameterized in Appendix B.

The daily total number of each salmonid species in each cell was summed and subsequently combined with species-specific mass and energy density estimates to convert numbers of fish to energy availability. Generalized additive models were used to estimate daily energy availability from salmonids, summed across all species, for each cell (Fig. B1). Energy availability was converted to energy gain as described in Appendix B. To this value, we added the energy gained from eulachon, approximated based on the timing and location of eulachon runs (Barrett et al., 1984; Spangler, 2002). We also added a static value of 40 MJ, primarily to parameterize the prey landscape from October to April. The timing and spatial distribution of this static value was approximated from acoustic presence/absence data of belugas from 13 acoustic moorings throughout Cook Inlet (Castellote et al., 2020; Appendix B). The specific value of 40 MJ was chosen after preliminary model runs indicated too little energy resulted in complete starvation and too much reduced seasonal fluctuations in blubber mass (see section *3.3. Sensitivity analysis*), operating under the assumption that CIBs experience seasonal fluctuations in prey availability. For all time steps, we assumed a reduced energy gain from foraging when the tidal phase was below slack, which was proportional to the percent of the cell that was exposed mudflats during low tide, corresponding to inaccessible foraging habitat. If a cell had no exposed mudflats then there was no influence of tidal phase on energy gain. As mentioned previously, the general assumption about reduced foraging during lower tides is not uniformly true across Cook Inlet; however, this assumption is simply intended to capture the general pattern that prey availability and foraging success is unlikely to be uniform throughout the day.

Since stomach fullness was a state variable, s, the energy gained from foraging was not only based on the prey landscape but also on the value of s. The maximum prey mass that could be consumed in a 6-hour time step was 22 kg, which was calculated based on maximum estimates of forestomach capacity (11 kg) calculated from the equation $s = 0.47L^{2.36}$, and clearance rates (3 hr), both of which were derived from data collected from fin whales (*Balaenoptera physalus*;

Vikingsson, 1997). There are anecdotal reports of forestomach capacities of belugas that suggest it may be higher than 11 kg (up to 22 - 28 kg; Quakenbush et al., 2015; Vladykov, 1964), but we chose not to use these here because they are based on so few observations. Since s represented the proportion of the forestomach that was full ($s = 0.5$ being empty and $s = 1.0$ being full), the value for the amount of prey that could be consumed decreased linearly from $s = 0.5$ to $s = 1.0$ with specific maximum consumption estimates of 22 kg ($s = 0.5$), 19.8 kg ($s = 0.6$), 17.6 kg ($s = 0.7$), 15.4 kg ($s = 0.8$), 13.2 kg ($s = 0.9$), and 11.0 kg ($s = 1.0$). These maximum consumption estimates were combined with average cell- and time-specific prey energy density estimates to convert from prey (in kg) to energy (in MJ). The energy gained from foraging was the minimum based on prey energy availability and maximum allowable consumption given s.

Our approach to quantifying E_{Gain} has limitations and is unlikely to be entirely representative of the prey landscape experienced by CIBs. Not only did we lack comprehensive data on prey abundance of key species like salmonids and eulachon, but we know virtually nothing about abundance of other prey species in any season nor how prey abundance relates to energy gain. What is important, however, is that the result is a temporally and spatially dynamic prey energy landscape characterized by seasonally abundant prey resources (Fig. B3). We have thus captured the essence of our understanding of the prey field that CIBs experience, even if the specific details are incomplete.

2.5. State dynamics

The blubber mass dynamics of a pregnant adult female beluga when foraging was

$$X(t + 1) = min\left[X(t) + \frac{E_{Gain} \cdot DEF - E_{Forage} - E_{HIF} - E_{Urine} - E_{MGestation} - E_{BGestation}}{ED_{Blubber}}, x_{max}\right]$$

Eq. 1

while the blubber mass dynamics of the fetus was calculated as

$$X_f(t + 1) = min\left[X_f(t) + \frac{E_{BGestation}}{ED_{FetalBlubber}}, x_{fmax}\right]$$

Eq. 2

In Eq. 1, E_{Forage} represents maintenance and locomotion costs (Eq. 4), $E_{HIF} = E_{Gain} \cdot HIF$ and $E_{Urine} = E_{Gain} \cdot DEF \cdot UEL$. The costs associated with the fetus, the energy density of fetal blubber, and the maximum value of fetal blubber mass all vary with time, but notation is omitted for simplicity. In nature, there is some lag between energy intake and blubber deposition, but here deposition (and catabolism) is assumed to occur within the same time step.

The blubber mass dynamics of a female that was traveling or resting were similar, except E_{Forage} was replaced with E_{Travel} (Eq. 5) or E_{Rest} (Eq. 6). For the latter two, $E_{Gain} = 0$, and since E_{HIF} and E_{Urine} are calculated relative to E_{Gain}, they also equaled zero when a whale was traveling or resting.

$$X(t + 1) = min\left[X(t) - \frac{E_{Travel} \; or \; E_{Rest} - E_{MGestation} - E_{BGestation}}{ED_{Blubber}}, x_{max}\right]$$

Eq. 3

The energetic costs of each behavior were calculated as

$$E_{Forage}(x, x_f, c, t) = COS \cdot h_{Swim}$$

Eq. 4

$$E_{Travel}(x, x_f, c, c', t) = COT \cdot d_{c \to c'} + RMR \cdot h_{remain}$$

Eq. 5

$$E_{Rest}(x, x_f, t) = RMR \cdot (6 - h_{Swim}) + COS \cdot h_{Swim}$$

Eq. 6

where $d_{c \to c'}$ is the distance (in km) between the current cell (c) and the new cell (c'), h_{remain} is the number of hours remaining in a time step once a whale reaches c', which was calculated based on an assumed transit rate of 5 km hr^{-1} and the distance traveled (Richard et al., 2001). Whales were allowed to travel to any cell within 120 km of their current cell (i.e., any cell they could reach in a single day). The energy cost of foraging was typically more energetically expensive than traveling (assuming a distance ≤ 30 km, the distance that could be traveled in single time step), particularly when considering the added costs of E_{HIF} and E_{Urine} when foraging.

Table 1. Key parameter values used in the SDP model. For state variables, values represent the range of possible values across which decisions were assessed, whereas the initiation value is how values were assigned to each state variable at $t = 1$ in the forward simulation. The same values for physiological variables in the backward iteration were used for the entire forward simulation. Source species refer to the species or taxonomic group that informed the parameter value; source citations can be found in the text.

Parameter	Notation	Value	Units	Initiation value	Source species
State variables					
Female blubber mass	$X(t)$ or x	80.0 – 543.0	kg	N(0.33, 0.038)[a]	Beluga
Fetal blubber mass	$X_f(t)$ or x_f	0 – 52.0	kg	<0.00001	Beluga
Cell	c	1 - 27		Random	
Tidal phase	p	Above or below slack		Below slack	
Stomach fullness	s	0.5 - 1		0.5	Fin whale
Physiological parameters					
Resting metabolic rate	RMR	3.0124	MJ hr^{-1}		Beluga
Cost of swimming	COS	5.3	MJ hr^{-1}		Beluga
Cost of transport	COT	1.087	MJ km^{-1}		Beluga
Digestive efficiency	DEF	95.0	% GEI		Pinniped/Odontocete
Urinary energy loss	UEL	8.0	% DEI[b]		Pinniped
Heat increment of feeding	HIF	10.0	% GEI		Pinniped
Blubber energy density	$ED_{Blubber}$	34.32	MJ kg^{-1}		Beluga

[a]The starting blubber mass for a female was calculated using a random number drawn from a normal distribution on the proportion of total body mass that is blubber (Cornick et al., 2016) and an assumed structural mass of 663 kg.

