Predicting the population consequences of acoustic disturbance, with application to an endangered gray whale population

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Abstract. Acoustic disturbance is a growing conservation concern for wildlife populations because it can elicit physiological and behavioral responses that can have cascading impacts on population dynamics. State-dependent behavioral and life history models implemented via Stochastic Dynamic Programming (SDP) provide a natural framework for quantifying biologically meaningful population changes resulting from disturbance by linking environment, physiology, and metrics of fitness. We developed an SDP model using the endangered western gray whale (Eschrichtius robustus) as a case study because they experience acoustic disturbance on their summer foraging grounds. We modeled the behavior and physiological dynamics of pregnant females as they arrived on the feeding grounds and predicted the probability of female and offspring survival, with and without acoustic disturbance and in the presence/absence of high prey availability. Upon arrival in mid-May, pregnant females initially exhibited relatively random behavior before they transitioned to intensive feeding that resulted in continual fat mass gain until departure. This shift in behavior co-occurred with a change in spatial distribution; early in the season, whales were more equally distributed among foraging areas with moderate to high energy availability, whereas by mid-July whales transitioned to predominate use of the location that had the highest energy availability. Exclusion from energy-rich offshore areas led to reproductive failure and in extreme cases, mortality of adult females that had lasting impacts on population dynamics. Simulated disturbances in nearshore foraging areas had little to no impact on female survival or reproductive success at the population level. At the individual level, the impact of disturbance was unequally distributed across females of different lengths, both with respect to the number of times an individual was disturbed and the impact of disturbance on vital rates. Our results highlight the susceptibility of large capital breeders to reductions in prey availability, and indicate that who, where, and when individuals are disturbed are likely to be important considerations when assessing the impacts of acoustic activities. This model provides a framework to inform planned acoustic disturbances and assess the effectiveness of mitigation strategies for large capital breeders.

Key words: bioenergetics; Eschrichtius robustus; individual-based model; population consequences of disturbance; stochastic dynamic programming.

INTRODUCTION
Noise pollution is a global problem for wild animal populations in terrestrial and marine environments (Hildebrand 2009, Buxton et al. 2017). As such, there has been an increased research effort to document the effects of noise on wildlife in the past few decades (Williams et al. 2015, Shannon et al. 2016). Anthropogenic noise can elicit behavioral or physiological responses that directly or indirectly impact the survival and fitness of wild animals, including changes in vocal or vigilance behavior, habitat use, and foraging behavior, and can have cascading effects on population dynamics and community structure (Francis et al. 2009, Barber et al. 2010, Shannon et al. 2016, Cox et al. 2018). Understanding
the impacts of anthropogenic noise on animal populations is essential for the development of standards for exposure and mitigation plans (Weir and Dolman 2007, Blickley and Patricelli 2010, Northrup and Wittemyer 2013) and is a topic considered to be an “urgent conservation priority” (Francis and Barber 2013).

Quantifying the consequences of acoustic disturbance on populations requires an integrative and mechanistic approach since noise can affect biological systems in a multitude of ways that then interact to influence fitness (Kight and Swaddle 2011). Much of the research to date has focused on two taxonomic groups, birds and marine mammals, although responses to anthropogenic noise have been documented across a diversity of vertebrate and invertebrate taxa (Shannon et al. 2016). Research on marine mammals has primarily focused on behavioral response studies of individuals to sound, revealing that acoustic disturbance generally elicits changes in feeding behavior and movement away from the source (Tyack et al. 2011, Pirotta et al. 2012, Derieter et al. 2013, Goldbogen et al. 2013, Miller et al. 2015, Dunlop et al. 2017) with behavioral responses that are context- (e.g., animal state, sound source) and species-specific (Ellison et al. 2012, Southall et al. 2016, Harris et al. 2018). There have been comparatively few studies investigating how these behavioral responses relate to biologically meaningful changes in populations, such as juvenile and adult survival and reproductive rates, in part due to the difficulty in quantifying the linkages between behavioral responses and survival or reproduction for large, wide-ranging species (Pirotta et al. 2018a).

The National Research Council developed the Population Consequences of Acoustic Disturbance (PCAD) framework in 2005 to address the issue of acoustic disturbance and biologically meaningful changes to marine mammal populations (Wartzok and Tyack 2008). Anthropogenic sources that may cause acoustic disturbance to marine mammals include oil and gas exploration surveys, large ships, renewable energy resources (e.g., offshore wind farms), and naval activities. This framework has since been expanded to include other forms of disturbance (population consequences of disturbance, PCoD). The PCoD framework details how disturbance may affect behavior, how behavior is linked to vital rates either through direct acute effects or indirectly via chronic effects, and how changes in vital rates influence population trajectories (New et al. 2014). The current approach assumes that changes in behavior affect maternal condition by reducing energy gain (interrupting foraging behavior) and/or increasing energy expenditure (cost of avoidance). The net loss of energy leads to compromised adult condition, reduced energy delivery to offspring, higher rates of offspring mortality, and elevated adult mortality. Implementation of these ideas requires quantifying the functions that link behavioral and physiological changes to vital rates and ultimately population effects (New et al. 2014, King et al. 2015, McHuron et al. 2018, Nabe-Nielsen et al. 2018). Bioenergetic models and short-term behavioral response studies can be used to quantify how disturbance affects time-energy budgets and the resulting energetic cost (Costa 2012, New et al. 2013, Villegas-Amtmann et al. 2017), but the larger challenge from the population perspective lies in understanding how energetic costs translate to changes in vital rates and population dynamics.

State-dependent behavioral and life history theory, as implemented by Stochastic Dynamic Programming (SDP), provides a natural framework in which to quantify the transfer functions from behavioral changes to population dynamics by linking environment, physiology, and metrics of fitness (Mangel and Clark 1988, Clark and Mangel 2000, Houston et al. 2006). SDP models have been used to study the effects of natural and anthropogenic environmental disturbance in a variety of species (Noren and Mangel 2004, Klaassen et al. 2006, Frid et al. 2009, Fischer et al. 2011, Satterthwaite and Mangel 2012), but they have only recently been proposed as a way to conceptualize the PCoD framework (McHuron et al. 2017, 2018, Pirotta et al. 2018b, 2019). Further efforts are needed to make this approach more accessible for PCoD applications, particularly because the development of these models is not trivial. The power of SDP models lies in the combination of a backward iteration and a forward simulation. In the backward iteration, physiological state variables (e.g., body mass, lipid reserves) and how they change in response to environmental conditions and behavior are linked to a metric of fitness to identify the optimal state- and time-dependent behaviors, which are then used in a Monte Carlo forward simulation to predict the population consequences of disturbance. Here we define fitness as expected reproductive success, which is a proxy for the ability of an organism to pass on its genes (McNamara and Leimar 2020). While anthropogenic disturbance can have strong selective properties, it is generally not within the evolutionary timeframe of long-lived species such that selection has not acted on them for even a couple of generations. Thus, disturbance can be simulated in the forward simulation to capture the consequences of evolved behaviors and ad-hoc adjustments as animals respond to the new, perturbed environment.

Here we illustrate the power of state-dependent behavioral and life history theory within the PCoD framework, applying the general approach described by McHuron et al. (2017) to a large, capital breeding cetacean. We chose the western population of gray whales (Eschrichtius robustus) as our motivating species for practical reasons associated with their biology, the existence of established long-term comprehensive datasets, and conservation concerns. The endangered population numbers <200 whales, and while currently growing (Cooke et al. 2017), this population exhibits high site fidelity to a geographically small foraging habitat off
northeast Sakhalin Island in Far East Russia (Weller et al. 2012, Mate et al. 2015). During the foraging season, whale distribution can overlap with oil and gas seismic surveys that, in some situations, can elicit behavioral responses, including changes in distribution, travel speed, and diving behavior (Gailey et al. 2007, Yazvenko et al. 2007, Forney et al. 2017).

We developed an SDP model to characterize the movement, feeding behavior, and physiological dynamics of pregnant females as they arrived on the feeding grounds and predicted the probability of female and offspring survival, with and without acoustic disturbance. These are key entries into the stage-structured model from which one predicts population forecasts, and we illustrate this approach using previously developed population models for this population. We show how the methods of state-dependent behavioral and life history theory can be applied to a specific existing ecological application and how the methods provide insight into and lead to testable hypotheses regarding the interplay among physiology, behavior, and vital rates of large capital-breeding cetaceans.

**Fig. 1.** Schematic diagram illustrating the structure of the backward iteration and forward simulation of the Stochastic Dynamic Programming (SDP) model and how these two components are coupled. Text colors indicate whether a variable in the forward simulation was fixed, stochastic (varying among whales and/or model time steps based on draws from distributions in Table 1), or part of a sensitivity analysis. Note that the number of time steps \( T \) in the backward iteration and forward simulation differ, as described in the Methods.
METHODS

We used backward iteration to determine the result of natural selection on behaviors (here travel and feeding) in response to physiological state, environmental conditions, and time within the foraging season (Fig. 1). We modeled behaviors on a daily time step and considered four behavioral options at each time step: leaving the feeding ground to start the migration to the breeding site (leaving), feeding (feeding) at the current location within a spatially discrete location (referred to as a cell; see Foraging environment, Fig. 2), traveling from the current

FIG. 2. (a) The study area off Sakhalin Island, Russia showing the size and location of each cell with bathymetric contours at 10, 20, and 50 m with (b) inset map showing the study area in the rectangle. Nearshore cells (1–7) are shown in white and offshore cells in black (8–11).
location but staying within the cell to feed (traveling and feeding), and traveling to a new cell (traveling). The behavior of traveling and feeding captures the essence of the behavior “feeding and traveling” described in Gailey et al. (2008) or “searching” described by Stelle et al. (2008), where whales travel at relatively slow speeds with consistent periods of diving. For simplification, we modeled this behavior as directed traveling followed by a period of feeding. We incorporated these behaviors into a forward Monte Carlo simulation to predict the consequences of disturbance on female survival and successful reproduction (Fig. 1). We have provided a thorough description of the model methodology in the main text because one of the objectives was to facilitate model applicability to other species, which requires an understanding of each component of the model.

The backward calculation is a precise, numerical iteration for the expected reproductive success, over the stochastic events of survival and finding food, and allows us to determine state, time, and location-dependent behaviors. To reduce computational complexity, we held female length constant within the short foraging season, and assumed that all offspring followed the same growth curve and that all females of a given length shared the same metabolic and behavioral parameters. While it is an oversimplification of natural conditions to assume fixed parameter values for a whale of a given length, introducing this complexity into the backward iteration was likely unnecessary given the relatively small variation in some of the factors used to calculate metabolic rates (e.g., respiration rates, Table 1). We accounted for spatial and temporal variation in food using the best data available. The forward calculation is a Monte Carlo simulation, in which we draw random variables – in this case concerning survival and the level of food encountered – at each time step for each individual. The forward Monte Carlo simulation also allowed us to incorporate variability in a variety of parameters for each individual, such as fat mass upon arrival, metabolic rates, and diving and travel parameters (Table 1, Fig. 1). We conducted sensitivity analyses on many of these parameters, which allowed us to understand how parameter changes impacted the distribution of behaviors and the impact of disturbance on fitness.

Backward iteration

Physiological state variables and their dynamics.—We used two physiological state variables to characterize females, fat mass $M_{fat}(t)$ in kg and fetal length $L_{fetus}(t)$ in m at the start of day $t$ on the foraging ground. While we assumed females did not increase their length during the foraging season or subsequent lactation period, we modeled dynamics separately for females ranging in length from 11 to 14 m in 0.1-m increments (Rice and Wolman 1971). In addition to the dynamics described in the following paragraphs, we set lower (5%) and upper bounds (40%) on fat mass relative to a female’s total maximum body mass (Pirotta et al. 2018a, Appendix S1: Table S1); if a female’s fat mass fell below the lower critical level, we assumed that she died from starvation.

