

A Dynamic State Model of Migratory Behavior and Physiology to Assess the Consequences of Environmental Variation and Anthropogenic Disturbance on Marine Vertebrates

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ABSTRACT: Integrating behavior and physiology is critical to formulating new hypotheses on the evolution of animal life-history strategies. Migratory capital breeders acquire most of the energy they need to sustain migration, gestation, and lactation before parturition. Therefore, when predicting the impact of environmental variation on such species, a mechanistic understanding of the physiology of their migratory behavior is required. Using baleen whales as a model system, we developed a dynamic state variable model that captures the interplay among behavioral decisions, energy, reproductive needs, and the environment. We applied the framework to blue whales (*Balaenoptera musculus*) in the eastern North Pacific Ocean and explored the effects of environmental and anthropogenic perturbations on female reproductive success. We demonstrate the emergence of migration to track prey resources, enabling us to quantify the trade-offs among capital breeding, body condition, and metabolic expenses. We predict that periodic climatic oscillations affect reproductive success less than unprecedented environmental changes do. The effect of localized, acute anthropogenic impacts depended on whales' behavioral response to the disturbance; chronic, but weaker, disturbances had little effect on reproductive success. Because we link behavior and vital rates by modeling individuals' energetic budgets, we provide a general framework to investigate the ecology of migration and assess the population consequences of disturbance, while identifying critical knowledge gaps.

Keywords: bioenergetic modeling, environmental changes, marine mammal, population consequences of disturbance, stochastic dynamic programming, uncertainty.

Introduction

Animals have to balance behavioral decisions against their body condition, their reproductive state, and the external environment (Houston and McNamara 1999; Clark and Mangel 2000). In some species and populations, migratory behavior has evolved to achieve this trade-off (Alerstam et al. 2003; Lennox et al. 2016). Migration allows individuals to exploit irregular resources resulting from seasonal changes in the environment and to ensure that the birth of their offspring occurs in areas likely to increase the probability of reproductive success (e.g., where predation risk is minimized; Alerstam et al. 2003). When breeding habitats do not provide sufficient food resources to sustain them, individuals can store energy as body reserves to support periods in which foraging is reduced. Pure capital breeders represent an extreme case in which the foraging habitat is completely decoupled from the breeding habitat (Stephens et al. 2014).

The complex life-history patterns of migratory animals result in wide-ranging movements over long time frames, which can hinder our ability to investigate even basic aspects of their biology and ecology. This is particularly true for marine environments, where animals are often inaccessible to human observers at the spatial and temporal scales relevant to the species' life history (Hussey et al. 2015). Yet, these species could be more susceptible to natural and

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human-induced fluctuations in environmental conditions because of the physiological constraints of migration (Lennox et al. 2016). Thus, the integration of behavioral and physiological research has been proposed as a way to gain a deeper understanding of biology (Weiner 1992) and to effectively tackle current conservation challenges (Cooke et al. 2014).

State-dependent behavioral and life-history theory, implemented via stochastic dynamic programming (SDP) and forward Monte Carlo (MC) simulations, provides a robust framework for quantifying the fitness implications of behavior and characterizing behavioral responses to natural environmental variation in different contexts (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). SDP models can be used to investigate optimal decisions based on an individual's internal physiological state and the state of the external environment over the course of the reproductive cycle. This is done by linking behavior to a measure of Darwinian fitness that accounts for both survival and reproduction (Mangel and Clark 1988). Since SDP models explicitly acknowledge the physiological basis of behavior, they can be employed to elucidate the biology of poorly known species and generate new, testable hypotheses on the evolution of behavioral and life-history strategies, while also identifying the parameters to which the results and the corresponding uncertainty are most sensitive (Mangel and Clark 1988; Weiner 1992). Moreover, disturbance from multiple stressors or rapid environmental change can be simulated under the assumption that anthropogenic activities are not part of the evolutionary history of these species (McHuron et al. 2017).