[b]Urinary energy loss was calculated as a percentage of energy intake after accounting for digestive efficiency

2.6. SDP Equations

When solving the SDP equations, we assume that all individuals act in such a way to maximize their expected reproductive success, which for this model is based on a single reproductive event and a female's probability of survival. The fitness function, $F(x, x_f, c, p, s, t)$, is defined as the expected total probability that a female will survive the year and her fetus, once born, will survive given that $X(t) = x$, $X_f(t) = x_f$, $C(t) = c$, $P(t) = p$, and $S(t) = s$, where the expectation is taken over the stochastic events of survival and food distribution, and taking into account errors in decision making as described later in this section.

At the last time step in the model, T, fitness was calculated as

$$F(x, x_f, c, p, s, T) = \phi(x) + \phi(x) \cdot \phi_f(x_f) \equiv \Phi(x, x_f)$$

Eq. 7

where $\phi(x)$ is the probability that a female with blubber mass x survives to the following year, and $\phi_f(x_f)$ is the probability that a fetus with blubber mass x_f at the time of birth $(t = T)$ survives to one year of age. The fitness associated with the newly born fetus (calf) was conditioned on female survival $(\phi(x) \cdot \phi_f(x_f))$ since we assumed the calf would die regardless of its own blubber mass if the female was not alive to provide milk. Since the relationships between survival probability and female and calf blubber mass are unknown, we parameterized these functions using estimates of the annual probability of reproductive female and young-of-the-year survival of CIBs from the model described in Himes Boor et al. (2023) and a sigmoidal function (Figs. A5 and A6).

Fitness at all other model time steps was calculated by iterating backwards through time, where fitness is the maximum future expected fitness across all three behaviors.

$$F(x, x_f, c, p, s, t) = max[V_{Forage}(x, x_f, c, p, s, t), V_{Travel}(x, x_f, c, p, s, t), V_{Rest}(x, x_f, c, p, s, t)]$$

Eq. 8

V_{Forage}, V_{Travel} and V_{Rest} are the fitness values associated with foraging, traveling, and resting, respectively, and the optimal behavioral decision is the one that maximizes a pregnant belugas future expected fitness across all potential behaviors. We used two-dimensional linear

interpolation to account for continuous physiological state variables that must be treated as discrete variables for computational purposes (Clark and Mangel, 2000).

We computed the fitness value of foraging $V_{Forage}(x, x_f, c, p, s, t)$, traveling $V_{Travel}(x, x_f, c, p, s, t)$, and resting $V_{Resting}(x, x_f, c, p, s, t)$ as

$$V_{Forage}(x, x_f, c, p, s, t) = e^{-\mu} \cdot F(x', x'_f, c, p, s, t + 1)$$

Eq. 9

$$V_{Travel}(x, x_f, c, p, t) = \max_{c \text{ over } \eta(c)} \left[e^{-\mu} \cdot F(x', x'_f, c', p', s', t + 1) \right]$$

Eq. 10

$$V_{Rest}(x, x_f, c, p, t) = e^{-\mu} \cdot F(x', x'_f, c, p, s, t + 1)$$

Eq. 11

where μ is the daily rate of background mortality (e.g., mortality due to predation, disease), and x' and x'_f are the future expected maternal and fetal blubber masses given the specific behavior and the values of other state variables (Eqs. 1 and 2). In Eq. 10, s' and p' are the expected stomach fullness and tidal state upon arrival given the time to travel from c to c', and $\eta(c)$ is all the cells within 120 km of c. We modeled μ as static across all behaviors so its inclusion here is irrelevant; however, we have included it to show how it could easily be incorporated as a spatially and/or temporally dynamic value. The optimal cell to travel to is the one that results in the maximum value of V_{Travel}. If at any time a female's blubber mass fell below x_{crit} then her fitness went to zero.

The above equations were solved backward starting at $t = T$ and resulted in the identification of the optimal time- and state-dependent behaviors. In addition to the optimal behaviors, we also calculated a probability distribution of behavior (Appendix C). This calculation relies on the differences between the specific values of fitness for each behavior and the optimal value, and an optimality parameter that determines how optimal a whale behaves. Very small optimality values result in a higher probability of selecting the optimal behavior, whereas larger optimality values result in more random behavior (i.e., as the value increases the probability of each behavior becomes more similar). Using a probability distribution, instead of simply the optimal behavior,

accounts for ties in fitness (when two behaviors have the same fitness value), the fact that animals may not always behave optimally (particularly when there are very small differences in fitness among behaviors), and that there may be 'errors' in decision making. This approach takes care of these issues in a natural and consistent way. We calculated probability distributions for both the behavior and travel decisions.

2.7. Forward simulation

We used the probability distribution of behaviors from the backward iteration in Monte Carlo simulations to determine the distribution of behaviors, changes in female and fetal blubber mass, and survival estimates in a population of 50 pregnant CIBs in undisturbed and disturbed environments (Fig. 1, Table 2, see *2.8. Disturbance scenarios*). Simulations started on the first day of pregnancy ($t = 1$). The initial values of the state variable for each female at $t = 1$ were selected as follows: randomly drawn from a normal distribution for female blubber mass; assumed to be a fixed value for fetal blubber mass, stomach fullness, and tidal phase; randomly drawn from values between 1 and 27 for cell (Table 1). Thereafter, values for female and fetal blubber mass were updated as described in section *2.5. State dynamics*, depending on the behavior that was selected. Stomach fullness was updated based on energy intake and time- and cell-specific estimates of prey energy density, tidal phase alternated between time steps, and cell changed depending on travel decisions. When the selected behavior was to travel and the new location was greater than could be transited in 6-hours, the time step was advanced according to the distance traveled and transit speed.

Since we used the probability distribution of behaviors from the backward iteration instead of the optimal one, each behavior had a probability of being chosen given the values of each state variable at the beginning of the time step. We used the following sequence to identify which behavior was chosen at each time step: 1) select a random number from a uniform distribution between 0 and 1, 2) randomly order behavioral choices, and 3) sequentially sum the probability of the behavioral choices based on their random order. The selected behavior was the one that caused the sum to exceed the value of the random number. We used the same approach to select which cell a whale selected when the chosen behavior was to travel. We did not include background mortality, the probability of mortality due to factors other than starvation, in the

forward simulations because we only ran a single replicate of 50 individuals per scenario, meaning that a random mortality in one scenario would greatly impact average population survival estimates.

2.8. Disturbance scenarios

Disturbance was included using seven hypothetical scenarios meant to mimic anthropogenic activities, changes in the availability of prey, and the interaction between the two (Table 2). These scenarios were implemented in the forward simulation only, meaning there was the potential for mismatch in the behavioral decisions from the backward iteration and the environments that were encountered in the forward simulation. The anthropogenic activity scenario was designed to represent any significant and sustained human disturbance, with specific values based on the activities occurring as part of the Port of Alaska Modernization Program in Knik Arm (Cell 1). This activity involves in-water pile driving and pile removal operations, the presence and movement of small boats and barges with heavy equipment, and other shore-based activities that overall cause both physical and underwater noise disturbance within CIB habitat. The parameters for this disturbance scenario were based on the current operations of this activity, which can span a single 6-hour period per day for 6 days per week from April to November in each year. These parameters captured the most extensive disturbance a beluga would likely encounter in this section of Cook Inlet. For the purposes of this modeling effort, and independently of the effectiveness of the mitigation program in place for this port project (e.g., NMFS, 2020, which is outside the scope of this paper), we assumed that a whale in Cell 1 at the time of disturbance would respond by leaving and traveling to another cell, determined using the probability of traveling to a given cell as described above. The prey availability scenarios described in Table 2 were intended to capture varying reductions in prey species during a presumed critical foraging time for CIBs. While we refer to them here using the species that informed the prey landscape (salmonids and eulachon, Table 2), results reflect changes in the overall prey landscape and are thus not specific to these prey groups.