Gray whales are capital breeders that need to acquire all of their energy needs for an entire reproductive cycle while on the foraging ground (Stephens et al. 2009). Thus, the daily energy requirements of a pregnant female gray whale while on the foraging grounds can be decomposed into two main categories: (1) costs associated with female maintenance and activity (field metabolic rate, FMR) and gestation (energy investment in fetal growth and the heat increment of gestation, HIG) while on the foraging grounds (current costs, $E_{Current}$), and (2) energy stored as fat to sustain the costs of FMR, gestation, and lactation from the time she leaves the foraging ground to the time she returns with a dependent calf (future costs, $E_{Future}$). The bioenergetics of gray whales have been comprehensively described by Villegas-Amtmann et al. (2015, 2017) and we generally relied on values, parameters, and equations from these two papers to estimate daily energy requirements (Appendix S1: Section S1, Appendix S1: Table S1). While there are significant data gaps in our understanding of the energy requirements of large cetaceans, these two papers are some of the most comprehensive efforts to date of cetacean bioenergetics with respect to both the parameterization of values and the incorporation of uncertainty into each energetic cost. There are also empirical data from gray whales on some key model inputs, such as respiration rates, oxygen extraction efficiency, tidal volume, and mass–length relationships, thereby increasing confidence that the values presented in these papers represent realistic estimates of energy requirements. The resulting estimates characterize all energy requirements at each time step ($E_{Total} = E_{Fetus} + E_{Future}$) and each individual component of current and future FMR ($E_{FMR}$ and $E_{FMR+Future}$), gestation ($E_{HIG}, E_{Fetus}, E_{Gestation+Future}$), and lactation ($E_{Lactation}$). Energy estimates are a function of female and fetal length, but for simplicity we omitted these notations.

The dynamics of fat mass on day $t$ are governed by the interplay between energy requirements and energy gain from foraging ($E_{Gain}$). Thus, females may not acquire all the energy to meet their current costs and deposit fat for future costs when foraging in a patch with low prey availability or quality. Below, we describe the three interplay scenarios and the associated equations and decisions used to calculate the fat mass dynamics for each scenario.

When foraging resulted in sufficient or surplus energy to meet a female’s current energy needs ($E_{Gain} \geq E_{Current}$) she gained any surplus energy as fat

$$M_{Fat}(t + 1) = M_{Fat}(t) + \min \left[ \frac{E_{Gain} - E_{FMR} - E_{HIG} - E_{Fetus}}{ED_{Fat}}, \Delta M_{Max} \right]$$

where $\Delta M_{Max}$ is the length-specific maximum fat mass that a female could gain per time step. We set this value
at 4% of body mass based on findings by Tamura and Konishi (2009) for pregnant Antarctic minke whales (Balaenoptera acutorostrata). We estimated the amount of prey consumed (kg) based on the predicted arrival mass (Appendix S1: Table S1) and multiplied this by the average energy density of amphipods (5.54 MJ/kg; Marsh et al., in press) to convert prey mass to energy density. This accounts for physiological limitations associated with foraging and prevents unrealistically large mass gains when a female encounters prey patches of extraordinarily high energy density.

When energy gain was not sufficient to meet all current costs, we assumed a female drew on her fat reserves to provide the remaining energy needed for FMR and fetal growth. We allowed the amount of energy allocated to fetal growth to vary as a function of female body condition (Christiansen et al. 2014) by comparing predicted fat mass \( M_{\text{predictedFat}} \) to actual fat mass. Predicted fat mass was calculated by summing predicted fat mass gain per time step obtained from estimates of \( E_{\text{Fetus}} \) and the energy density of fat (\( E_{\text{Fat}} \), 39.7 MJ), assuming fat gain was amortized equally across each time step (Appendix S1: Section S1). If a female had the same or more fat reserves as the average predicted fat mass at a particular time step \( \left( \frac{M_{\text{predictedFat}}(t)}{M_{\text{predictedFat}}(t)} \geq 1 \right) \), fat reserves were taken to provide all needed energy costs for the fetus so that

\[
M_{\text{Fat}}(t+1) = M_{\text{Fat}}(t) + \frac{E_{\text{Gain}} - E_{\text{FMR}} - E_{\text{HIG}}}{E_{\text{Fat}}} 
\]

(3)

where the energy allocated to the fetus declined as a function of the ratio of fat mass to predicted fat mass so that

\[
E_{\text{AFetus}} = E_{\text{Fetus}} \cdot \frac{M_{\text{Fat}}(t)}{M_{\text{PredictedFat}}(t)} 
\]

(4)

Thus, there was a penalty in the form of slower fetal growth when a female was not on track to meet future energetic needs for fasting after leaving the feeding ground. When a female did not gain enough energy to meet her own needs then any energy deficit was again met with her fat reserves and we assumed that she did not allocate any energy towards fetal growth so that

\[
M_{\text{Fat}}(t+1) = M_{\text{Fat}}(t) + \frac{E_{\text{Gain}} - E_{\text{FMR}} - E_{\text{HIG}}}{E_{\text{Fat}}} 
\]

(5)

When a female was traveling between two cells (traveling), we allowed feeding to occur in the remaining time once she reached her new cell. In these situations, we assumed that a female used her own fat reserves to meet energy requirements, with energy allocation to fetal growth dictated by maternal body condition as above (Eqs. 2–4).

We converted fetal growth from the growth curve in Sumich et al. (2013) to discrete time, letting \( \Delta L_{\text{Fetus}} \) represent the per time step fetal growth if a female allocated the predicted amount of energy to the fetus. When a female allocated less energy than predicted to the fetus, we assumed that fetal growth was reduced such that

| Table 1. Behavioral and physiological parameters for the backward iteration and forward simulation. |
|-----------------------------------|--------|--------|----------|----------|
| Diving parameters                 |        |        |          |          |
| Dive time, foraging (%)           | 0.73   | beta (6.7, 2.5) |          | Appendix S1 Section S2 |
| Dive cycle (s)                    | 221.7  | log normal (5.33, 0.39) | 120, 2100 | Appendix S1 Section S2 |
| Travel parameters                |        |        |          |          |
| Travel speed (km/h)               | 3.53   | gamma (3.16, 0.93) | 1.5, 13.4 | Appendix S1 Section S2 |
| Linearity                         | beta   |          |          |          |
| Traveling/feeding                 | 0.8    | (2.1, 0.52) |          | Gailey et al. (2005) and similar reports |
| Traveling                         | 0.9    | (7.2, 0.8) |          |          |
| Within-cell travel time (h)       | 1      | log normal (1, 1) | 0.25, 5.99 | Estimated |
| Physiological                     |        |        |          |          |
| Respiration rate (breaths/d)      | 1.305  | normal (1305, 22) | 0, 7000   | Villegas-Amtmann et al. (2017) |
| Initial fat mass (kg)             | NA     | normal (20%, 300) | \( x_{\text{crit}}, x_{\text{max}} \) 10% and 15% | Appendix S1 Table S1 |
| Initial fetal length (m)          | NA     | normal (0.21, 0.1) | 0.21, 3.62 | Sumich et al. (2013) |
| Other                             |        |        |          |          |
| Arrival time                      | 15 May | normal (1 or 15 June, 5 d) | estimated |          |

Notes: When a distribution was used, the type of distribution is listed, with parameter values shown in parentheses. Values are also shown for those parameters that were evaluated in the sensitivity analysis.
\[
L_{\text{Fetus}}(t+1) = L_{\text{Fetus}}(t) + \Delta L_{\text{Fetus}} \times \frac{E_{\text{AFetus}}}{E_{\text{Fetus}}} \quad (6)
\]

When a female allocated no energy to fetal growth the dynamics were simply
\[
L_{\text{Fetus}}(t+1) = L_{\text{Fetus}}(t). \quad (7)
\]

The foraging environment.—We divided the foraging environment into seven nearshore cells and four offshore cells (Fig. 2), with \(C(t)\) denoting the cell where a whale was located at the start of time \(t\). We set the eastern boundaries of three nearshore cells (cells 1, 3, 5) to match those of the detailed benthic prey sampling grid (Blanchard et al., in press), whereas the eastern boundary of the remaining nearshore cells (cells 2, 4, 6, and 7) was based on the historic benthic sampling grid (Blanchard et al., in press). The boundaries of the four offshore cells (cells 8–11) were based on a combination of the historic benthic sampling grid and whale sightings in the area over time.

We used a single value to characterize the probability of mortality in each cell based on the annual non-calf survival estimates \(\phi\) from Cooke (2010). The daily rate of mortality \(\mu\) was the same across all foraging cells and time periods due to a lack of data about spatial and temporal variability in mortality \((\mu = 4.14 \times 10^{-5}\)).

We characterized each foraging cell by a state variable \(X(t)\) that described the energy density of prey species from six groups (Amphipoda, Bivalvia, Cumacea, Isopoda, Pisces/Actinopterygii, and Polychaeta) present in benthic grab samples collected in the Sakhalin feeding area in 2015 (Blanchard et al., in press; Maresh et al., in press). The energy per unit area \((\text{MJ/m}^2)\) for each foraging cell during three defined periods (early, 15 May–14 July; mid, 15 July–26 August; late, 27 August–7 November) was calculated using repeated Monte Carlo sampling of prey biomass and energy density (Maresh et al., in press).

We fit the resulting estimates to a log-normal distribution and converted this to a discrete distribution with \(N = 20\) equally spaced values running from \(x = 0\) to \(x = 1.05x_{\text{max}}\), where \(x_{\text{max}}\) was the maximum observed energy density for that cell (Appendix S1: Table S2). We let \(\bar{X}(c, t)\) denote a random variable corresponding to the energy that a whale encounters in cell \(c\) during day \(t\) and let \(p(x|c, t)\) denote the probability that \(\bar{X}(c, t) = x\). Thus, if \(\pi(c, t)\) and \(\sigma(c, t)\) denote the log-normal parameters for the benthic energy in cell \(c\) on day \(t\) and \(p(x|c, t)\) is the probability of a whale encountering energy density \(x\)

\[
p(x|c, t) = \frac{1}{\sum_{c' = 0}^{\text{Gain}} \exp \left[ -\frac{(\ln(x') - \pi(c, t))^2}{2\sigma(c, t)^2} \right]} \frac{\exp \left[ -\frac{(\ln(x) - \pi(c, t))^2}{2\sigma(c, t)^2} \right]}{x\sigma(c, t)\sqrt{2\pi}}.
\quad (8)
\]

The denominator is a normalization constant, used to guarantee that \(p(x|c, t)\) sums to 1; this allows us to convert from a continuous version of the log-normal distribution to a discrete one. In the following equations, we will use the notation \(E_{X(c, t)}\) to denote the expectation over \(x\) using the distribution in Eq. 8. We provide a brief description of the temporal and spatial variability in prey availability in the Results section, as this is a major driver of the behaviors that emerge from the model.

**Energy gained from foraging.**—The energy gained \(E_{\text{Gain}}\) per time step is a function of prey energy availability, whale foraging behavior, and the amount of energy available after fecal and urinary energy losses (metabolizable energy). To calculate the number of dives that occur during feeding, we used data from behavioral observation of Sakhalin Island whales during undisturbed periods to estimate the mean proportion of time spent diving and the mean surface-dive cycle time while feeding or traveling and feeding (Table 1, Appendix S1: Section S2). To calculate \(E_{\text{Gain}}\), we multiplied the number of dives by the estimated energy excavated per dive \((15.5 \text{~m}^2; \text{Thomson and Martin} 1984)\), the foraging efficiency of whales feeding on amphipods \((0.95; \text{Thomson and Martin} 1984)\), and an estimate of metabolizable energy \((0.84)\) derived from assimilation efficiency of minke whales (Martensson et al. 1994) and urinary energy losses of pinnipeds (Gomez et al. 2016).