In this study, we present an SDP framework to model the movement, foraging, and reproductive behavior of a migratory mammal through the various phases of its breeding cycle. We use long-lived female baleen whales, specifically, eastern North Pacific (ENP) blue whales (*Balaenoptera musculus*), as a case study to demonstrate the strength of the approach. In particular, we highlight the ability of the SDP framework to provide new insights into the biology of migratory animals for which it is challenging to collect empirical evidence. Furthermore, there are growing concerns regarding the effects of global climate changes (Hazen et al. 2012; Poloczanska et al. 2013; IPCC 2014) and expanding human activities on the marine environment (Halpern et al. 2008; Maxwell et al. 2013). Our case study also illustrates the value of predictive models that capture fundamental biological and ecological processes to support scientifically sound management measures (New et al. 2014; Christiansen and Lusseau 2015; King et al. 2015; Pirota et al. 2015; Villegas-Amtmann et al. 2015), despite large gaps in empirical knowledge (Harwood and Stokes 2003; Inger et al. 2009).

Under most regulatory frameworks, the ways in which baleen whales may change their diving, vocal, or movement

behavior in response to disturbance (Nowacek et al. 2007; Goldbogen et al. 2013; DeRuiter et al. 2016) are relevant only if they alter the population's status (e.g., European Habitats Directive 92/43/EEC, US Marine Mammal Protection Act). Assessing the population consequences of disturbance requires a mechanistic understanding of how behavior affects an individual's energy budget (National Research Council 2005; New et al. 2014; National Academies of Sciences 2016) and how this varies with prey availability (Miller et al. 2011; Williams et al. 2013; Seyboth et al. 2016). Since nutritional status and body condition are tightly associated with survival and reproductive success (Lockyer 1986), changes in behavior and physiology can affect an individual's fitness and reverberate at the population level (New et al. 2014).

We show how SDP methods can be used to develop testable hypotheses regarding the mechanisms that drive the evolution of behavioral and physiological strategies, as well as assess responses to fluctuations in the environment. This solid characterization of the population's ecology and evolved responses to environmental variation enabled us to investigate the consequences of anthropogenic disturbance on vital rates. Our approach provides insights into biological processes that are difficult to sample directly, such as the energetic basis of migration and reproduction in baleen whales. In addition, it identifies critical knowledge gaps, offers guidance on how to address situations where incomplete information is available, and could be extended to other species with comparable life histories.

Methods

Case Study

Developing the model required a series of simplifying assumptions that may not fully reflect the biology of the population under analysis. These arise from the need to maintain model tractability and from uncertainty in the available data. The use of simplified biological assumptions will be common when dealing with species like baleen whales, where the model must rely on the existing literature and any potential associated biases. The assumptions used in the model can be interpreted as research hypotheses, which can be addressed by targeted data collection.

ENP blue whales are believed to constitute the largest remnant population of this species (Thomas et al. 2016) and, in their evolutionary history, have experienced environmental fluctuations (e.g., El Niño Southern Oscillation [ENSO]) and longer-term climate changes (Hazen et al. 2012) that affect prey density and distribution. In recent ecological time, they have been exposed to a series of anthropogenic stressors, including shipping traffic, military exercises, oil and gas exploration, and proposed offshore renewable developments (Thomas et al. 2016). How the effects of these human activities may interact with environmental fluctuations is unclear.

ENP blue whales spend summer months along the coast from California to British Columbia (fig. 1), feeding on high densities of krill (euphausiids) in the California Current (Croll et al. 2005). In this area, whales primarily target adult euphausiids belonging to the species *Euphausia pacifica* and *Thysanoessa spinifera* (Fiedler et al. 1998). Satellite telemetry data suggest that individuals follow the seasonal increase in productivity (Bailey et al. 2010; Irvine et al. 2014), which is characterized by a peak that shifts to higher latitudes as the summer progresses (Schwing et al. 1996; Henson and Thomas 2007). In late autumn, blue whales migrate to their breeding grounds in the Gulf of California, off the southern tip of the

Baja California Peninsula, and near the Costa Rica Dome (Bailey et al. 2010).