2.9. Sensitivity analysis

We explored the sensitivity of model output to uncertainties in key parameter inputs. Specifically, we ran separate backward iterations using altered parameter values for optimality, a

different terminal fitness function, and different winter prey energy gain values (one higher and one lower than the baseline scenario). We refer to these two prey sensitivity scenarios as 'reduced winter prey' or 'increased winter prey' for ease of reference even though they affected more than just the winter months. This approach, re-running the backward iteration using the altered winter prey landscape, means that behavioral choices are perfectly matched to the environment. That is, what a whale expects to encounter in the forward simulation is what they encounter. This contrasts with the approach used for the disturbance scenarios, where prey availability was altered only in the forward simulation.

While metabolic rates are one of the most influential factors on estimates of energy costs (Bejarano et al., 2017; Winship et al., 2002) and can influence SDP model output (McHuron et al., 2021; Pirotta et al., 2018b), we did not explore the sensitivity of the model to this parameter (or to parameters that influenced it, like the percentage of time spent swimming when foraging). This was because we had no empirical knowledge on the energy gained from foraging, making the specific values used for metabolic parameters of less importance in this effort. This reasoning is also why we present the ratio of energy gains and costs in the results in addition to presenting absolute values.

Table 2. Scenario names for each of the 7 hypothetical disturbance scenarios, the real-world process each scenario is intended to mimic, and details on how each scenario was implemented in the model. In the description of the real-world process, the term 'foraging season' refers to the time when it is assumed that belugas exhibit intensive foraging and large mass gains.

| Scenario name(s)	Real-world process	Model implementation
Disturbance	Disturbance from anthropogenic activity, such as that from the Port of Alaska Modernization Project in Knik Arm	A 6-hour disturbance in Cell 1 for 6 consecutive days each week between May 1 and November 1 that caused whales to travel to a different cell
No eulachon	Absence of high energy prey early in the foraging season	Energy gained from foraging in Cells 2 and 6 was 0 from May 5 - June 9
75% salmon 50% salmon	Reduced availability of prey during most of the foraging season	Energy gained from foraging was 75% or 50% of baseline value from June 10 - October 31 in all cells
75% salmon/eulachon 50% salmon/eulachon	Reduced availability of prey during the entire foraging season	Energy gained from foraging was 75% or 50% of baseline value from May 5 - October 31 in all cells
Disturbance + 75% salmon/eulachon	Disturbance from anthropogenic activity in an environment with reduced prey during the entire foraging season	Combination of each individual scenario

3. Results

Initial runs of the model revealed two movement patterns that led us to alter the model to better match known behavior of CIBs. The first was that the model indicated a high probability of traveling to and foraging in Cells 15 (Kenai) and 16 (Kasilof) in July and August because of an abundance of spawning salmon in these rivers at that time (Appendix D, Fig. D1). This timing coincides with the drift gillnet fishery that includes the mouth of these rivers, as well as the commercial fishery and personal use dipnetting in the rivers, and is a period when belugas are largely absent (see **Discussion**). Because of this, we removed foraging in these two cells (Cell 15 and Cell 16) as a behavioral choice in the backward iteration from July 1 - August 31. The second deviation from observed beluga behavior was that use of Cell 1 (Knik Arm), which in initial model runs was very low during the entire year despite evidence that belugas use this area intensively during the late summer and fall (Castellote et al., 2020; McGuire et al., 2020a; Shelden et al., 2015). This is also the cell where the Port of Alaska is located, and in our model, the cell where the anthropogenic disturbance was simulated. While we had escapement and harvest data for sockeye and coho salmon in Cell 1, primarily from July - September, with a peak in August, total daily numbers of fish were low compared with other cells during that time in our dataset. This may be because small and medium size sockeye and coho runs occur in numerous rivers and creeks in Knik Arm, and so likely add up to a substantial number of fish, but escapement is only monitored in one location for each species. To (somewhat) correct for this, we used the prey data from July 5 - September 20 from Cell 6 (Susitna) to characterize Cell 1 during August 15 - October 31 (Appendix B). This effectively extended the length of time abundant prey were available to CIBs (Fig. B3). The results below are from models with these modifications.

3.1. Baseline scenario

Foraging activity was highest in the summer and lowest in the spring, with an average of 81.1% (summer, June - Aug), 67.4% (fall, Sept - Nov), 66.8% (winter, Dec - Feb), and 61.7% (spring, Mar - May) of time spent foraging (Table 3, Fig. D2). When not foraging, simulated pregnant CIBs spent more time resting than traveling in the spring (32.0% resting vs. 6.3% traveling) and

winter (32.1% vs. 1.1%), whereas time spent between the two behaviors was more evenly distributed in the summer (8.2% vs. 10.7%) and fall (15.9% vs. 16.7%).

Variation in cell use primarily followed temporospatial changes in the prey landscape. From May - August, simulated pregnant CIBs primarily used, in no particular order: Cell 6 (Susitna), Cell 2 (Turnagain Arm), Cell 3 (Chickaloon Bay), Cell 4 (Potters Creek), Cell 16 (Kasilof), Cell 22 (Ninilchik), and Cell 1 (Knik Arm; Fig. 3). Spatial use in other months can be found in Fig. D3; we do not provide a description here because the spatial location of prey resources used to parameterize the model during these months was informed by the current habitat use of belugas. As such, spatial predictions of habitat use during these months are not truly an emergent model property.
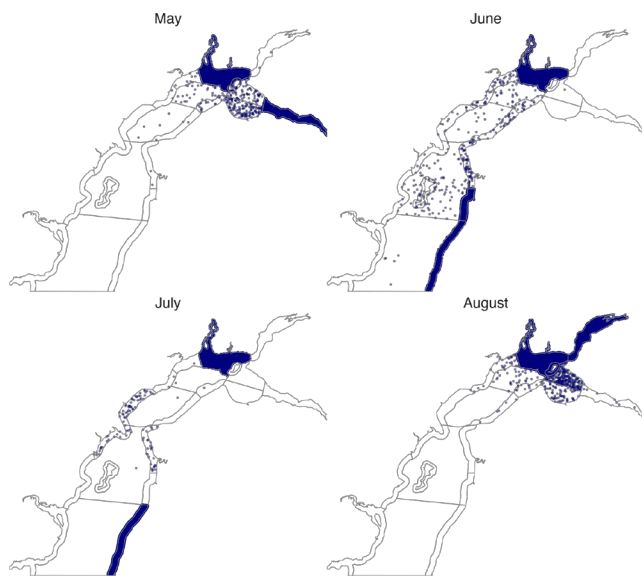
Figure 3. Spatial use of mid and upper Cook Inlet cells by simulated pregnant belugas from May – August. Each blue dot corresponds to an occurrence in that cell so that individual dots in high use areas are indistinguishable. Within-cell locations were generated by randomly sampling locations within the cell polygon since model output simply returned what cell an animal was in at any given time.