The resulting values represented \(E_{\text{Gain}}\) for a whale that was feeding in cell \(c\) at time \(t\) in a patch with energy class \(x\). To estimate \(E_{\text{Gain}}\) for the other behavioral states, we assumed that the amount of time spent feeding, hence the number of foraging dives, was reduced due to time spent traveling to a new location within the same cell (traveling and feeding) or a new cell (traveling). When traveling within the same cell, we reduced the time available for foraging by one hour, which was sufficient for local spatial information about prey resources to be lost based on average travel speed and linearity (Appendix S1: Section S2). When traveling to a new cell, we reduced the time available for foraging based on the mean transit time between a whale’s current cell \(c\) and the new cell \(c’\). We determined the mean distance between unique cell combinations by calculating the distance between 1000 random points in each cell (ArcGIS V. 10.2; ESRI, Redlands, California, USA); we converted distances to transit times based on the average travel speed and linearity of whales (Table 1).

**Fitness function and end condition.**—Our metric of fitness \(F(m, l, c, x, t)\) was the sum of the expected probability that the female and the fetus survived to return to the foraging grounds at the next feeding cycle, given that she was in cell \(C(t) = c\) with food level \(\bar{X}(c, t) = x\) and physiological states \(M_{\text{Fat}}(t) = m\) and \(L_{\text{Fetus}}(t) = l\), where the expectation was taken over the stochastic events of survival and food distribution, and taking into account
erred in decision-making as described in Errors in decisions and the probability distribution of behavior (McNamara et al. 1997, Clark and Mangel 2000).

We calculated the probability a female survived to return to the foraging grounds in the following year based on her length and fat mass, using the methods of Villegas-Amtmann et al. (2017), who assumed a fixed number of days in transit from the foraging grounds to the breeding lagoons (assumed here to be Baja California). To account for females leaving the foraging ground before the end of the season and thus having additional days off the feeding ground before giving birth that need to be met from fat stores, we calculated survival curves for females of each length as a function of the day they left the foraging ground (Appendix S1: Fig. S1). In these cases, we adjusted a female’s departure fat mass for additional days she would spend before reaching the lagoons, which we calculated using breathing rates of pregnant females during the southbound migration (Villegas-Amtmann et al. 2017).

The probability that a fetus survived to return to the foraging grounds as a calf (hereafter “calf survival”) was a function of fetal length, maternal fat stores, and the departure day from the foraging ground (Appendix S1: Fig. S1). For the first component, we assumed a sigmoidal survival curve and assigned the maximum probability of returning to the foraging grounds (0.818; Gabriele et al. 2001) to a fetus that was at the predicted length at the end of the foraging season according to the fetal growth curve from Sumich et al. (2013). For the second component, if a female could not meet her own energy needs using fat mass reserves, both she and the calf died before returning to the foraging grounds. If a female could meet her own energy needs, we followed Villegas-Amtmann et al. (2017), who described the probability a female would successfully wean her calf based on her fat mass reserves upon departure from the foraging ground. The resulting fitness was adjusted as described above to (1) reflect the influence of early departure from the foraging ground on female fat reserves and (2) account for discrepancies in where pregnancy costs were incurred between our model and Villegas-Amtmann et al. (2017). The two fitness components were multiplied together to calculate the fetal fitness function.

The SDP equations.— After we determined fitness at the time a female must leave the feeding ground, iterating backwards in time allowed us to compute the fitness values of the different behaviors at previous times and from them optimal behavior and the probability of suboptimal behaviors (Mangel and Clark 1988, Clark and Mangel 2000). We let $V_F(m, l, c, x, t)$, $V_L(m, l, c, x, t)$, $V_{TF}(m, l, c, x, t)$, and $V_{c\rightarrow c'}(m, l, c, x, t)$ denote, respectively, the fitness value of leaving the foraging ground entirely, feeding at the current location, traveling within the current cell, or traveling from the current cell $c$ to cell $c'$ and where $M_{Fat}(t) = m$, $L_{Fetus}(t) = l$, and $X(c, t) = x$.

We used two-dimensional linear interpolation to account for continuous physiological state variables that must be treated as discrete values in the implementation of the SDP model (Clark and Mangel 2000).

We computed the fitness value of leaving $V_L(m, l, c, x, t)$ using the methods described for the end condition.

We computed the fitness value of feeding $V_F(m, l, c, x, t)$ assuming that after feeding in the current time step, a whale moved within the cell where she could encounter a prey patch with an energy density that differed from her current location. We let $p_c$ denote the probability that the energy density at the new spatial location was the same as at the current location (Appendix S1: Section S3). Assuming that a whale survived the current time step, which occurred with probability $e^{−\mu}$, at the start of the next she would be in the same cell at a location with the same energy density with probability $p_c$ and at a location with a different energy density with probability $1 − p_c$. In the latter case, future fitness was an expectation over the distribution of resources in the cell. Consequently

$$V_F(m, l, c, x, t) = e^{−\mu} \left[ p_c F(m_{TF}^l, l_{TF}^c, x, t + 1) + (1 − p_c) E_{X(c+1)=x'} \left\{ F(m_{TF}^l, l_{TF}^c, x', t + 1) \right\} \right]$$

(9)

The first term inside the square brackets on the right-hand side corresponds to a spatial location with the same energy density, where $m_{TF}^l$ and $l_{TF}^c$ are the predicted values of fat mass and fetal length at the next time step given feeding and $m, l, c, x$, and $t$. The second term inside the square brackets on the right-hand side corresponds to finding a spatial location where energy density is independent of the energy density in the current location ($x'c$). The values of $m_{TF}^l$ and $l_{TF}^c$ reflect this. In that case, we averaged over all the possible energy densities between 0 and the maximum for the current cell and time (denoted by $E_{X(c+1)=x'}$) using Eq. 8.

When computing the fitness value of traveling and feeding $V_{TF}(m, l, c, x, t)$, we assumed that when a whale moved within a cell without first feeding at her current location, she moved far enough so that local spatial information about prey was lost. Thus

$$V_{TF}(m, l, c, x, t) = e^{−\mu} E_{X(c+1)=x'} \left\{ F(m_{TF}^l, l_{TF}^c, x, t + 1) \right\}.$$  

(10)

We computed the fitness value of traveling from cell $c$ to $c'$ from

$$V_{c\rightarrow c'}(m, l, c, x, t) = e^{−\mu} E_{X(c+1)=x'} \left\{ F(m_{c\rightarrow c'}^l, l_{c\rightarrow c'}^c, c', t + 1) \right\}$$

(11)
where \( e^{-\mu|c'|} \) is the probability of surviving when traveling between the current and target cell. There were 10 values of \( V_{c_{t+1}}(m, l, c, x, t) \) for each \( c \), one for each of the potential cells a female could move to from her current cell.

**Errors in decisions and the probability distribution of behavior.**—We computed a probability distribution of behavior as opposed to using the behavioral decision that maximized fitness (optimal behavior; McNamara et al. 1997, Clark and Mangel 2000). This approach accounts for relatively small differences in fitness among behaviors that may result in non-optimal behavioral decisions, and accounts for situations in which ties in fitness arise (i.e., two or more behaviors have the same fitness value). Using this approach takes care of such issues in a natural, consistent way, and also prevents all individuals in the forward simulation from congregating in a single cell with the behavior that gives the highest fitness level. We included a modifier on this probability to account for the positive association between gray whales and amphipods (Oliver et al. 1984, Dunham and Duffus 2001, Budnikova and Blokhin 2012). See Appendix S1: Section S4 for a detailed description of these equations and Appendix S1: Fig. S2 for an example of the output from the backward iteration.

**Forward Monte Carlo simulation**

We used forward Monte Carlo simulation to develop behavioral predictions and to incorporate anthropogenic disturbance (Fig. 1). To add more precision to our forward predictions, the time step in the Monte Carlo simulation was 6 h (rather than 24 h, as it was in the backward iteration). We ran the simulation 100 times for each female length and disturbance scenario described below (including the undisturbed conditions). We created 100 populations from these simulations, where the number of whales (Appendix S1: Section S5, Appendix S1: Fig. S3) and lengths of whales within population were drawn from distributions ranging from 5–34 pregnant whales and 11–14 m in length (12.7 ± 0.6 m; Villegas-Amtmann et al. 2015), respectively. Replicates were randomly selected from the 100 length-specific replicates to identify the individuals that would comprise each population. The composition of populations (number of females and lengths) was the same across all scenarios. Females had a starting fat mass and fetal length based on draws from truncated normal distributions (Table 1). Females arrived on the foraging grounds on the same day (15 May), entering via one of the nine cells not bounded by other cells, and were required to depart by 6 November so that they could reach the breeding lagoons in Baja California.

The physiological dynamics in the forward simulation were the same as the backward iteration, with the exception that we drew parameters from distributions to incorporate individual variability and scaled energetics to a 6-h period (Table 1, Fig. 1). This included parameters associated with FMR, traveling (e.g., time, speed, linearity) and foraging (length of the dive cycle, percentage time spent diving). For each individual, we allowed parameters to vary among time steps with the exception of FMR, which was fixed across the entire simulation.

For each 6-h time step, we determined a female’s behavioral state by first drawing a random number uniformly distributed between 0 and 1 and then randomly summing the probabilities from Eq. S8 until the random number fell between two behaviors. The behavior adopted by a whale was the one that caused the sum to exceed the random number. We used a similar approach to determine the prey energy class a whale encountered, with the probability based on the log-normal probability distribution for the current cell (Eq. 8). When the selected behavior was traveling and feeding, we used the travel time, travel speed, and linearity to calculate the distance traveled and compared this to the distance at which spatial correlation in prey resources was lost (Appendix S1: Section S3). If the travel distance was greater than the distance at which spatial correlation was lost, the new energy class was determined as previously described. Otherwise, we used the method of the structure function (Mangel 1994, Mangel and Adler 1994) extended for multiple resource levels to compute the probability that a female was at a spatial point with the same energy density as the one she left. We compared that to a uniformly random number to determine if the new point had the same energy density as the old point (if not, it was drawn randomly from the appropriate log-normal distribution as described above). When a female traveled to a new cell, we used the travel speed, linearity of travel, and distance traveled to calculate travel time. Because the maximum distance between two cells was often >50 km, it could take females several time steps to reach their new cell; this jump in times was accounted for in the physiological dynamics and probability of mortality. We placed an upper limit of 24 h on traveling between cells because random draws occasionally resulted in parameter combinations that were inconsistent with the natural behavior of whales (i.e., low travel speed and linearity and large distances). Whales could forage for the remaining time when the travel time to the new cell was not an integer, with prey density at the new location determined as described above.

**Disturbance scenarios.**—We loosely modeled our disturbance scenarios on acoustic disturbance from seismic surveys, which have occurred in close proximity to the western gray whale feeding grounds in the summers of 1997, 2001, 2010, 2012, and 2015. Seismic surveys have typically been conducted in proximity to nearshore foraging areas (Gailey et al. 2007, Muir et al. 2016a). We did not include other forms of human-related disturbance that whales may experience on the foraging grounds that are energetically costly, such as fishing gear entanglement (Bradford et al. 2009, van der Hoop et al.
2016, Lowry et al. 2018). We simulated a total of 30 disturbance scenarios that varied in the start date of disturbance within the foraging season (15 June [early] or 15 August [late]), the spatial location of the disturbance (cells), the effect of multiple concurrent or sequential surveys, and the probability of disturbance (Table 2). The initiation dates of the disturbances were based on the earliest date it would generally be safe to conduct a seismic survey without encountering large ice floes (early), and a date later in the season that was within the time it would still be safe to initiate a survey without encountering rapidly deteriorating weather conditions (late). The duration of each disturbance lasted for a total of three weeks, consistent with typical operations in this area. Disturbances occurred in no fewer than two cells and no more than four cells at a single time and were restricted to cells 1–6. We paired adjacent cells during all disturbance scenarios (e.g., if cell 2 was disturbed so was cell 1). We assumed that whales experienced disturbance with one of two fixed probabilities (30% or 60%), which we interpreted as the combination of area ensonified (probability of exposure) and the dose-response curve (probability of behavioral response given exposure). We assumed that when a whale was disturbed, which occurred when the probability of disturbance was greater than a random number uniformly distributed between 0 and 1, it responded by leaving the current location and traveling to the nearest undisturbed cell. In these cases, the amount of time spent traveling and any energy gained from feeding upon reaching the undisturbed cell was dictated as described previously for traveling.