In contrast to pure capital breeders (Stephens et al. 2014), ENP blue whales continue feeding in their breeding grounds, where substantial euphausiid populations occur throughout the winter (Gendron 1992; Etnoyer et al. 2006). Most whales leave the breeding grounds in spring, moving northward, primarily along the coast, stopping for several days to feed on krill available along the Baja California Peninsula (Bailey et al. 2010). The foraging patches off Baja California and in the Gulf of California are mainly dominated by the subtropical species *Nyctiphanes simplex*, which is smaller and thus

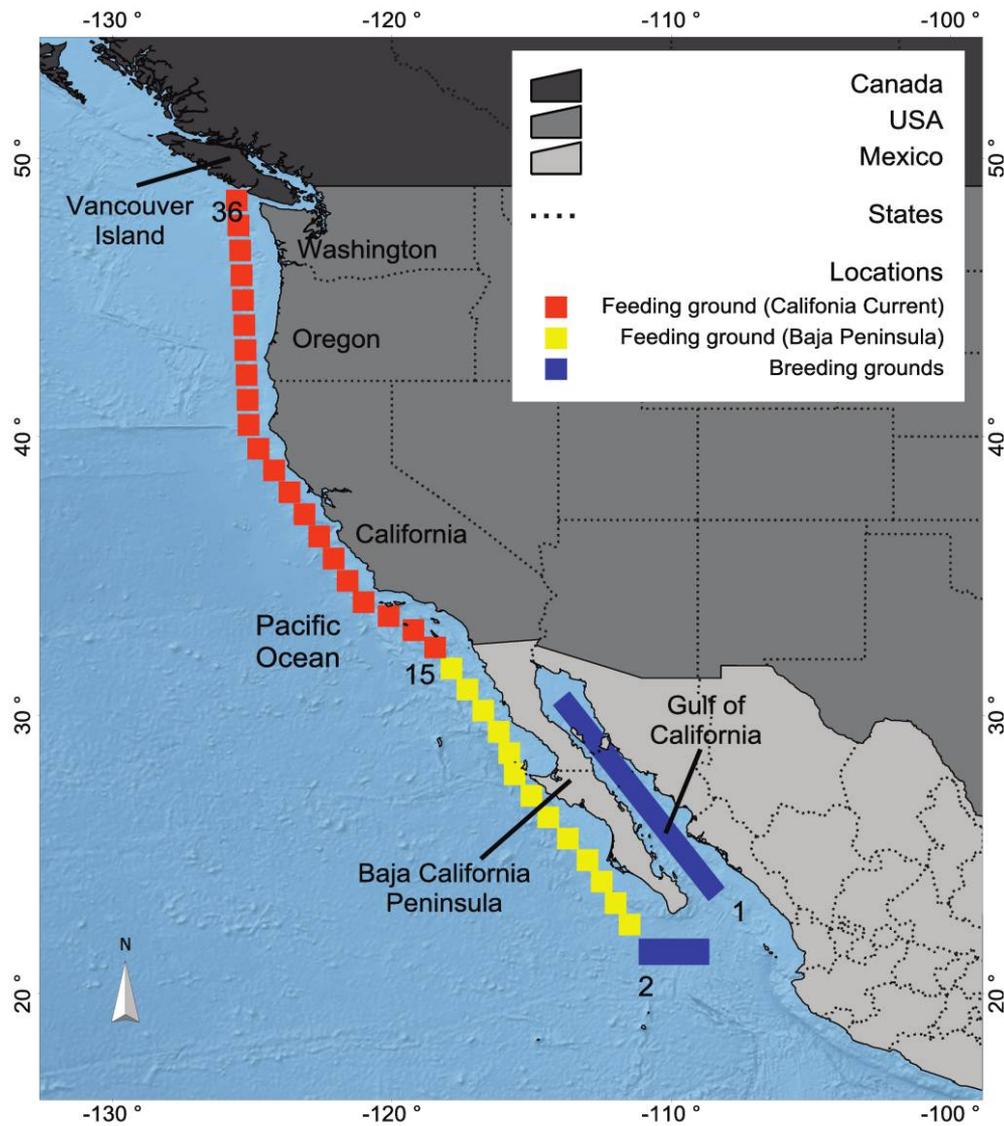


Figure 1: Map of the study area, showing the 36 100 × 100-km locations used in the model. Relevant locations are numbered for reference. Larger boxes for the breeding grounds indicate whales’ ability to roam within those areas.

less energy-rich than the euphausiids targeted in the California Current but appears to be subject to fewer seasonal fluctuations (Gendron 1992; Gómez-Gutiérrez 1995). In this study, we focus on the subset of the population that breeds in the Gulf of California and off the southern tip of Baja California because it is unclear what proportion of the ENP population uses the Costa Rica Dome and whether the region supports a separate, nonmigrating population of blue whales (Calambokidis et al. 2009).