Daily mean gross energy costs of pregnant CIBs in the baseline scenario ranged from 150.1 to 192.6 MJ day^{-1}, with the highest values in summer when the time spent foraging was greatest

(Table 3). Fetal energy costs were at their highest point during the second summer of gestation, with a maximum of 70.3 MJ day^{-1} spent on fetal maintenance and growth just prior to parturition. Daily mean energy gain exceeded costs by 4.8%, 82.8%, 13.8% in the spring, summer, and fall, respectively, but were 25.8% lower than mean daily energy costs in winter (Table 3). Daily mean prey consumption was 48.2 kg day^{-1} (summer), 25.5 kg day^{-1} (fall), 16.8 kg day^{-1} (winter), and 19.7 kg day^{-1} (spring). Across the entire gestation period, average energy consumption of a single whale exceeded energy costs by 30.1% (100,486 MJ vs 77,225 MJ). Most prey consumption occurred during the summer (52.9%) compared with other seasons (9.3% - 22.9%), which was due to both intensive foraging activity on abundant prey and because the gestation period spanned two summers (from April to August in the following year). When broken up by year, a greater mean percentage of the total prey was consumed in the first summer compared with the second (29.0% vs. 23.9%), but when differences in the length of each summer were considered, the average daily rate of prey consumption was higher in the second summer (52.7 kg day^{-1} vs. 45.9 kg day^{-1}).

Table 3. Summary of mean energy costs and gains, blubber changes, and behavioral time budgets by season for pregnant Cook Inlet belugas in the baseline scenario, averaged across all 50 individuals in the simulation. Total energy costs and gains were summed by season across the entire 475-day gestation period. The gain contribution represents the percentage of the total energy gained in each season relative to the maximum gain.

	Summer	Fall	Winter	Spring
Energy costs (MJ)				
Daily	192.6	150.1	139.3	150.4
Total	30,429	13,805	12,535	20,455
Energy gain (MJ)				
Daily	383.4	195.6	105.2	181.1
Total	53,172	14,898	9,375	23,041
Gain:Cost				
Daily	1.83	1.14	0.74	1.05
Total	1.75	1.08	0.75	1.13
Daily blubber change (kg)	2.10	-0.35[a]	-0.63	1.18

Gain contribution (%)	53.0	14.8	9.3	22.9
Behavior (% time)				
Forage	81.1	67.4	66.8	61.7
Travel	10.7	16.7	1.1	6.3
Rest	8.2	15.9	32.1	32.0

[a] This value was negative despite a positive gain:cost ratio because belugas had reached their maximum blubber mass during the first part of the season, meaning that blubber gains were zero despite a net energy gain.

Female blubber mass dynamics exhibited strong seasonality, with rapid increases in May and early June during the simulated eulachon runs (Fig. 4). Regardless of initial starting blubber mass, all pregnant CIBs reached the maximum blubber mass allowed in the first summer. The timing of when that maximum was first reached depended on initial starting mass, but it occurred no later than mid-July. Blubber masses were largely maintained at the maximum until the beginning of October; after this time, blubber masses steadily declined until the following May. At the lowest point in the second calendar year, mean female blubber mass was 275.2 kg or 29.3% of body mass. Maximum daily blubber mass changes were +9.3 kg in spring and summer, +1.5 kg in fall, and -0.11 kg in winter. These values were low in the fall because whales had largely reached the maximum allowed blubber mass during that time. All pregnant CIBs were able to maximize their blubber mass just prior to parturition. Fetal blubber mass dynamics followed an exponential pattern, with very small gains between April and December, and rapid growth thereafter until the following August. At the time of birth, mean fetal blubber mass was 51.7 kg. Mean female and calf survival probability at the end of the simulation were 98.7% and 97.4%, respectively.
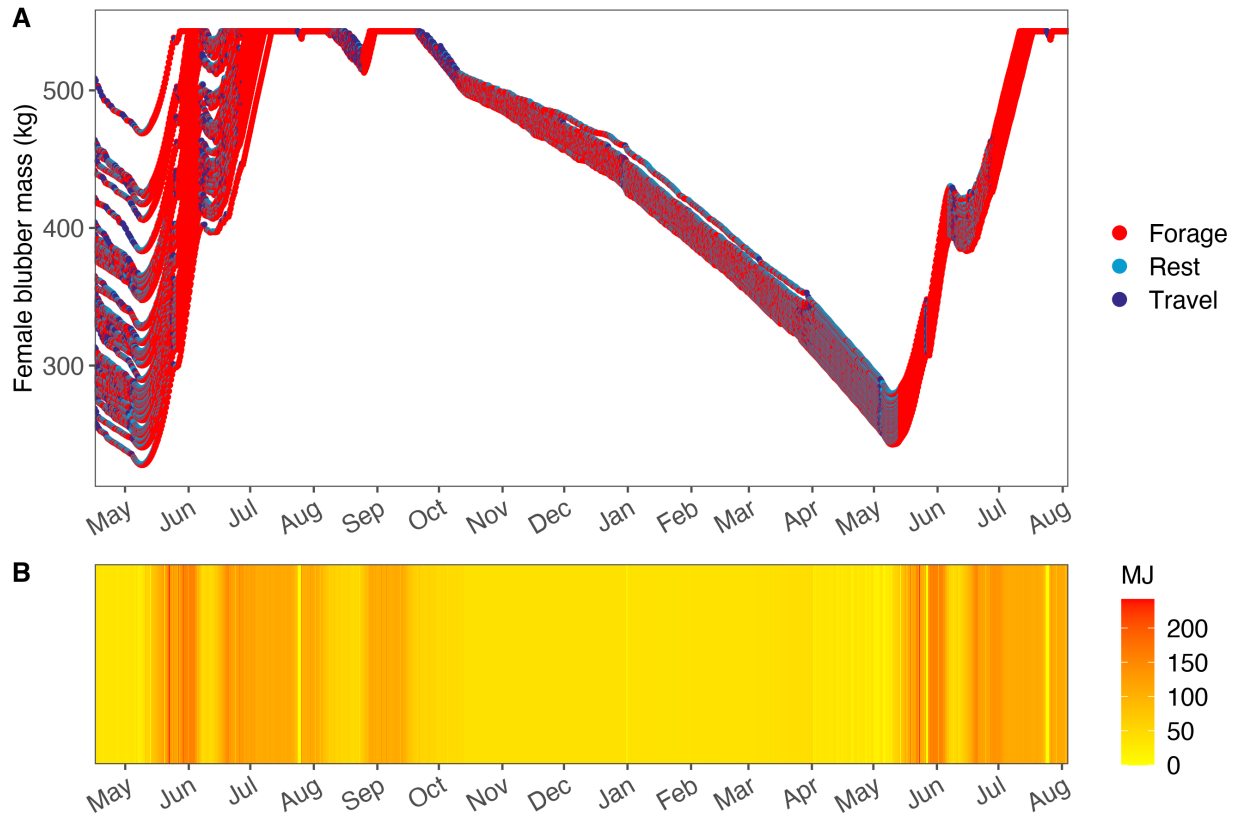
Figure 4. Female blubber mass dynamics (A) and energy gain (B) at 6-hour time steps across gestation, color-coded by behavior (A) or energy gain (B). In A, values for each of the 50 simulated belugas is shown, whereas values in B represent the maximum value across all whales at each time step. Both plots present output from the undisturbed baseline scenario. The percentage of time spent in each behavior can be found in Fig. D2.
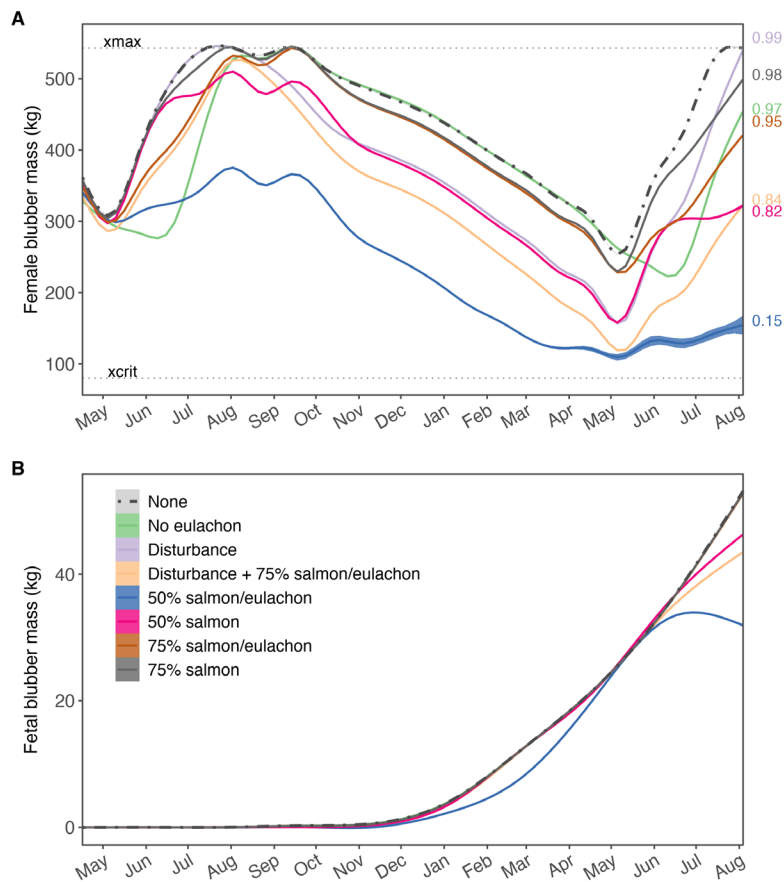
3.2. Disturbance scenarios