Table 2. Disturbance scenarios implemented in the forward simulation, including the probability a pregnant whale would be disturbed, whether the disturbance began on 15 June (early) or 15 August (late), and which cells were disturbed.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Disturbance probability</th>
<th>Timing</th>
<th>Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–12</td>
<td>0.3 or 0.6</td>
<td>early or late</td>
<td>1 and 2, 3 and 4, 5 and 6</td>
</tr>
<tr>
<td>13–24</td>
<td>0.3 or 0.6</td>
<td>early or late</td>
<td>1–4, 1–2 and 5–6, 3–6</td>
</tr>
<tr>
<td>25–30</td>
<td>0.3 or 0.6</td>
<td>early and late</td>
<td>1–2 then 3–4, 1–2 then 5–6, 3–4 then 5–6</td>
</tr>
</tbody>
</table>

Note: In all scenarios, each disturbance event lasted for three weeks.

RESULTS

Prey availability: Empirical results

There was considerable spatial variability in energy availability, with the largest discrepancy between the nearshore and the offshore cells (Appendix S1: Table S2, Appendix S1: Fig. S4). The mean energy availability in cells ranged from 0.22–0.50 MJ/m² (nearshore) and 0.98–3.52 MJ/m² (offshore), with maximum values of 5.26 and 24.54 MJ/m², respectively (Appendix S1: Table S2). In the three nearshore cells with temporal data, variability across the three time periods was less pronounced than the differences between nearshore and offshore cells (Appendix S1: Fig. S5). In general, nearshore prey energy density was lower in the south (cell 1), particularly in the later time periods, compared with the northernmost cell (cell 7). Although the nearshore northern cell had higher prey energy density compared to most other nearshore cells, amphipods made up the lowest proportion of that energy. The southeast corner of the offshore area (cell 11) had both the highest prey energy density in the entire defined foraging area, with a mean value over 12 times that of the lowest mean energy density, and the greatest proportion of energy from amphipods of all cells (Appendix S1: Table S2).
Undisturbed conditions: Model output

Upon arrival on the foraging grounds, the behavior of pregnant females was characterized by an initial period of relatively random behavior that resulted in minimal mass gain (Fig. 3). The length of this period varied with female length, arrival fat mass, arrival time, and metabolic rate, with whales switching to a period of intensive foraging between July and August (depending on the scenario) resulting in large gains of fat mass (Fig. 3). Whales began concentrated foraging earlier in the season when they showed up in poorer body condition, whereas they delayed this switch under the scenario where metabolic expenditure was reduced by 50%. The switch from more random behavior to foraging was characterized by movement of most whales to the offshore cell with the greatest prey availability (cell 11), which contrasted with earlier in the season when whales were present in more equal proportions in nearshore and offshore cells (Fig. 4, Appendix S1: Fig. S6). The increased presence of whales in the offshore cells later in the season occurred regardless if we considered only whales that were feeding or traveling or feeding (i.e., those assigned to a particular cell at a given time in the forward simulation), or if we also included whales that were moving between two cells within the nearshore or offshore areas.

Changes in fat mass across the season varied considerably across female lengths and sensitivity scenarios (Fig. 3, Appendix S1: Fig. S7). While some of the variation associated with female length was because of parameterized differences in food intake capabilities, it was also due to differences in how much time females spent foraging (Appendix S1: Fig. S8). In most scenarios, there was a strong dichotomy in the fat mass at departure relative to the maximum allowed fat mass; almost all females ≥12.7 m reached or were close to their maximal allowable fat mass, whereas very few females <12.2 m left with more than 50% of the allowed values (Appendix S1: Fig. S9). This size-specific pattern was less apparent for the metabolic sensitivity scenario, where females of almost all lengths departed with an average of at least 60% of their maximum allowable fat mass. When females were excluded from cell 11, they experienced minimal net fat mass gain regardless of length, with almost all individuals falling below the critical fat mass limit and dying when excluded from all offshore cells (Fig. 4, Appendix S1: Fig. S6). Females of all lengths generally compensated for variation in arrival body condition by increasing the amount of time spent foraging, whereas they decreased the amount of time foraging when metabolic rates were reduced (Fig. 3, Appendix S1: Fig. S8). These alterations resulted in a

Fig. 3. (a) Cumulative number of foraging time steps (behaviors of feeding and traveling and feeding) and (b) fat mass of pregnant gray whales across the foraging season as a function of whale length. Gray dots represent trajectories of individual whales from 50 of the 100 population replicates from the undisturbed, baseline scenario. Loess-smoothed trajectories of data points are shown for each whale length for ease of visualization.
similar fat mass at departure as in the baseline scenario for the largest (≥13.0 m) females (Fig. 3, Appendix S1: Fig. S9). Variation in arrival dates had little to no impact on fat mass gain or foraging behavior (Appendix S1: Figs. S6–S9).

Female survival was high and similar across all lengths and sensitivity scenarios, except for scenarios where females arrived in reduced body condition or where they were excluded from the cell with the highest energy availability (Fig. 5, Appendix S1: Fig. S10). When arrival fat mass was distributed around 10% or 15% of body mass, mean female survival was reduced from 0.99 to 0.92 or 0.98, respectively. Cell exclusions resulted in reductions in survival; mean survival was reduced to 0.91 when whales were excluded from cell 11, whereas almost all whales died (mean survival = 0.06) when they were excluded from all offshore cells (Fig. 5a, c). These reductions in female survival were driven by an increase in starvation, which accounted for 24% of all mortalities in the baseline scenario but 48–99% in scenarios with reduced female survival. The smallest females generally had slightly higher survival probabilities, presumably because they had lower absolute energy requirements than larger females. The probability that a female would successfully return to the foraging grounds the following year with a calf was virtually zero for almost all females <11.8 m in the baseline scenario (Fig 5b). This value steadily increased until a female reached a length of about 13.7 m, after which the rate of increase began to slow. A 50% reduction in metabolic rates led to a noticeable increase in calf survival for smaller females, whereas arriving in poorer body condition had the opposite effect (Fig. 5, Appendix S1: Fig. S11). Exclusion from cell 11 resulted in a very low probability of calf survival for almost all females (calf survival at or near 0), regardless of length (Fig. 5). Female and calf survival in the remaining scenarios (prey spatial correlation, exclusion from other offshore cells) were generally similar to that in the baseline scenario (Appendix S1: Figs. S10–S11).

**Disturbed conditions: Model output**

Individual females were disturbed and left their current cell for the nearest undisturbed cell between 0 and 17 times across all disturbance scenarios, with the average female disturbed 1.2–5.5 times across the foraging season depending on the disturbance scenario (Appendix S1: Fig. S12). Under the baseline parameters, the scenario that had the highest average disturbance per whale occurred when whales experienced a 60% probability of disturbance in cells 1, 2, 5, and 6 early in the season. Whales in this scenario were disturbed an average of 5.5 times, although there were also five other scenarios where the average times a whale was disturbed was ≥5. The average number of disturbance events was insensitive to variation in metabolic rates, arrival times and body condition at arrival, the prey spatial correlation coefficient, and exclusion from some offshore cells (cells 8–10). When whales were excluded from cell 11 or all offshore cells, disturbance increased because there was a higher probability of being in a disturbed cell.
given all simulated disturbances occurred in nearshore cells. The level of disturbance experienced by an individual was affected by length, such that the smallest females were generally disturbed the most and the largest females the least (Appendix S1: Figs. S12–S13). This was because smaller whales were more likely to be in nearshore areas during the times of the simulated disturbance (and in general), hence increasing their potential exposure to disturbance (Appendix S1: Fig. S14).

Disturbance had almost no discernable adverse effects on population-level female (Cohen’s $d = -0.04$ to 0.21) or calf survival (Cohen’s $d = -0.001$ to 0.06) using the baseline parameter values (Appendix S1: Table S3). There was only one disturbance scenario where female survival exceeded the threshold for a small adverse impact, with female survival decreasing from 0.99 to 0.98. There was little effect of variation in arrival time and body condition, metabolic rate, the prey correlation coefficient, or cell access on the conclusions with regards to the effects of disturbance (Appendix S1: Table S4).

When we calculated Cohen’s $d$ values by pooling across female length categories (instead of by averaging within and then across population replicates), disturbance did appear to have variable impacts on females of different lengths (Fig. 6, Appendix S1: Fig. S15). This general pattern was true regardless of whether we used only the females in our simulated populations (where there were fewer larger and smaller whales, Fig. 6) or all 100 replicates for each whale length (Appendix S1: Fig. S15), however, the specific lengths that were affected varied between the two. For both population-level and female length comparisons, the average number of disturbances to an individual whale did not appear to be a good indicator of the impact of disturbance on female or calf survival (Appendix S1: Figs. S16–S17).

**Population impacts: Model output**

Because disturbance had comparatively little impact on female and calf survival, we chose to explore the population consequences of changes in calf and female survival as a result of exclusion from offshore cells using the altered survival rates with the additional Cooke (2010) rates and a Leslie matrix (Appendix S1: Section S6, Appendix S1: Table S5, Appendix S1: Fig. S18). Exclusion from cell 11, where mean calf survival was 0.003, resulted in a very gradual population decline with a zero probability of extinction at 100 yr, assuming that exclusion occurred across many years. Exclusion from all offshore cells in just a single year, where mean female survival was 0.06, led to an initial population decline with recovery after 16 yr. This one-year exclusion had additional long-term population ramifications because after 100 yr, population size was 36% of what it would have been without the exclusion, assuming neither population reached carrying capacity. Poor female survival across many years led immediately to a functionally extinct population, with the remaining population consisting entirely of males and juveniles, and juvenile females dying once they reached reproductive age.
We developed a state-dependent behavioral and life history model that extended initial efforts by McHuron et al. (2017) and Pirotta et al. (2018b, 2019) to quantify the population consequences of disturbance on marine mammals. This approach overcomes a key challenge in implementing the PCoD framework by providing a natural link between behavioral changes and vital rates. The development of SDP models requires that one carefully characterize the biology of the focal species, the key aspects of the environment (e.g., prey fields, natural mortality), and identifies metrics of fitness. SDP models are data intensive and can be challenging to parameterize, particularly for large marine species that spend their entire lives at sea and often cover vast geographic areas. By focusing on species that are comparatively data rich, we gain an understanding of how disturbance may affect other species with similar life history characteristics while highlighting parameters that are particularly influential on model output and should therefore be a focus of future data collection efforts. In addition to the conservation need for a species-specific model, Sakhalin Island gray whales are a tractable population given their high site fidelity, relatively small foraging area, and the availability of key data sets. We discuss the results of our initial effort within the context of Sakhalin Island gray whales and capital-breeding cetaceans in general, identifying testable hypotheses and key areas of future research that are important for using SDP models to implement the PCoD framework. While we focused on acoustic disturbance from seismic surveys, it is relatively simple to model other types of disturbance (acoustic or otherwise) with SDP models, as this typically only requires adjustments to the forward simulation (e.g., the disturbance landscape, the behavioral response of individuals to the disturbance). It also is possible to develop forward simulations for a variety of hypothetical prey/disturbance scenarios, which may be desirable for examining the range of potential population responses to future disturbance activities.