Mating in blue whales is thought to occur in low-latitude breeding grounds in winter (Lockyer 1981; fig. 1). Gestation lasts for 11 months, during which a female has to acquire significant energy reserves to support gestation, migration to the feeding grounds and back, to the breeding grounds (where birth is thought to occur), and part of the subsequent lactation (Lockyer 1981). Lactation is extremely costly in marine mammals, since the calf has to rapidly accumulate lean tissues to grow as well as fat mass for insulation and to sustain its energy needs in the transition to autonomous feeding (Oftedal 1997). There are no data on the duration of lactation in ENP blue whales, so we used information from Antarctic blue whales (*Balaenoptera musculus intermedia*), whose calves follow their mothers on the spring migration and are weaned on the feeding grounds at 7 months (Lockyer 1981). The amount of energy a female transfers to her calf during lactation is expected to affect her offspring's size and condition at weaning and, thus, its survival probability (e.g., McMahan et al. 2003; Miller et al. 2011). Since a female cannot accrue all the necessary energy for reproduction within the breeding area, the accumulation of sufficient reserves in the feeding grounds is critical for the success of a reproductive event (a self-sufficient weaned calf) and, ultimately, a female's reproductive fitness (interpreted as offspring recruited to the population; New et al. 2014).

Stochastic Dynamic Programming Model

Our model covers one reproductive cycle, that is, the period in a female's life history ranging from her departure from the breeding ground (90-days pregnant), through gestation of the fetus while migrating to the feeding grounds and back, to the birth of the calf and the end of lactation. The time horizon is, therefore, $T = 454$ days, between April 1 in the first year and the end of June of the following year (date of weaning). A whale shifts from pregnancy to lactation at $t_b = 244$, when the calf is born, fixed here for simplicity. On each day, a whale may stay in her current location to feed and rest, travel forward for an entire day to the next location, or travel backward to the previous location. On the breeding grounds, a whale may also move within the corresponding location, which captures whales' roaming behavior in these areas during winter to access food or mates (Bai-

ley et al. 2010). On days when she does not travel, there will be some movement within the location, but we assume this movement involves energy expenditure that is comparable to resting (Williams 1999).

State Variables

Full details on the state variables and all associated parameters are provided in appendix A (apps. A–D are available online). The state variables (table 1) are

a) Blubber mass (kg) of the female at time t , $X(t) = x$, which is a measure of the female's energy stores (Lockyer 1986; Miller et al. 2011; Williams et al. 2013). This can vary between a minimum of $x_{\min} = 2,000$ kg and a maximum of $x_{\max} = 22,000$ kg (Lockyer 1976).

b) Current location, $L(t) = l$, simplified as the position along a south-to-north axis representing the range over which the species migrates. This corresponds to the Gulf of California and the southern tip of Baja California in the south, which are the winter breeding grounds, to the waters south of Vancouver Island, which is the northernmost extent of the summer migration. Each location corresponds to a patch size of 100 km by 100 km (Bailey et al. 2010; Wiedenmann et al. 2011). Within the locations representing the breeding grounds, whales can roam and take part in all relevant behaviors, including feeding.

c) Current patch type, $I(t) = i$. There are three patch types, based on available prey species: low-quality food patches (*N. simplex*), high-quality food patches (*T. spinifera* and *E. pacifica*), and patches with no food. Patch quality is determined by the differences in the size of krill species, which results in variation in the total available biomass and, thus, the energy a female acquires per unit of water engulfed. A female that travels for the day has a probability $\lambda(l, i)$ of finding patch type i in location l . We estimated this probability using existing long-term satellite telemetry data (Mate et al. 1999; Bailey et al. 2010; Irvine et al. 2014; app. A; telemetry data available via the Animal Telemetry Network (<http://oceanview.pfeg.noaa.gov/ATN/>)). Given current patch type i , location l , and day t , a whale that stays in the patch and feeds has a probability $p(i, l, t, j)$ of encountering krill density j . The probability $p(i, l, t, j)$ varies spatially and seasonally to reflect yearly fluctuations in the environment along the migratory route. We used the upwelling index provided by the Environmental Research Division, Southwest Fisheries Science Center, NOAA Fisheries, as a proxy for this variable (Schwing et al. 1996; figs. A2, A3; figs. A1–A3 are available online) and assumed that whales can sense prey density and distribution in a patch.