Female blubber mass dynamics in the disturbance scenarios generally followed similar seasonal patterns as in the baseline scenario, but the specific values at any given time varied among scenarios (Fig. 5A). If prey were abundant during the summer, pregnant whales achieved reasonably high blubber masses at the end of the simulation under the no eulachon scenario (461.2 kg out of a maximum allowed of 543.0 kg). When prey energy gain was reduced to 75% of baseline values from May to October (75% salmon/eulachon scenario), mean terminal blubber mass was reduced by 22.3% (422.3 kg or 38.9% of body mass); most whales were able to achieve maximum allowable mass gains or close to it in the first summer and fall, but because it took them longer to do so, this ultimately resulted in reduced blubber mass at the time of

parturition. When this 75% reduction only applied to values from mid-June to October (75% salmon scenario), mean terminal blubber masses were 498.6 kg (42.9% of body mass). This was still below baseline but considerably higher than values from the 75% salmon/eulachon scenario, indicating that availability of energy-rich prey buffers against changes in prey availability for other species, even if it only occurs during a short time window. Reductions in prey energy gain to 50% of baseline had considerable impacts on blubber mass gain, with mean terminal blubber masses of 153.6 kg (18.7% of body mass, 50% salmon/eulachon scenario) and 317.6 kg (32.3% body mass, 50% salmon scenario).

The simulated disturbance had no effect on terminal blubber masses when prey were abundant, with all whales still achieving a mean of 540 kg of blubber mass at the end of the simulation (Disturbance scenario). When it coincided with reductions in prey energy gain (Disturbance + 75% salmon/eulachon scenario), terminal blubber masses were on average 76.5% of what they were in the absence of disturbance (75% salmon/eulachon scenario), indicating synergistic effects between prey availability and disruptions to foraging activity. The number of disturbances experienced by simulated belugas was similar between the two scenarios, with an average of 41.3 (Disturbance scenario) and 42.1 times (Disturbance + 75% salmon/eulachon scenario) per whale. The simulated disturbance resulted in more lost time than the nominal disturbance time (a single 6-hour time step for 6 days of the week), as whales were forced to travel to a new cell and subsequently chose to travel back, only to be disturbed again the following day. Thus, this simulated disturbance reflects the effects of 6 lost foraging days per week and may be a more severe energetic effect than actual responses to a daily 6-hour disturbance since whales may simply move a short distance away or remain in the vicinity of the disturbance.

Mean terminal fetal blubber masses remained unchanged from the baseline (51.5 - 51.7 kg) for all disturbance scenarios except for the two scenarios where prey energy gain was 50% of the baseline (33.1 kg and 44.3 kg) and the scenario that paired reductions in prey energy gain with anthropogenic disturbance (43.9 kg; Fig. 5B).

Mean female survival probability ranged from 14.7% - 98.7% (Table D1). In almost all scenarios with reduced energy gain from prey or changes in prey availability, mean survival was reduced by a minimum of 1.7% below baseline values (Fig. 5A). The one exception was for the 75% salmon scenario, where the availability of energy dense prey early in the season allowed whales to maintain survival rates despite small reductions in energy gain from other prey resources. For scenarios where prey energy gain was 50% of baseline values, poor survival was due to both adult mortality and poor body condition at the end of the simulation. Model predictions of calf survival followed similar patterns as female survival, which was to be expected given it was in part conditioned on female survival. For scenarios with a 50% reduction in prey energy gain or where anthropogenic disturbance co-occurred with a reduction in prey energy gain, this reduction was because of both reduced female and calf condition at time of birth. Even in the absence of maternal mortality, when calf survival was calculated solely based on calf condition, it was still reduced by 2.1% to 14.5% below baseline in these three disturbance scenarios.

Figure 5. Female (A) and fetal (B) beluga blubber mass dynamics across gestation for the seven disturbance scenarios. The results from the baseline scenario with no disturbance is shown in the dashed black line. Data were smoothed using a generalized additive model for ease of visualization. Smoothed lines are shown with 95% confidence intervals. In A, the upper and lower critical levels for female blubber mass are shown as dashed horizontal lines. The resulting mean values of female survival probability for each simulation are shown to the right of the plot. See Table 2 for a description of disturbance scenarios.

3.3. Sensitivity scenarios

The sensitivity analysis scenarios largely resulted in similar temporal patterns in female blubber mass fluctuations as in the baseline scenario, with the lowest values observed in early May just prior to the start of the simulated eulachon run. Summer and fall behavior remained largely unchanged from baseline, as simulated belugas still exhibited intensive foraging when prey were abundant. Sensitivity scenarios largely impacted the magnitude of seasonal fluctuations, with more abundant winter prey resulting in belugas that were in good body condition year-round, and less abundant winter prey resulting in a minimal blubber mass that was on average 130 kg lower than the baseline scenario (Fig. 6). In the absence of disturbance, female and calf survival in all sensitivity scenarios were the same or very similar as in the baseline scenario (98.0 - 98.7% and 96.7 - 97.4%, respectively; Table D1).