Baleen whales share a life history strategy that typically consists of a long-distance migration between breeding/calving grounds and productive foraging grounds. Survival and reproductive success are therefore largely dependent on the presence of abundant resources on the foraging grounds that allows whales to gain substantial fat stores to support metabolic and reproductive costs in the following year (Lockyer 1984). At Sakhalin Island, benthic survey data indicated that prey availability varied drastically between the nearshore and offshore cells; prey biomass and energy density in the nearshore cells were quite low compared with other gray whale foraging areas, whereas cell 11 in the offshore area was at the upper range relative to other gray whale foraging areas (Dunham and Duffus 2001, Coyle et al. 2007, ...)
Brower et al. 2017, Blanchard et al. 2019). While we characterized the prey landscape using data from a single year, a trend of higher prey biomass in the offshore cells has been consistently observed for at least the past 15 yr (Blanchard et al. 2019). There may still be localized patches of high prey energy density in the nearshore area, as relatively high energy densities of amphipods have been documented very close to shore (<7 m water depth). These areas are underrepresented in our benthic dataset because they are logistically challenging to sample (Blanchard et al. 2019 and references therein), but future efforts to do so are important for accurately characterizing the prey landscape that gray whales experience.

Spatial differences in prey availability affected the predicted behavior and distribution of whales, with whales shifting from an initial distribution that was relatively equal between nearshore and offshore cells to predominate use of the offshore cell 11 by mid-August. This pattern was present regardless of variation in arrival time, body condition at arrival, and metabolic rates, although the timing varied depending on these parameters. There were also some length-specific differences in the timing and severity of this response, likely due to interactions between total metabolic demands, which increase with body size, and future expected fitness. The predicted concentration of whales in the offshore area from the model, where the average amphipod biomass routinely exceeds 100 g/m² (Blanchard et al. 2019), is consistent with observations that eastern gray whales aggregate in areas with amphipod densities in excess of 100 g/m² (Dunham and Duffus 2001, Brower et al. 2017). A considerable number of gray whales have been found in the offshore area between June and November since the first observation of its use in 2001, with intra-seasonal and inter-annual variability in both distribution and abundance (Meier et al. 2007, Muir et al. 2016b). These observations support the predictions of our model that the offshore foraging area provides important habitat for pregnant gray whales at Sakhalin Island.

Our model results are consistent with studies of gray and other baleen whales, showing that habitat use and movements on the foraging grounds are influenced by prey abundance and distribution (Dunham and Duffus 2001, Moore et al. 2003, Hazen et al. 2009, Laidre et al. 2010). The specific patterns of cell use predicted here are limited by the resolution and specific values of the benthic data, and therefore may not be representative of the actual movements of gray whales in any one year. There is interannual variation in the biomass and composition of benthic prey communities at Sakhalin Island, particularly with respect to amphipods (Blanchard et al. 2019), and thus a continued need for benthic sampling to quantify inter-annual and intra-seasonal variation at finer resolutions than what we modeled here. We can, however, develop predictions about how pregnant gray whales at Sakhalin Island should be distributed in relation to prey availability in any given year. Specifically, the model output indicates that early in the foraging season, pregnant gray whales are likely to be more broadly distributed among areas with moderate to high prey availability, but by mid-August (or earlier depending on arrival condition) should be concentrated in areas of high prey availability.

The model indicated that pregnant whales generally did not exhibit consistent fat mass gains until habitat use shifted to the offshore area, except when metabolic rates were reduced by 50% below the baseline. This was due to the combination of relatively low prey availability in nearshore cells and because we allowed for non-optimal behaviors to be selected when fitness values were relatively similar to the optimal behavior. When whales arrived with half of their maximum allowable fat mass, they did not need the entire foraging period to reach their maximum fat mass and thus their behavior early in the season was more random. On average, simulated whales doubled their fat mass across the foraging season, although larger whales exhibited average increases of 144% above their starting fat mass. These values are roughly similar to empirical measurements from minke whales that doubled their blubber mass across the 180-d foraging season (Christiansen et al. 2013). Baleen whales can also store considerable amounts of fat in muscle and visceral organs (Lockyer et al. 1985, Lockyer 1986, Niess et al. 1998), which may explain why our values for larger females are higher given they are meant to represent all fat stores and not just blubber. Alternatively, it is possible that we overestimated the energy gain from foraging, either in how much prey they are actually able to ingest or in how much energy from that prey is available for fat accumulation. If this were the case though, we would expect that whales would begin intensive foraging earlier in the season, which would likely result in similar levels of fat mass gain from the model.

The delay between arrival and the onset of intensive foraging generally allowed whales in our model to compensate for variation in arrival condition and time through changes in time-activity budgets. Intermediate-sized females experienced reduced reproductive success when they arrived in poorer body condition, indicating this flexibility likely decreases with body size. While detailed time-activity budgets across the foraging season are lacking for baleen whales, Lemos et al. (2020) found that the body condition of gray whales foraging in Oregon was similar between June and July and did not begin to increase until sometime between July and August. Temporal variation in body condition across the foraging season was absent in a year when whales arrived in relatively good body condition (Lemos et al. 2020), providing some support for our model observations that whales may not necessarily need to feed intensively across the entire foraging season. A similar pattern of increasing body condition from July onward has been detected for western gray whales at Sakhalin Island (Bradford et al. 2012), but it is unknown whether body condition is stable early in the foraging season.
increases in blubber deposition across the foraging season have been detected for other baleen whales (Vikingson 1990, Christiansen et al. 2013), but this does not necessarily discredit the potential for non-linear changes because the length of the foraging season, prey availability, metabolic demands, and maximum intake rates can vary among populations and/or species.

There were length-specific differences in the predicted patterns of fat mass gain, with the largest females exhibiting the greatest rate of fat mass gain while the smallest females gained relatively little or no fat mass across the foraging season. These patterns were in part driven by the parameterization of length-specific differences in absolute fat stores that allowed a large (long) female to invest more in her calf than a small (short) female and therefore increase the probability of calf survival. Because the average probability that a whale <11.8 m would successfully wean a calf was low (<20%), there was less discrepancy in future expected fitness values among behaviors for smaller whales, leading to more random behavior as long as females had enough fat to meet their metabolic needs until the following season. Based on photogrammetry, Perryman and Lynn (2002) observed female gray whales with calves on the northbound migration that were <11.8 m, suggesting that we may have underestimated calf survival for at minimum small females and potentially all size classes. While this would have affected absolute values for calf survival, these underestimates are unlikely to affect the general patterns predicted by our model given that size-specific variation in energy transfer to offspring has been documented in capital-breeding marine mammals (Crocker et al. 2001, Christiansen et al. 2018).

For baleen whales, empirical data indicates that most age and reproductive classes exhibit increases in body condition across the foraging season (Vikingson 1990, Christiansen et al. 2013, George et al. 2015). While this is somewhat contradictory to our model output, there is some evidence that pregnant baleen whales gain mass at a faster rate than non-pregnant ones (Vikingson 1990, Irvine et al. 2017) and that small pregnant whales may still have low lipid stores at the end of a foraging season (Irvine et al. 2017). We did not model potential transitions from a pregnant to non-pregnant state (abortion), but if we had, whales that exhibited a lack of intensive feeding would likely have been those that would have terminated their pregnancy during the season. Extension of our model timeline to include multiple years is needed to determine if our observations here are simply an artifact of model structure, the fact that it was limited to a single year and did not include growth costs nor a future increase in fitness associated with growing larger, or whether they indicate that there may be behavioral differences among females of different lengths and reproductive states.

Predicted vital rates were strongly influenced by the ability to access areas of high prey availability later in the season, with exclusion from these areas leading to a near zero probability of calf survival, or in the extreme case, mortality of all but the smallest individuals. As mentioned previously, length-specific variation in mortality was likely driven by differences in absolute metabolic requirements, with smaller whales better able to meet their metabolic demands with less prey. The SDP model developed by Pirotta et al. (2019) for blue whales (Balaenoptera musculus) indicated a similar trend, with most whales dying from starvation when a simulated disturbance occurred in the central part of their feeding ground. Physical exclusion from all offshore foraging cells (or other areas with high prey availability) is unlikely, but these results highlight the relatively dramatic effects that decreases in prey availability could have on large capital breeders. Reductions in prey availability, either due to actual decreases or shortened foraging seasons, have been linked with decreases in body condition, reproductive success, and survival of gray whale populations (Moore et al. 2001, 2003, Perryman et al. 2002, Grebmeier et al. 2006, Salvadeo et al. 2015, Gailey et al. 2020) and baleen whales in general (Braithwaite et al. 2015, Meyer-Gutbrod et al. 2015, Seyboth et al. 2016). At Sakhalin Island, annual sea ice conditions in the year prior to birth explained about 77% of the variation in calf survival, with whales returning in poorer body conditions in the year following a shortened foraging season (Bradford et al. 2012, Gailey et al. 2020). While our model predicts that whales may have some ability to compensate for delayed arrival time and reductions in arrival body condition, that ability is likely reduced when these factors co-occur. In addition, pregnant females that extend their foraging season risk giving birth outside of the lagoons (Shelden et al. 2004), which could impact calf survival. In our population simulations, the absence of highly abundant prey in even a single year led to the death of whales in relatively good body condition, regardless of the metabolic scenario, which had long-term population ramifications even though the population was able to recover from the initial decline caused by these mortalities. In reality, the population effects would be much worse given that lactating females are likely to be the most susceptible to changes in prey availability because they arrive on the foraging grounds in poor body condition (Bradford et al. 2012, Lemos et al. 2020). While this scenario is quite extreme, our results are relevant given the high number of eastern gray whales in poor body condition that stranded along the west coast of North America in 2019 (Christiansen et al. 2020), which led to the declaration of an unusual mortality event for this population.

Simulated disturbances in the nearshore area had little to no adverse effect on female or calf survival at the population level, regardless of spatial or temporal variation in disturbances. Mass gain was not critical in the early part of the foraging season, when gray whales were more likely to be in the nearshore cells to experience disturbance. In the later part of the season, when most mass gain occurred, whales were largely foraging in the
offshore area where there was no simulated disturbance. Smaller females generally experienced more disturbances than larger ones because they were more likely to be in nearshore cells when simulated disturbances occurred, likely due to interactions between metabolic requirements and behavioral choices associated with expectations related to the probability of calf survival. An increase in the average number of disturbances per individual did not necessary translate to greater adverse population-level effects in our simulations, indicating that the absolute number of disturbances a whale experiences may not be the only indicator that should be considered when planning disturbance activities. These findings do not necessarily imply that seismic activities at Sakhalin Island do not have adverse affects on gray whales. Instead, our results provide the framework under which these impacts can be assessed in individual years; specific impacts will likely depend on interactions among the size composition of the population, arrival body condition, and how prey availability and distribution overlap with seismic activities. Our model was also focused on the chronic effects of disturbance on energy gain of pregnant females and did not consider other disturbance-related effects (Wright et al. 2007, Rolland et al. 2012, Finneman 2015), the cumulative impacts of multiple stressors (Crain et al. 2008), or impacts on other demographic groups.

Gray whale research efforts at Sakhalin Island have been conducted annually for the last two decades, providing an opportunity to test model predictions and collect additional data to improve parameter estimates. For example, existing efforts that include focal follows, drone surveys, and photo-identification can be used to better inform parameters related to body condition, the length-distribution of mature whales, and behavioral responses of whales to disturbance. The addition of newer technologies, such as coupling drone technology with hormone analyses, would provide a better understanding of energetic costs and the relationships among body size, body condition, pregnancy rates, and perinatal/calf mortality (Christiansen et al. 2014, 2016, Pallin et al. 2018). Such data are needed for refining the fitness functions, which are critical components affecting model-derived estimates of vital rates and can be influential on conclusions regarding the population consequences of disturbance (Pirotta et al. 2018b).

CONCLUSIONS

Acoustic disturbance can adversely affect individuals in a variety of ways that have the potential for cascading effects on the biology and population dynamics of a species and the communities they inhabit (Slabbekeorn and Rippester 2008, Barber et al. 2010, Shannon et al. 2016, Cox et al. 2018). Biologically meaningful effects are often assessed within an energetic framework because the ability to acquire energy is critical for survival and reproduction. The SDP model we developed here is a tool that can be used to generate testable hypotheses, test existing hypotheses, and inform research needs, planned disturbances, and the effectiveness of mitigation strategies. As illustrated here, SDP models are a useful tool for implementing the PCoD framework because they are able to capture the essence of a species’ biology and underlying ecological/evolutionary processes while allowing for disturbance to occur within the context of a temporally and spatially dynamic environment. While we used western gray whales as our motivating species, our model can be relatively easily adapted to other species with similar life history characteristics and to incorporate other types of disturbance.