d) Blubber mass of the calf $M(t) = m$, expressed as a proportion of its total mass at time t . This can vary between $m_{\min} = 0.05$ and $m_{\max} = 0.44$ and only applies during lactation.

Table 1: Value of the state variables and associated parameters

State variable, parameter	Description	Value	Reference
Blubber mass:			
x_{\max}	Max. blubber mass	22,000 kg ^a	Lockyer 1976, 1981
x_{\min}	Min. blubber mass	2,000 kg ^a	Wiedenmann et al. 2011
x_{abo}	Threshold mass for abortion	8,000 kg ^a	Lockyer 1976, 1981
x_{lac}	Threshold mass for lactation	8,000 kg ^a	Lockyer 1976, 1981
Location:			
Breeding ground, Gulf of California and off southern tip of Baja California	...	1–2	Bailey et al. 2010
Feeding ground, Baja California	...	3–14	Bailey et al. 2010
Feeding ground, California Current	...	15–36	Bailey et al. 2010
d	Location radius and distance covered per day	100 km	Bailey et al. 2010; Braithwaite et al. 2015
Patch type:			
$\lambda(l)$	Vector of probabilities of encountering different patch types (given location l)	(0.6, 0, 0.4) for l in [1,14]; (0, 0.7, 0.3) for l in [15,36]	Analysis of satellite tracking data
Low-quality food patch type (<i>Nyctiphanes simplex</i>)	...	1	...
High-quality food patch type (<i>Thysanoessa spinifera</i> and <i>Euphausia pacifica</i>)	...	2	...
No food patch type	...	3	...
Calf's proportion of blubber mass:			
m_{\max}	Max. % blubber mass of calf	0.44	Reilly and Fedak 1990; Noren and Mangel 2004
m_{\min}	Min. % blubber mass of calf	0.05	Whittemore 1998; Malavear 2002
m_{50}	% blubber mass of calf at which survival probability is 0.5	0.27	Lockyer 1976, 1981 ^a
γ	Steepness of fitness function	8	...

^a These values were derived from the cited source as described in app. A.

Fitness Metric

We let $\varphi_s(M(T) = m)$ denote the probability of a calf recruiting into the population, given its blubber as proportion of total mass is m at the time of weaning (T). Assuming that $\varphi_s(m)$ is sigmoidal, we set

$$\varphi_s(m) = \frac{m^\gamma}{m^\gamma + m_{50}^\gamma}, \quad (1)$$

where γ determines the steepness of the curve and m_{50} is the inflection point, at which the proportion of the calf's mass that is blubber results in a 50% chance of the calf recruiting (fig. A1).

Prior to calf recruitment, the female is lactating. We define the fitness function when lactating as

$$F_{\text{lac}}(x, m, l, i, t) = \max E\{\varphi_s(M(T)) | X(t) = x, M(t) = m, L(t) = l, I(t) = i\}, \quad (2)$$

that is, the maximum expected value of the terminal fitness taken over all possible behavioral decisions and environmental stochasticity, given the current value of the state variables $X(t) = x$, $M(t) = m$, $L(t) = l$, and $I(t) = i$. If we define $V_b(x, m, l, i, t)$ as the fitness value of behavioral choice b_i during lactation (stay, move forward, move backward, or move within the breeding location), then

$$F_{\text{lac}}(x, m, l, i, t) = \max\{V_b(x, m, l, i, t)\}. \quad (3)$$

Because calves have limited swimming abilities in the first weeks after birth (e.g., Cartwright and Sullivan 2009), we set an arbitrary threshold of lean mass (4,500 kg) that the calf must reach before being able to travel outside the breeding grounds with its mother. This results in the mother-calf pairs staying in the breeding grounds for the first 40 days after parturition.