Disturbance scenarios generally had similar effects on survival and reproductive success as in the baseline values with respect to order, but the magnitude of the impact and specific value of survival varied among scenarios (Table D1). For example, when the amount of prey energy gained from foraging was increased from 40 MJ to 55 MJ (increased winter prey), all disturbance scenarios had similar female (98.3 - 98.7%) and calf (97.1 - 97.4%) survival estimates as the non-disturbance scenario except for the 50% salmon/eulachon scenario. Survival estimates for this scenario were 62.6% (female) and 57.9% (calf), considerably higher than corresponding values from the baseline scenario (14.7% and 12.4%, respectively). When winter prey energy was reduced to 30 MJ, survival estimates were not only lower, but complete mortality was observed during the winter and spring in all but two of the disturbance scenarios (75% salmon and 75% salmon/eulachon).
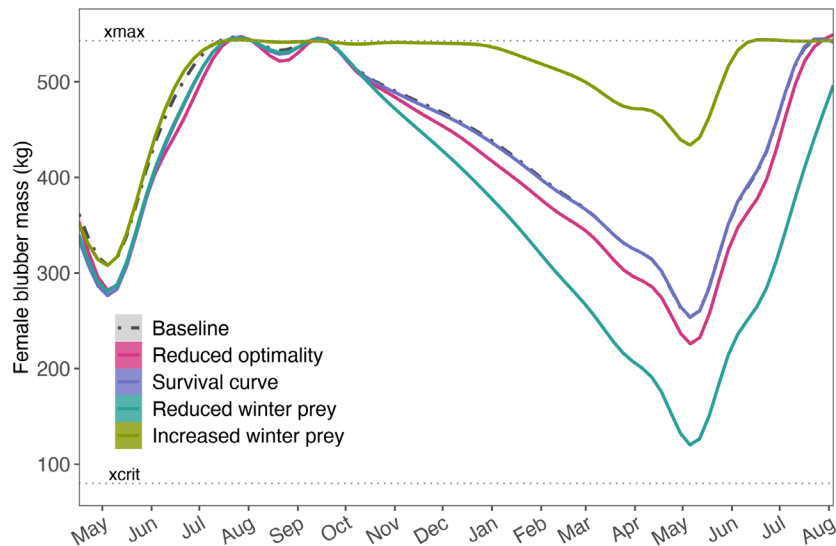
Figure 6. Blubber mass dynamics of female belugas across gestation for the baseline scenario and four sensitivity scenarios. Data were smoothed using a generalized additive model for ease of visualization. The upper and lower critical levels for female blubber mass are shown as dashed horizontal lines.

4. Discussion

The development of the SDP model described in this paper represents the first step in achieving the end goal of developing a lifetime population consequences of disturbance (PCoD) model to help inform management decisions for the recovery of CIBs. With a population of just under 300 individuals, tools like this are critical to better understand the current causes of the CIB decline, predict how anthropogenic activities and future environmental changes may impact this population, and develop mitigation measures to help alleviate such effects. While there are limitations to what we can infer from our results, primarily because relatively little is known about beluga prey preferences and prey availability in Cook Inlet, our model provides insights into the conditions under which reductions in reproductive success and survival might be expected, and provides a tangible product to managers to illustrate the value of behavioral models and the need for obtaining currently unavailable data that can be incorporated into the existing model framework. It also highlights a key discrepancy in spatial use of the Kenai and Kasilof rivers between model output and empirical data that warrants further attention. Below we

provide a discussion of key outputs and how they compare with empirical data, highlighting areas of further research to obtain critical data for the successful application of this model by managers (Table 4).

4.1 Time-activity budgets

Seasonal fluctuations in foraging effort and body condition have been documented in many beluga populations and are assumed to reflect seasonal changes in prey availability (Breton-Honeyman et al., 2016; Cornick et al., 2016; Huntington and The Communities of Buckland, 1999; Kilabuk, 1998; Koski and Finley, 2002). In our model, a seasonal pattern of increased foraging effort emerged in response to abundant prey from May - September, which is consistent with empirical observations. Foraging was still the predominant behavior in other months, but there was an increase in the occurrence of resting behaviors from October to April. The sensitivity analyses for winter energy gain resulted in changes in the magnitude of blubber reserve fluctuations, with less pronounced fluctuations in blubber reserves when winter prey energy was increased. Seasonal fluctuations in foraging effort and hence blubber mass still occurred even when winter prey energy gain was great enough for simulated whales to maintain high blubber masses year-round, indicating the mere presence of seasonality in prey resources (regardless of how it affects energy balance) is sufficient to induce variation in foraging effort. These model outputs provide support for assumptions that prey availability for CIBs is lower in the winter than during summer months, which are based on observations of intensive foraging in summer on salmon and eulachon, pronounced differences in blubber thickness between spring and fall, and slower transit rates in summer compared with winter (Goetz et al., 2012b; Huntington, 2000). Data from acoustic moorings are also suggestive of lower levels of feeding activity by CIBs during winter, but also could reflect foraging on benthic prey or in unmonitored offshore waters (Castellote et al., 2020). While foraging effort was reduced from October to April, prey energy gain during these months was still critical in ensuring simulated pregnant CIBs survived, even when they were able to maximize their blubber reserves during summer months.

Given key knowledge gaps in prey availability, quantitative comparisons between model output and empirical data are largely uninformative and should be cautiously interpreted. For example,

the percentage time spent foraging in winter and spring was still considerably high (61.7 - 67.4%), but this value is based on our assumptions that the prey landscape during this time is comprised of continuously available prey with a low energy return while foraging. If instead the prey landscape from October to April was temporally and/or energetically non-uniform, it is likely that different values for time-activity budgets would emerge from the model. Model predictions of the occurrence of foraging behavior may be slightly high, particularly during summer when the model indicated belugas should spend over 80% of their time foraging. In comparison, Lydersen et al. (2001) found that belugas from Svalbard spent roughly 63% of the summer and autumn in presumed foraging behaviors, with a peak monthly estimate of 72%. While this would seem to provide support that our model overestimated the amount of time spent foraging, CIBs and those in Svalbard consume different prey species and it is possible that differences in time-activity budgets simply reflect the underlying temporal variation in prey availability.

The potential overestimate in time spent foraging speaks more to errors in the model parameterization rather than errors in the model itself, which could be resolved with additional data. In our model, prey were available at most model time steps, but this may not be an accurate assumption since it is possible that prey abundance or foraging efficiency fluctuates throughout the day as environmental conditions change. For example, Chinook and sockeye salmon entering the Kenai River took advantage of the flood tide to move rapidly into the river (Welch et al., 2014), which would likely influence beluga foraging behavior. In addition, we assumed that there were no restrictions on prey availability during the 'above slack' phase; however, the tidal cycle and how it affects habitat and prey availability is much more complex and there still may be access issues at some high tide levels that limit foraging opportunities. Behaviors were also assumed to occur for the entire time step when a whale may not need 6 hours of continuous foraging to achieve high rates of prey energy gain, particularly when prey are abundant or when a whale's stomach is partially full. This assumption would result in overestimates of the amount of time spent foraging.

4.2. Energy balance and blubber mass dynamics

During intensive foraging in the summer, simulated whales consumed an average of 48.2 kg day^{-1} (about 4% of mean body mass during the summer), almost 2 times their energy requirements, resulting in a maximum blubber gain of 9.3 kg day^{-1} (about 1% of body mass). This allowed them to rapidly increase their body condition from 29.3% blubber mass (relative to total body mass) to 45% between May and mid-July in the first summer of gestation. Model predictions of prey consumption and rates of blubber mass gain may be too high given the potential overestimate in foraging effort, although these consumption estimates are feasible for marine mammals, particularly for species that exhibit seasonal fluctuations in foraging effort. For example, Owen et al. (2017) estimated that humpback whales (*Megaptera novaeangliae*) consumed 1.2 - 3.4 times their daily energy requirements, whereas Savoca et al. (2021) estimated that baleen whales consumed between 5 - 30% of their body mass daily, depending on prey type. A cross-sectional study of belugas from Bristol Bay, Alaska, indicated that adults increased blubber mass (relative to total body mass) from 33% in May to 48% in September (Cornick et al., 2016), a rate that is roughly two times lower than our model estimates. These estimates are not directly comparable to our model output since they are cross-sectional, were not collected from reproductively active females, and may be artificially depressed if whales reached such high blubber masses prior to the sampling in September (i.e., if blubber mass plateaued prior to sampling). They do, however, provide some indication that further adjustments to model parameters that influence the rate of blubber mass gain may be needed, such as the prey landscape or stomach fullness.