Our results indicate that which individuals and where and when individuals are disturbed are likely to be important factors when assessing the population consequences of disturbance on capital-breeding cetaceans, even for a single reproductive group. The results also highlight the susceptibility of baleen whales to dramatic changes in prey resources, which is a particular concern for western gray whales at Sakhalin Island because, while amphipod densities remain high in the offshore area despite recent declines (Blanchard et al. 2019), they have a small population size with high site fidelity to the current foraging area. The physiological and behavioral patterns that emerged from our model are ultimately driven by how the model was parameterized and our assumption of how optimal whales behaved, as these dictate predictions of behaviors from the backward iteration. This highlights the need to accurately parameterize models and to conduct sensitivity analyses when there is uncertainty in parameters. Despite this, many of the general patterns that emerged from our model, such as the importance of foraging areas with high density prey and length-specific variation in behavior, appeared robust to variation in parameter values or were based on underlying assumptions that are well rooted in empirical data (e.g., size-specific variation in metabolic demands and energy stores). In particular, the potential for length-specific differences in behavior and movement patterns could lead to size-specific disparities in disturbance exposure, which should be taken into consideration when assessing the impacts of disturbance on capital-breeding cetaceans. Future efforts to extend the model timeline, incorporate additional reproductive states, and compare model output with empirical data are needed to evaluate model predictions, identify whether mitigation strategies differ among reproductive groups, and better evaluate the population consequences of disturbance on western gray whales.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Rodger Melton, whose insight and dedication to gaining a scientific understanding of the population consequences of acoustic disturbance set a high bar and inspired us. Our work was funded by an ExxonMobil grant (A19-0699-001) and was part of an extensive Exxon Neftegas Limited monitoring program developed to
understand population level consequences of gray whale responses to the 2015 seismic survey activities. All authors contributed to the study design; G. Gailey and L. Schwarz analyzed data used in the model; E. McHuron, M. Mangel, and L. Schwartz developed and implemented the model; and E. McHuron led the manuscript writing with input from all authors. During preparation of this manuscript, E. McHuron was supported by a Lenfest Ocean Program grant 00031535 and M. Mangel was partially supported by ONR grant N00014-19-2494. The spatial and temporal prey biomass and caloric value data used in this manuscript were collected as part of the 2015 monitoring program. Collection of the respiratory and tracking data used to parameterize the model was funded by Exxon Neftegas Limited and Sakhalin Energy Investment Company Ltd. These efforts would not have been possible without the following people/groups that contributed to the analysis of datasets central to the model: Arny Blanchard, Laurie Ainsworth, Jen Maresh, Vladimir Nechauvuk, Mike Jenkerson, Pacific Oceanological Institute of the Far East Branch of the Russian Academy of Sciences, and JASCO Applied Sciences.

**LITERATURE CITED**


Reproductive success is influenced by krill (Euphasia superba) density and climate. Scientific Reports 6:28205.


Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2440/full

Output from the forward simulations (McHuron et al. 2021) can be found in the Dryad Digital Repository at https://doi.org/10.7291/D1VM2B.

Appendix S1
Section S1: Energetic Costs

Energy requirements

We computed daily Field Metabolic Rates (FMR) by

\[ FMR = 0.02 \cdot \%O_2 \cdot R_s \cdot V_{\text{tidal}} \]  \hspace{1cm} (S1)

where 0.02 is the amount of heat projected in MJ L\(^{-1}\) O\(_2\) consumed, \(\%O_2\) is the proportion oxygen efficiency per breath, \(R_s\) is the phase-specific respiration rate (number of breaths per day while foraging, migrating, or on the breeding lagoons), and \(V_{\text{tidal}}\) is the tidal lung volume. We used a value of 0.11 for \(\%O_2\) based on data from a captive gray whale (Sumich 2001, Villegas-Amtmann et al. 2015), and breathing rates from observations of free-ranging gray whales during each phase (Table 1). We computed tidal volume by

\[ V_{\text{tidal}} = 0.014 M_{\text{Arrival}}^{1.04} \]  \hspace{1cm} (S2)

where \(M_{\text{Arrival}}\) is the mass of the female in kg (Table S1).

We computed the daily cost of gestation based on the chemical composition of the fetus, the energy density of fat and protein, the energy associated with other tissues, and the Heat Increment of Gestation (HIG). We predicted the daily fetus length and mass from Eqs. 4 and 6 of (Sumich et al. 2013), and used the resulting change in mass (\(\Delta M_{\text{Fetus}}\)) to calculate the daily energy composition of the fetus where

\[ E_{\text{Fetus}} = \Delta M_{\text{Fetus}} \cdot \%_{\text{Lipid}} \cdot E_{\text{Lipid}} + \Delta M_{\text{Fetus}} \cdot \%_{\text{Protein}} \cdot E_{\text{Protein}} \]  \hspace{1cm} (S3)

We used values of 0.06 and 0.125 for the relative contribution of lipid and protein to fetal mass (Sumich 1986, Villegas-Amtmann et al. 2015), respectively. and assumed the energy composition of fat and protein to be 39.7 and 23.8 MJ kg\(^{-1}\) (Kleiber 1961), respectively. We computed the energy associated with the HIG following Villegas-Amtmann et al. (2015) with slight modifications to estimate daily costs.
where the HIG was allocated to each day based on the ratio between the mass of new tissue added \( (M_{\text{Fetus}}) \) to the mass of the fetus at birth \( (M_{\text{Fetus}_{\text{born}}}) \). We calculated the daily energy cost of additional tissues (e.g., placenta) assuming fetal costs represented 80.7% of the cost of gestation. The total future cost of gestation was calculated by summing the daily costs from the time a female left the foraging ground to the end of gestation.

We used a value 135 MJ 10\(^3\) to represent the total cost of lactation, computed by Villegas-Amtmann et al. (2017) for western gray whales by summing calf FMR and growth costs across the ~6.5 month lactation period.

\[
E_{\text{HIG}} = (18.41 \cdot M_{\text{Fetus}_{\text{born}}}^{1.2}) \cdot \frac{M_{\text{Fetus}_{\text{born}}}}{M_{\text{Fetus}}}
\]  \( (S4) \)

*Daily predicted fat mass*

We amortized the total future energy costs equally across the foraging period to calculate the per timestep energy gain needed to support metabolic demands and reproduction once a female left the foraging grounds. We converted these values to fat mass gain per timestep \( (\Delta M_{\text{Fat}}) \) using the energy density of fat \( (ED_{\text{Fat}}, 39.7 \text{ MJ kg}^{-1}) \), assuming that all energy was stored as fat. A female’s predicted fat mass at each timestep was calculated using length-specific estimates of \( \Delta M_{\text{Fat}} \) and fat mass at arrival. These predicted fat mass values were used to assess how a female should allocate energy to her fetus, as described in the main text.
Section S2: Behavioral parameters

Travel speed, feeding dive time, and surface-dive time data were collected from whales foraging off Sakhalin Island from 2002 – 2010 via focal follows that recorded behavioral state and respiratory events, and by theodolite tracking (see Gailey et al. 2016 for further details). This long-term dataset was filtered to isolate periods when no significant anthropogenic activity occurred, defined as undisturbed periods. Focal follows of known calves were excluded in the analysis. Individual whales often could not be identified, so each focal follow was treated as independent. For each behavior, data were limited to focal follows with 10 or more observations.

For travel speed, we calculated the parameters of a gamma distribution for each focal follow. To determine the population distribution, the log of the parameters of the gamma distribution was assumed bivariate normal. Using Bayesian inference and the Fortran program MTG (Metropolis within Gibbs sampling), means, variances, and covariance of the bivariate normal were estimated. Priors on means and covariance were uniform. Priors on variances were uniform >0 on the inverse. Sample interval was set to reduce lag-1 autocorrelation to <0.1 for posterior samples. Each of the 15,000 posterior samples of the bivariate normal was used to draw one set of gamma distribution parameters. Those gamma distribution values were then used to draw 10 behavioral posterior values. For ease in programming and later sampling, the posterior samples were found to be gamma distributed. Using the posterior samples, point values were determined for the parameters of the overall gamma distribution with a limit on the maximum value based on data (Table 1).

Surface-dive time was better described as a lognormal distribution. We calculated the mean and standard deviation of the log of surface-dive time for each focal follow. To determine population level surface-dive time, we assumed that the means of the lognormal distributed
normally, and standard deviations were gamma distributed. The parameters of the normal and gamma distributions were estimated jointly using MTG. The prior on the normal mean was uniform. Priors for the gamma parameters and the inverse of the variance of the normal distribution were uniform > 0. Sample interval was set to reduce lag-1 autocorrelation to < 0.1. Each of the 15,000 posterior samples of parameters from the normal and gamma distributions were used jointly to draw one sample of the mean and standard deviation of the lognormal. The lognormal parameters were then used to draw 10 samples of surface-dive time. For ease in programming and later sampling, the parameters of the lognormal distribution of the posterior samples on surface-dive time were then determined with a limit on the minimum and maximum values based on data (Table 1).

For the proportion of time spent diving while feeding, each feeding dive time was divided by its respective surface-dive time. The distribution of the data was best fit with a beta distribution with provided mean and standard deviation (Table 1).
Section S3: The spatial correlation parameter $p_c$ of prey resources

The spatial correlation parameter characterizes the fine scale structure of the resource environment. In the backward iteration, we used three different values, a baseline ($p_c = 0.5$) and then conducted sensitivity analyses for two larger values ($p_c = 0.7$ or $p_c = 0.9$). In the forward Monte Carlo simulation, we need to distinguish between cases in which the animal moves to a point in which energy density is independent of the current value and one in which it is not. In the former case, we sampled from the distribution of energy in the current cell. In the latter case, we needed to compute the probability that the energy density at the new location is the same as the energy density at the location from which the animal moved. To do this, we estimated the distance at which spatial correlation was lost using the prey distributions determined in 2015 (Blanchard et al. accepted); we estimated this to be about 2.5 km for the inshore cells and about 2 km for the offshore cells corresponding to $p_c = 0.5$. 
Section S4: The probability distribution of behavior and association with amphipods

To compute a probability distribution of behavior, we let $V^*(m,l,c,x,t)$ denote the optimal value of fitness given $M_{fat}(t) = m$, $L_{fetus}(t) = l$, and $\tilde{X}(c,t) = x$. That is,

$$V^*(m,l,x,c,t) = \max[V_L(m,l,c,x,t), V_F(m,l,c,x,t), V_{TF}(m,l,c,x,t), V_{c\rightarrow c'}(m,l,c,x,t)]$$

and the fitness cost of different behaviors are

$$
\begin{align*}
\Delta_L(m,l,c,x,t) &= V^*(m,l,c,x,t) - V_L(m,l,c,x,t) \\
\Delta_F(m,l,c,x,t) &= V^*(m,l,c,x,t) - V_F(m,l,c,x,t) \\
\Delta_{TF}(m,l,c,x,t) &= V^*(m,l,c,x,t) - V_{TF}(m,l,c,x,t) \\
\Delta_{c\rightarrow c'}(m,l,c,x,t) &= V^*(m,l,c,x,t) - V_{c\rightarrow c'}(m,l,c,x,t)
\end{align*}
$$

These are all $\geq 0$ and only 0 when the optimal behavior is followed.

We let $p_L(m,l,c,x,t)$, $p_F(m,l,c,x,t)$, $p_{TF}(m,l,c,x,t)$ and $p_{c\rightarrow c'}(m,l,c,x,t)$ denote respectively the probability of leaving the foraging ground entirely, feeding at the current location, traveling within the current cell, or traveling from the current cell $c$ to $c'$ given that a whale is in cell $c$ at time $t$ and that $M_{fat}(t) = m$, $L_{fetus}(t) = l$, and $\tilde{X}(c,t) = x$. To account for the association between gray whales and amphipods (Oliver et al. 1984, Highsmith and Coyle 1992, Dunham and Duffus 2001, Moore et al. 2003, Budnikova and Blokhin 2012), we let $\rho_a(c,t)$ denote a modifier that increased the probability of being in a particular cell when a large proportion of the total energy available came from amphipods (Appendix S1: Table S2). We then set
In these equations the denominator is a normalization constant that ensures that the sum over all the probabilities is 1 (i.e., the whale must do something) and $\zeta$ is a tuning parameter on the errors in decisions. When $\zeta$ is much bigger than any of the costs, then the probabilities in Eq. S7 are essentially a uniform distribution (i.e., behavior is random). Alternatively, when $\zeta$ is much smaller than the smallest cost in Eq. S6, then Eq. S7 will pick out the optimal behavior with a very high probability (or fitness ties with equal probability). We chose a value for $\zeta$ that resulted in an activity budget in the undisturbed forward simulation that approximately matched estimates of the percentage of time spent in each behavioral category derived from field observations during periods of no known anthropogenic disturbance (G. Gailey, unpublished data).

We found $F(m,l,c,x,t)$ by averaging across the fitness values of different behaviors

$$F(m,l,c,x,t) = p_L(m,l,c,x,t)V_L(m,l,c,x,t) + p_F(m,l,c,x,t)V_F(m,l,c,x,t) + p_{TF}(m,l,c,x,t)V_{TF}(m,l,c,x,t) + \sum_{c \neq c'} p_{c \rightarrow c'}(m,l,c,x,t)V_{c \rightarrow c'}(m,l,c,x,t)$$

(S8)
The probability that a whale adopted a particular behavior given her fat mass, the length of the fetus, current location, food density, and time on the feeding ground (Appendix S1: Eq. S7) was the output of the backward iteration that we used in the forward Monte Carlo simulation.
Section S5: Population Size of Pregnant Females

We sampled the estimates of survival and reproduction based on mark-recapture from Cooke (2010); we used medians as mean and estimated 95% posterior intervals from other percentiles and fit beta densities to emulate the distributions described in Cooke (2010). Following Cooke (2010), we used the samples of survival and reproduction and the dominant eigenvector of the Leslie matrix to estimate the proportion of non-calf animals in the "resting or potentially pregnant" category and the proportion of animals in the "lactating" category. We multiplied the non-calf population size from Cooke et al. (2007) by the proportion of individuals in the “resting or potentially pregnant” or “lactating” categories to obtain the number of animals in each of those categories. In the stable age distribution, the number of lactating females was thus a minimum for the number of pregnant whales and the number of pregnant and resting females was a maximum for the number of pregnant whales. We sampled from this range using the results from the Leslie matrix to obtain the probability distribution for the number of pregnant females in a simulated cohort (Appendix S1: Fig. S2). Although the potential range of pregnant females from this procedure was 5-34 whales, the range of 11-22 whales contained about 97% of the probability.
Section S6: Leslie matrix

We simplified the Leslie matrix from Cooke (2010) (Fig. S18, Table S5). Females mature at 6 – 12 years old. Calving state is the period when a female is with a calf. Calves wean at roughly 6 – 8 months old. Pre-calving state indicates a female’s first pregnancy, a resting period two or more years after the last calving event, or a pregnancy two or more years after a calving event. Post-calving state is the year directly after the last calving event. Females that have rested for a year or more have a higher probability of returning with a calf in subsequent years.

Assuming a stable population distribution, we sampled the above transition probability distributions (N = 50000), supplied the sample values in the Leslie matrix, and calculated the dominant eigenvector of the Leslie matrix to estimate the proportion of animals in every category. Using population size estimates from Cooke et al. (2007) (mean = 121, sd = 4.5), we sampled the non-calf population size from a normal distribution and multiplied the proportion in the above categories by that population size. We then projected the populations with defined initial numbers in each demographic group out for 100 years, testing four different scenarios: reduced reproductive rate for 100 years (α and β = 0.003), reduced survival for reproductive females for 100 years (S_{Age > 5} = 0.06), reduced survival for reproductive females for the first year, and no reduction in survival or reproduction. We calculated population size and the probability of extinction after 100 years. Results are in the main text.
Table S1. Length-specific estimates of body mass of adult female gray whales used to estimate metabolic rates (Mass_{Met}), critical (x_{crit}) and maximum (x_{max}) allowed values for fat mass, and fat mass upon arrival at the foraging grounds assuming females arrived with a fat mass that was 20%, 15%, or 10% of their body mass.

<table>
<thead>
<tr>
<th>Length (m)</th>
<th>Mass_{Met} (kg)</th>
<th>x_{crit} (kg)</th>
<th>x_{max} (kg)</th>
<th>Arrival fat mass (kg)</th>
<th>Arrival mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>20%</td>
<td>15%</td>
</tr>
<tr>
<td>11.0</td>
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<td>7,169</td>
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<tr>
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<td>Mass$_{Me}^a$ (kg)</td>
<td>$x_{crit}^b$ (kg)</td>
<td>$x_{max}^b$ (kg)</td>
<td>Arrival fat mass (kg)</td>
<td>Arrival mass (kg)$^c$</td>
</tr>
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<td>15%</td>
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<td>3,912</td>
</tr>
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</table>

$^a$From Villegas-Amtmann et al. (2015)

$^b$Calculated assuming mass estimates in the second column represented whales with a fat mass of 35% of their body mass. This assumption was based on the fact that data were derived from animals on their southbound migration where they presumably would be at their fattest

$^c$Calculated based on estimated structural mass derived from second column and arrival fat mass of 20% of body mass
Table S2. Summary of prey energy data by time period and cell, including the estimated mean prey energy density (MJ m$^{-2}$) from a fit of a log-normal distribution to the data of six primary prey species, and the proportion of energy from amphipods (Maresh et al. accepted). The proportion of energy from amphipods was calculated by dividing the prey energy from amphipods m$^{-2}$ by the total prey energy m$^{-2}$ per time period and cell. Means are presented ± SD with minimum and maximum values shown in parentheses. Time periods are as follows: May 15 – July 14 (Early), July 15 – August 26 (Mid), August 27 – November 7 (Late), May 15 – November 7 (All, indicating low temporal resolution of data). See Maresh et al. (accepted) for a detailed description of benthic data collection and analysis.

<table>
<thead>
<tr>
<th>Period</th>
<th>Cell</th>
<th>Lognormal values</th>
<th>Energy density (MJ m$^{-2}$)</th>
<th>Proportion amphipods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>1</td>
<td>-1.37 ± 0.70</td>
<td>0.32 ± 0.23 (0.02 - 1.52)</td>
<td>0.45 ± 0.32</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-1.10 ± 0.60</td>
<td>0.40 ± 0.26 (0.02 - 2.34)</td>
<td>0.50 ± 0.26</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-1.15 ± 0.73</td>
<td>0.41 ± 0.32 (0.02 - 2.36)</td>
<td>0.43 ± 0.27</td>
</tr>
<tr>
<td>Mid</td>
<td>1</td>
<td>-1.67 ± 0.76</td>
<td>0.24 ± 0.20 (&lt;0.01 - 1.43)</td>
<td>0.53 ± 0.35</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-1.31 ± 0.76</td>
<td>0.36 ± 0.32 (0.01 - 5.26)</td>
<td>0.57 ± 0.28</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.91 ± 0.64</td>
<td>0.49 ± 0.34 (0.02 - 2.78)</td>
<td>0.37 ± 0.28</td>
</tr>
<tr>
<td>Late</td>
<td>1</td>
<td>-1.70 ± 0.64</td>
<td>0.22 ± 0.16 (0.01 - 1.38)</td>
<td>0.33 ± 0.35</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-1.14 ± 0.68</td>
<td>0.40 ± 0.30 (0.01 - 3.01)</td>
<td>0.54 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-1.41 ± 0.90</td>
<td>0.35 ± 0.33 (&lt;0.01 - 2.45)</td>
<td>0.47 ± 0.31</td>
</tr>
<tr>
<td>All</td>
<td>2</td>
<td>-1.01 ± 0.14</td>
<td>0.24 ± 0.29 (&lt;0.01 - 1.71)</td>
<td>0.24$^a$</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>-1.98 ± 1.26</td>
<td>0.24 ± 0.29 (&lt;0.01 - 1.71)</td>
<td>0.22 ± 0.30</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>-2.07 ± 1.32</td>
<td>0.25 ± 0.34 (&lt;0.01 - 2.39)</td>
<td>0.26 ± 0.30</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-1.24 ± 1.08</td>
<td>0.46 ± 0.51 (&lt;0.01 - 3.30)</td>
<td>0.10 ± 0.16</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-0.31 ± 0.85</td>
<td>1.05 ± 1.06 (0.02 - 14.14)</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>-0.77 ± 1.49</td>
<td>0.98 ± 1.38 (&lt;0.01 - 8.63)</td>
<td>0.22 ± 0.30</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.20 ± 1.12</td>
<td>1.93 ± 2.08 (0.02 - 12.37)</td>
<td>0.26 ± 0.30</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>0.78 ± 1.11</td>
<td>3.52 ± 3.90 (&lt;0.01 - 24.54)</td>
<td>0.10 ± 0.16</td>
</tr>
</tbody>
</table>

$^a$Average of cells 4 and 6
Table S3. Mean probability of female and calf survival ± SD and associated Cohen’s $d$ values for 30 disturbance scenarios. Calf survival represents the probability a fetus will survive to return to the foraging grounds in the following year. Mean and SD were calculated by averaging across the 100 replicate populations.

<table>
<thead>
<tr>
<th>Disturbance Scenario</th>
<th>Probability of survival</th>
<th>Cohens’s $d$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Calf</td>
</tr>
<tr>
<td>Undisturbed</td>
<td>0.99 ± 0.02</td>
<td>0.29 ± 0.22</td>
</tr>
<tr>
<td>1 – Cells 1 &amp; 2 Early 0.3</td>
<td>0.99 ± 0.02</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>2 – Cells 1 &amp; 2 Early 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>3 – Cells 1 &amp; 2 Late 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>4 – Cells 1 &amp; 2 Late 0.6</td>
<td>0.98 ± 0.06</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>5 – Cells 3 &amp; 4 Early 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>6 – Cells 3 &amp; 4 Early 0.6</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>7 – Cells 3 &amp; 4 Late 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>8 – Cells 3 &amp; 4 Late 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>9 – Cells 5 &amp; 6 Early 0.3</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>10 – Cells 5 &amp; 6 Early 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>11 – Cells 5 &amp; 6 Late 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>12 – Cells 5 &amp; 6 Late 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.29 ± 0.22</td>
</tr>
<tr>
<td>13 – Cells 1 to 4 Early 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>14 – Cells 1 to 4 Early 0.6</td>
<td>0.99 ± 0.02</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>15 – Cells 1 to 4 Late 0.3</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>16 – Cells 1 to 4 Late 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.29 ± 0.22</td>
</tr>
<tr>
<td>17 – Cells 1,2,5,6 Early 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.29 ± 0.22</td>
</tr>
<tr>
<td>18 – Cells 1,2,5,6 Early 0.6</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>19 – Cells 1,2,5,6 Late 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>20 – Cells 1,2,5,6 Late 0.6</td>
<td>0.99 ± 0.02</td>
<td>0.27 ± 0.23</td>
</tr>
<tr>
<td>21 – Cells 3 to 6 Early 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.29 ± 0.22</td>
</tr>
<tr>
<td>22 – Cells 3 to 6 Early 0.6</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>Disturbance Scenario</td>
<td>Probability of survival</td>
<td>Cohens’s d</td>
</tr>
<tr>
<td>----------------------</td>
<td>------------------------</td>
<td>------------</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Calf</td>
</tr>
<tr>
<td>23 – Cells 3 to 6 Late 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>24 – Cells 3 to 6 Late 0.6</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>25 – Cells 1 to 2 (Early), 3 to 4 (Late) 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>26 – Cells 1 to 2 (Early), 3 to 4 (Late) 0.6</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>27 – Cells 1 to 2 (Early), 5 to 6 (Late) 0.3</td>
<td>0.99 ± 0.03</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>28 – Cells 1 to 2 (Early), 5 to 6 (Late) 0.6</td>
<td>0.99 ± 0.02</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>29 – Cells 3 to 4 (Early), 5 to 6 (Late) 0.3</td>
<td>0.99 ± 0.05</td>
<td>0.28 ± 0.22</td>
</tr>
<tr>
<td>30 – Cells 3 to 4 (Early), 5 to 6 (Late) 0.3</td>
<td>0.99 ± 0.04</td>
<td>0.28 ± 0.22</td>
</tr>
</tbody>
</table>
Table S4. Mean probability of female and calf survival ± SD and Cohen’s $d$ values for the 12 sensitivity scenarios related to exclusion from one or more cells, variation in mean arrival date and fat mass, and metabolic expenditure. The same disturbance scenario (Cells 1, 2, 5, 6 Late 0.6) was used for all sensitivity analyses. Calf survival represents the probability a fetus will survive to return to the foraging grounds in the following year. Mean and SD were calculated by averaging across the 100 population replicates.