Model estimates of summer prey consumption were considerably higher than daily food consumption of belugas in aquaria, which average around 11 - 15 kg day^{-1} (Kastelein et al., 1994). Such discrepancies are not unexpected, particularly given that belugas in zoological institutions are fed daily, do not experience seasonal fluctuations in food availability, and are unlikely to experience the same energetic costs as free-ranging belugas because of different environmental conditions and activity patterns. Estimates from belugas in aquaria are also largely derived from non-reproductive individuals. For comparison, three harvested CIBs with relatively full stomachs had between 15.0 – 27.8 kg of salmon in their stomachs, along with other prey items (Quakenbush et al., 2015). Additional data on beluga energetics and foraging success would help refine our estimates of energy expenditure and gain, including metabolic data

to identify any seasonal variation in metabolic rates and behavioral data to quantify activity levels during foraging.

4.3. Spatial use

Spatial predictions can be an emergent property of this model, but here they are not entirely so because we used the spatial distribution of CIBs to characterize the prey landscape from October to April. For these months, we can conclude that spatial variation in prey abundance would generate the general patterns we observe in nature, but they are not confirmatory since the distribution and abundance of prey during these months is unknown. Because model output from May to August was largely informed by the prey data themselves (either the harvest/escapement data or timing and locations of eulachon runs) rather than beluga distributions, we limit our discussion below to these months.

Empirical data on the spatial use of CIBs comes from aerial surveys (Goetz et al., 2012a), vessel sightings (McGuire et al., 2020a), acoustic moorings (Castellote et al., 2021, 2016), opportunistic sightings (Shelden et al., 2015), traditional ecological knowledge (Carter and Nielsen, 2011; Huntington, 2000), and limited satellite tracking data (Goetz et al., 2012b; Hobbs et al., 2005; Shelden et al., 2018, 2015). Results from these studies indicate that CIBs are largely concentrated in upper Cook Inlet during summer and fall, with concentrated use of the Susitna Region (from Beluga River to the west to Little Susitna River to the east), Knik and Turnagain Arms, Chickaloon Bay, and the east and west coasts of the inlet to West and East Foreland. From 2008 to 2022, few if any belugas were seen in Knik Arm during aerial surveys in the month of June for unknown reasons (Shelden et al., 2017, 2015), but have been consistently detected from visual and acoustic surveys as early as April, with peak presence in the fall (Castellote et al., 2020; McGuire et al., 2020a). A northeastward range contraction occurred from the 1970s to the early 2000s, resulting in belugas being concentrated in upper Cook Inlet close to Anchorage (Rugh et al., 2010; Shelden et al., 2015; Shelden and Wade, 2019). The reason for this contraction is unknown, but hypotheses include changes in habitat (including prey availability), predation risk by killer whales (*Orcinus orca*), or the abandonment of poorer quality habitat as the population declined (Rugh et al., 2010).

Model output of spatial use from May - August indicated high use of Cell 6 (Susitna), with intermittent use of Cells 1 (Knik Arm), 2 (Turnagain Arm), 3 (Chickaloon Bay), 4 (Potters Creek), 16 (Kasilof), and 22 (Ninilchik). These results are generally consistent with empirical observations showing concentration of CIBs in the upper inlet during these months, with some key deviations. While the model predicted use of Turnagain Arm during May, there were very limited occurrences of whales in this cell in August, which is inconsistent with observations during this month (McGuire et al., 2020a). Model predictions indicated some use of the mid inlet in June (Cells 16 and 22) and July (Cell 22); CIBs are not currently observed in these areas during summer months, but oral histories indicate belugas were sometimes abundant in both areas from the 1920s – 1930s until the 1980s – 1990s (Dutton et al., 2012). Similarly, initial model runs indicated the Kenai and Kasilof rivers and surrounding areas should be important habitat for CIBs, particularly in July and August. Belugas have been notably absent from these rivers during these months in recent years, although they have used this area historically (Carter and Nielsen, 2011; Dutton et al., 2012; Huntington, 2000; Shelden et al., 2015), which is why we excluded foraging in these cells during July and August in our final model despite available and abundant prey data. Use of the Kenai River does occur in other months, with whales typically being acoustically and visually detected starting in September and continuing throughout the winter and into early May (Castellote et al., 2020; McGuire et al., 2020a).

Mismatches between model output and empirical data are likely driven by the lack of prey data for areas of critical beluga habitat (upper Cook Inlet cells) or indicative that prey availability is unlikely to be the sole driver of the CIB range contraction, and habitat use more generally. In parameterizing the prey landscape, all cells with data included the period of range contraction (2000s onward), with some cells also having escapement or harvest data dating back as early as the 1960s (Table B1). Thus, model predictions that belugas should use cells in mid Cook Inlet are not because of biases in the temporal distribution of prey data (pre versus post contraction). Hypotheses about changes in spatial use due to predation risk or contraction to optimal habitats during a population decline are neither supported nor refuted by our model. The influence of predation risk on habitat use could easily be tested by incorporating a spatially (and if desired temporally) explicit mortality parameter in the backward iteration, which accounts for the fact that perceived risk of predation may influence behavioral decisions about habitat use (Castellote

et al., 2022). In this model, we used a single value because there is very limited information on the presence of transient killer whales in Cook Inlet (Shelden et al., 2003). The Kenai River also supports a large commercial fishery and sport and personal fisheries during the summer, which may make this area suboptimal due to disturbance or accessibility issues. While such disturbances can easily be incorporated into the model, either in the backward iteration or forward simulation, it is challenging to do so in a meaningful way without a better understanding of the prey landscape and how belugas perceive and respond to fishing activity. For example, removal of foraging as a behavioral choice in the Kenai and Kasilof cells during July and August resulted in predicted habitat use similar to what is currently observed, but without knowing how accessible this habitat is to belugas and what the prey availability is during those times of accessibility, we can only conclude that accessibility issues should remain as a potential hypothesis. Further efforts are thus needed to understand why belugas do not use these mid inlet areas in July and August during peak prey abundance, particularly given indications that prey availability may be hindering population recovery (Warlick, 2022). One area that remains a considerable unknown is the role that cultural information plays in influencing habitat use, and how the loss of older individuals from the population may alter this information (Wade et al., 2012; Williams and Lusseau, 2006).

The movement of simulated pregnant CIBs was largely confined to a few discrete cells. While it has been reported that belugas will often remain in the same location for weeks when prey are abundant (Citta et al., 2016; Hobbs et al., 2005; Lydersen et al., 2001), other factors in the model could have led to this behavior. These factors include 'perfect' knowledge of the environment in the baseline scenario (i.e., they encountered the expected environment in the forward simulation), that whales may make decisions based on reasons unrelated to energy gain, and the lack of environmental features that may facilitate movement or make it more energetically beneficial to move (e.g., tidal activity). For example, some belugas in Svalbard moved to other distant foraging areas despite abundant prey in their current location, which the authors hypothesized may be adaptive behavior in a fluctuating environment (Lydersen et al., 2001). Incorporating environmental uncertainty into behavioral decisions in SDP models is possible, but this added complexity may not be overly informative since Cook Inlet is relatively small and there may be more uniformity in responses of prey communities to environmental fluctuations.

Tidal activity influences CIB behavior but incorporating these effects into a model are challenging because relationships appear to be site-specific (Howe et al., 2015; Huntington, 2000), indicating behaviors may be driven by more than just energy savings.