<table>
<thead>
<tr>
<th>Sensitivity Scenario</th>
<th>Female survival</th>
<th></th>
<th></th>
<th>Calf survival</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed</td>
<td>Disturbed</td>
<td>Cohen’s $d$</td>
<td>Undisturbed</td>
<td>Disturbed</td>
<td>Cohen’s $d$</td>
</tr>
<tr>
<td>No Cell 8</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.04</td>
<td>0.13</td>
<td>0.30 ± 0.21</td>
<td>0.30 ± 0.21</td>
<td>0.02</td>
</tr>
<tr>
<td>No Cell 9</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.03</td>
<td>0.03</td>
<td>0.30 ± 0.21</td>
<td>0.30 ± 0.21</td>
<td>0.00</td>
</tr>
<tr>
<td>No Cell 10</td>
<td>0.99 ± 0.04</td>
<td>0.98 ± 0.06</td>
<td>0.12</td>
<td>0.29 ± 0.22</td>
<td>0.29 ± 0.22</td>
<td>0.02</td>
</tr>
<tr>
<td>No Cell 11</td>
<td>0.91 ± 0.22</td>
<td>0.89 ± 0.26</td>
<td>0.11</td>
<td>0.00 ± 0.01</td>
<td>0.00 ± 0.01</td>
<td>-0.02</td>
</tr>
<tr>
<td>No Offshore cells</td>
<td>0.06 ± 0.16</td>
<td>0.06 ± 0.16</td>
<td>0.01</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.15</td>
</tr>
<tr>
<td>Arrival - June 1</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.04</td>
<td>0.04</td>
<td>0.26 ± 0.22</td>
<td>0.27 ± 0.21</td>
<td>-0.03</td>
</tr>
<tr>
<td>Arrival - June 15</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.03</td>
<td>-0.02</td>
<td>0.25 ± 0.20</td>
<td>0.25 ± 0.21</td>
<td>0.03</td>
</tr>
<tr>
<td>$pc = 0.7$</td>
<td>0.99 ± 0.02</td>
<td>0.99 ± 0.04</td>
<td>-0.10</td>
<td>0.30 ± 0.22</td>
<td>0.30 ± 0.22</td>
<td>0.00</td>
</tr>
<tr>
<td>$pc = 0.9$</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.06</td>
<td>-0.06</td>
<td>0.31 ± 0.21</td>
<td>0.30 ± 0.21</td>
<td>0.01</td>
</tr>
<tr>
<td>Arrival fat mass - 10%</td>
<td>0.92 ± 0.25</td>
<td>0.90 ± 0.26</td>
<td>0.06</td>
<td>0.22 ± 0.24</td>
<td>0.22 ± 0.24</td>
<td>0.01</td>
</tr>
<tr>
<td>Arrival fat mass - 15%</td>
<td>0.98 ± 0.06</td>
<td>0.98 ± 0.07</td>
<td>-0.04</td>
<td>0.25 ± 0.23</td>
<td>0.25 ± 0.23</td>
<td>-0.01</td>
</tr>
<tr>
<td>Metabolism - 50% reduction</td>
<td>0.99 ± 0.03</td>
<td>0.99 ± 0.04</td>
<td>0.06</td>
<td>0.36 ± 0.17</td>
<td>0.36 ± 0.18</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table S5. Leslie matrix for the population. Transition probabilities were beta distributed based on posterior distributions of parameters from a mark-recapture model (Table 3 in Cooke 2010).

<table>
<thead>
<tr>
<th>Females Transition from / to</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age 1</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Age 2</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Age 3</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Age 4</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Age 5</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Maturing</td>
<td>S(1 - µ)</td>
<td>Sµ</td>
</tr>
<tr>
<td>Pre-calving</td>
<td>S(1 - α)</td>
<td>Sa</td>
</tr>
<tr>
<td>Calving</td>
<td>Sf</td>
<td></td>
</tr>
<tr>
<td>Post-calving</td>
<td>S(1 - β)</td>
<td>Sβ</td>
</tr>
</tbody>
</table>

We used medians as means and estimated 95% posterior intervals from other provided percentiles:

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter description</th>
<th>Mean</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_f</td>
<td>Survival probability: calf (age 0.5) to age 1.5</td>
<td>0.69</td>
<td>0.0045</td>
</tr>
<tr>
<td>S</td>
<td>Survival probability (age 1.5+)</td>
<td>0.985</td>
<td>0.00001</td>
</tr>
<tr>
<td>µ</td>
<td>Maturation probability (annual, from age 6)</td>
<td>0.35</td>
<td>0.02</td>
</tr>
<tr>
<td>α</td>
<td>Calving probability (for newly mature and rested animals)</td>
<td>0.62</td>
<td>0.014</td>
</tr>
<tr>
<td>β</td>
<td>Calving probability (after 1 or more years resting)</td>
<td>0.51</td>
<td>0.007</td>
</tr>
<tr>
<td>f</td>
<td>Calf female sex ratio</td>
<td>0.44</td>
<td>0.0012</td>
</tr>
</tbody>
</table>
Figure S1. Survival functions for a pregnant female (a) and her fetus (b). In a, the probability of survival depended on a female’s fat mass (kg), her length (not shown), and the day of departure from the foraging ground. As such, a pregnant female needed to have progressively higher fat reserves to achieve the same probability of survival if she departed from the foraging grounds earlier in the season. For ease of presentation, the survival function for a single female length (14 m) is shown. In b, the survival of her calf was dependent on fetal length, maternal fat mass, and the day of departure from the foraging grounds (not shown). As such, females with greater fat reserves had a higher probability of calf survival at a given fetal length and departure day. Survival based solely on fetal length is also shown for comparison. As described in the main text, we use these survival functions to compute the terminal fitness function for the SDP model.
Figure S2. Example of the probability distribution of behavior from the backward iteration as a function of female fat mass (kg), shown for a 13.0 m female with a fetus of 2.915 m encountering a prey patch of energy class 4 in Cell 11 on day 140 (October 1st). A female encountering energy class 4 in Cell 11 expected to gain the maximum allowable fat mass in that time step. The probability of “Feeding” (Feed) or “Traveling or Feeding” (MoveFeed) was high, particularly at exceptionally low or intermediate fat masses, presumably due to an increased risk of starvation or because of considerable fitness gains, respectively. The category Move11 is empty because the female is already in Cell 11.
Figure S3. The probability distribution of pregnant females used to create populations in the forward Monte Carlo simulation.
Figure S4. The distribution of prey energy density within each cell used to characterize the prey energy landscape experienced by Sakhalin Island gray whales on the foraging grounds. A single distribution is shown for each cell for ease of visualization; temporal variation within cells is shown in Appendix S1: Fig. S5. Note the differences in scale between the nearshore and offshore cells.
Figure S5. Temporal variation in prey energy density for the three nearshore cells for which samples were collected at more than one time period. Time periods are as follows: May 15 – July 14 (Early), July 15 – August 26 (Mid), August 27 – November 7 (Late).
Figure S6. Temporal variation in the distribution of whales in the nearshore and offshore cells for four different scenarios. Individual points represent the percentage of the population (summed across all 100 population replicates) in either nearshore or offshore cells for each scenario per time step. Note this includes females “Feeding”, “Traveling or Feeding”, and those “Traveling” between two cells in the same cell type (nearshore, offshore).
Figure S7. Net fat mass change across the foraging season as a function of female length for the baseline and each sensitivity scenario. Gray dots represent values for individual females and colored points the average with 95% confidence intervals. Baseline values are shown by dark gray diamonds in each plot for comparison.
Figure S8. The proportion of time a female spent foraging (“Feeding” + “Traveling and Feeding”) as a function of female length for each sensitivity scenario. Gray dots represent values for individual females and colored points the average with 95% confidence intervals. Baseline values are shown by dark gray diamonds in each plot for comparison.
**Figure S9.** Departure fat mass relative to maximum allowed fat mass as a function of female length for each sensitivity scenario. Gray dots represent values for individual females and colored points the average with 95% confidence intervals. Baseline values are shown by dark gray diamonds in each plot for comparison.
Figure S10. The probability of female survival as a function of female length for each sensitivity scenario. Gray dots represent values for individual females and colored points the average with 95% confidence intervals. Baseline values are shown by dark gray diamonds in each plot for comparison.
Figure S11. The probability a fetus would survive to return to the foraging grounds in its first year (calf survival) as a function of female length for each sensitivity scenario. Gray dots represent values for individual females and colored points the average with 95% confidence intervals. Baseline values are shown by dark gray diamonds in each plot for comparison.
Figure S12. The mean number of disturbances per whale as a function of female length for 30 different disturbance scenarios under the baseline parameters.
Figure S13. The mean number of disturbances per whale as a function of female length for 12 different sensitivity scenarios. The disturbance scenario involved simultaneous disturbance to Cells 1, 2, 5 and 6 late in the season at a 60% probability of disturbance.
Figure S14. Temporal variation in cell type use by pregnant gray whale females in the absence of disturbance for the baseline scenario for three whale lengths. Individual points represent the percentage of whales in each length category (summed across all 100 population replicates) in either nearshore or offshore cells per time step. Note this includes females “Feeding”, “Traveling and Feeding”, and those “Traveling” between two cells in the same cell type (nearshore, offshore).
Figure S15. Cohen’s $d$ values showing the effect of disturbance on female (a) and calf (b) survival as a function of female length for the baseline scenario and a subset of sensitivity scenarios. Values greater than zero indicate survival was higher in the undisturbed than the disturbed scenario, with gray boxes depicting the value indicative of some adverse effect on survival estimates. This figure contrasts with Fig. 6 in that it uses all 100 replicates for female length.
Figure S16. The relationship between the Cohen’s $d$ value for the probability of female (a) or calf (b) survival and the mean number of disturbances experienced by a whale for the baseline (purple dots) and sensitivity (blue triangles) scenarios.
Figure S17. The relationship between the Cohen’s $d$ value for the probability of female (a) or calf (b) survival and the mean number of disturbances experienced by a whale. Separate plots are shown for females of three different lengths. In all plots, purple dots represent disturbance scenarios using baseline parameter values and blue triangles represent disturbance using sensitivity parameter values.
Figure S18. Stage-structured model of the population.
Literature Cited


Accepted. Benthic studies adjacent to Sakhalin Island, Russia, 2015 I: benthic biomass and community structure in the nearshore gray whale feeding ground. Environmental Monitoring and Assessment.


Villegas-Amtmann, S., L. K. Schwarz, J. L. L. Sumich, and D. P. Costa. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to