4.4. Environmental change and disturbance

In the CIB Recovery Plan, anthropogenic disturbance and prey availability are listed as high and medium threats to population recovery, respectively (National Marine Fisheries Service, 2016). Cumulative effects from multiple stressors are also listed as a threat of high concern, and while there are significant barriers to assessing these impacts in marine mammal populations, the combination of multiple stressors is increasingly identified as a concern for marine mammal populations (Cervin et al., 2020; National Academies of Science, Engineering, and Medicine 2017; Pirotta et al., 2019; Silva et al., 2021; Williams et al., 2021).

The model output provides insight into specific conditions under which disturbance could impact CIB vital rates, at least when the only consideration is direct impacts on energy balance. Specifically, the lack of an effect of the simulated anthropogenic disturbance in isolation suggests that if prey are abundant during the summer and early fall, and prey during winter is above some critical threshold, pregnant CIBs at asymptotic length should be able to cope with intermittent disruptions to foraging gain during these months, such as those experienced by the Port of Alaska Modernization Program. There were synergistic impacts when the simulated anthropogenic disturbance co-occurred with reductions in prey availability, highlighting the need to assess anthropogenic impacts on CIBs within the context of resource availability. Given that body conditions of the current population are unknown, it is impossible to know whether the scenario showing no energetic impacts of anthropogenic disturbance on pregnant CIBs is applicable. Drone technology cannot yet be used to estimate body condition in CIBs, as it has for other cetaceans (e.g., Christiansen et al., 2020; Stewart et al., 2021), because the waters of Cook Inlet are too turbid to photograph below the surface. Other data, however, suggest that conditions in the Inlet may be suboptimal. For example, a recent estimate of the interbirth interval of CIBs (Himes Boor et al., 2023; Warlick, 2022) was considerably longer than previously documented for CIBs and other beluga populations (Harwood et al., 2015; Jacobson et al., 2020; Mosnier et al., 2015; Suydam, 2009). In other cetacean species, longer interbirth intervals (or reduced

calving rates) have been associated with poor body condition and adverse environmental conditions (Gailey et al., 2020; Ijsseldijk et al., 2021; Kershaw et al., 2021; Meyer-Gutbrod et al., 2021; Seyboth et al., 2021), providing some indication that CIBs are unlikely to be in optimal body condition and that synergistic impacts may be more likely for this population. The average lifespan of CIBs also appears to be considerably shorter than the potential lifespan of belugas, although causes of mortality are largely unknown (McGuire et al., 2021).

Adverse effects of reductions in prey energy gain on survival probability, meant to simulate a reduction in prey availability, were in large part driven by effects in the second summer of pregnancy. When energy gain was reduced to 75% of baseline values, access to prey into October allowed whales to achieve near maximum fat masses during the first summer of gestation. This was not possible in the second summer because parturition occurred at the beginning of August, resulting in reduced female blubber masses at the time of birth. Under scenarios where prey energy gain was severely reduced (50% of baseline), whales were unable to achieve large gains in mass in the summer and fall. There was an increase in the percentage of time spent foraging during the fall to help compensate for this reduced prey gain, although it was insufficient to offset such severe reductions in prey energy gain. Even for pregnant females that survived simulations with 50% reduced prey, such a prolonged reduction could result in starvation since some females experienced a net loss in blubber mass across the simulation. The availability of energy dense prey early in the season (modeled here as eulachon), even if only for a relatively short period of time, helped buffer against reductions in prey energy gain, particularly when those reductions were severe, highlighting the importance of spring eulachon runs for CIBs.

Much of the focus on understanding CIB prey preferences has been on salmonids since they appear to be a critical prey resource for this population during summer and early fall when belugas are accumulating blubber reserves to presumably help sustain them during reduced prey availability in other times of the year. While model results indicate that prey availability during this time is indeed critical, they also highlight the importance of understanding prey availability during other times of the year. Indeed, it was the interplay between the 'winter' and 'summer' prey availability that was important, as changes in winter prey either exacerbated or buffered

against adverse effects on energy gain during the summer months. We modeled prey availability as a reduction in energy availability within a given cell, however, our results would also apply if prey shifted their distribution to areas that were less accessible to belugas or if energy gained from foraging is effectively reduced in some other way.

Sea ice concentration, which was not included in our model, is important to consider in future efforts because of its influence on beluga habitat use (Asselin et al., 2011; Hornby et al., 2016; Loseto et al., 2006). In Cook Inlet, belugas are commonly found in very open (1 - 24% ice concentration) and open (25 - 68%) pack ice in the winter (Goetz et al., 2012b), but associate with habitats that range from ice free to compact pack ice (up to 92%; Moore et al., 2000; Shelden et al., 2018). Reductions in sea ice concentrations may allow belugas to expand their winter range (Heide-Jørgensen et al., 2010), but also may indirectly impact behavior through ecosystem changes (Hauser et al., 2018). Incorporating the effects of sea ice on habitat accessibility in our model is relatively straightforward and could be achieved in one or more ways. For example, it could be modeled by increasing the probability of mortality at high sea ice concentrations (because of increased difficulty in finding breathing holes), or belugas could simply be excluded from accessing cells with high ice concentrations (similar to how we excluded belugas from the Kenai and Kasilof rivers). Both options would require little change to the existing model structure to incorporate. Effects of sea ice on prey availability, if known, could simply be incorporated into the existing spatially and temporally explicit prey landscape, requiring no additional modifications to the model. There also may be thermoregulatory changes associated with reduced sea ice and increased warming, but a better understanding of how water temperature, body condition, and metabolic rates interact is needed before such effect could meaningfully be incorporated into the model.

4.5. Conservation implications

Behavioral models can provide relevant information to managers for planning human activities and mitigating associated risks to wildlife populations. A key feature of SDP models is that decisions (here the decision to forage, travel, or rest) are an emergent model property based on the assumption that animals act to maximize the expected future value of a reward (here reproductive success), which allows for predictions to be based on a population that can

potentially adapt their behavior to novel environmental conditions. The model described herein is an initial effort to fill a critical information gap for management of CIBs, a population that has a 19 – 32% probability of extinction in the next 150 years if vital rates and environmental variability remain unchanged (Warlick, 2022). Our model provides insight into habitat use and distribution of CIBs, notably that prey availability alone is unlikely to have caused the range contraction, necessitating further efforts to understand why belugas are not currently using areas of Cook Inlet that presumably have abundant prey, like the Kenai River. Perhaps most importantly, model output indicates that the effects of disturbance from human activities on CIBs are inextricably linked with prey availability, making it impossible to accurately assess the effects of anthropogenic disturbance in isolation. This elevates the importance of better understanding CIB behavioral responses to disturbances and collecting prey and beluga body condition data, which also would help increase the utility of the model described in this paper through parameterization and/or calibration. Such data are challenging to collect in Cook Inlet but recent efforts using environmental DNA have been successful in characterizing temporal variability in prey communities (Z. Gold and K. Parsons pers comm).

Table 4. Overview of some key data needs that would improve the ability of the model to inform management decisions for Cook Inlet belugas. While each data need has the potential to influence all model outputs, we highlight in gray the most likely emergent properties that would be influenced by each data need. We also highlight data needs that could be used for model validation. See discussion for additional description of data needs.

Data need	Time-activity budgets	Blubber mass	Spatial use	Env. change/disturbance	Validation
Body condition					▓
Metabolic rates[a]	▓	▓			
Fine-scale behavior[b]	▓	▓			▓
Response to disturbance[c]			▓	▓	
Prey landscape	▓	▓	▓	▓	

[a]Includes variation in metabolic rates associated with season, body size, age class, and reproductive status

[b]Needed to better estimate energetic costs of modeled behaviors and to validate model output of time-activity budgets

[c]Refers to the behavioral responses of belugas to anthropogenic disturbances, such as pile driving, vessel traffic, and fishing activities

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