If, at any time during lactation, the mother's blubber mass is equal or below the starvation threshold x_{\min} , she

dies. Her calf can survive depending on its current value of m and the energy required to survive and grow until 7 months, when weaning would have occurred. Finally, the dependent calf dies whenever the proportion of its mass that is blubber falls below 0.05; that is,

$$F_{\text{lac}}(x, m, l, i, t) = 0 \text{ if } m \leq m_{\text{min}}. \quad (4)$$

Prior to lactation, the female is pregnant. We define fitness when pregnant, $F_{\text{preg}}(x, l, i, t)$, in analogy to equation (2). Given the current value of the state variables $X(t) = x$, $L(t) = l$, and $I(t) = i$, the fitness function for the pregnancy phase, $F_{\text{preg}}(x, l, i, t)$, is 0 if $x < x_{\text{abo}}$, where x_{abo} is the threshold level of blubber mass below which a fetus is aborted. Abortion can occur at any time during pregnancy, although for simplicity, the energy contained in the fetus cannot be reabsorbed. If we let $V_{b_p}(x, l, i, t)$ denote the fitness value of behavioral choice b_p during pregnancy, then

$$F_{\text{preg}}(x, l, i, t) = \max\{V_{b_p}(x, l, i, t)\}. \quad (5)$$

We linked the two phases (lactation and pregnancy) using sequential coupling (Mangel and Clark 1988; Clark and Mangel 2000). On the last day of the pregnancy ($t = 243$), a female needs to be in the breeding ground, otherwise her fitness is set to 0 (i.e., the newborn calf dies). The fitness at the end of pregnancy defines the expected fitness at the beginning of lactation:

$$F_{\text{preg}}(x, l, i, t) = F_{\text{lac}}(x', m_0, l, i, t + 1), \quad (6)$$

where $F_{\text{preg}}(x, l, i, t) = 0$ for all $L(t) = l > 2$ (i.e., outside the breeding grounds) and for $x < x_{\text{abo}}$, $m_0 = 0.06$ (i.e., the calf's proportion of blubber mass at birth, assuming that a calf is born with minimum blubber mass to allow survival), and x' is the female's blubber mass at t , minus the costs of the last day of gestation and the costs of resting for the entire day (see details in apps. B, C).

We obtained the cost of traveling for a day from allometric estimates of the minimum cost of transport provided by Williams (1999) and approximated the cost of feeding using the rorqual average active metabolic rate described in Potvin et al. (2012). The amount of time spent feeding in a day depended on the encountered krill density, the size of the buccal cavity, and digestion times (Wiedenmann et al. 2011; Goldbogen et al. 2015). We assumed that whales feed only in daylight hours (Fiedler et al. 1998). When not feeding, a whale rested, with a resting metabolic rate twice the value of its basal metabolic rate, following Potvin et al. (2012). We estimated the costs of supporting the growing fetus at different stages of gestation based on Lockyer (1981) and used information on calf growth rate, calf metabolic rate, and lactation from Lockyer (1981) and Oftedal (1997). We assumed reproductive females were at their average asymptotic length

(22 m; Gilpatrick and Perryman 2008). The full state dynamics and parameters are described in appendix B (table B1, available online).

Equations (1)–(6) are known as the SDP equations (additional details in app. C) and are solved backward starting at $t = T$ (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). The backward iteration of the SDP equations resulted in the identification of the optimal behavior during pregnancy, $b_p^*(x, l, i, t)$, and lactation, $b_l^*(x, m, l, i, t)$, given the value of the state variables at each time step (Mangel and Clark 1988; Clark and Mangel 2000).

Forward Iteration

We used $b_p^*(x, l, i, t)$ and $b_l^*(x, m, l, i, t)$ to simulate the behavior and state dynamics of 200 females through time, starting on April 1. This sample size captured individual variability while ensuring manageable run times and array sizes. Each whale's initial condition was drawn from a uniform distribution $X(1) \sim U(x_{\text{abo}}, x_{\text{max}})$, and the initial location $L(1)$ was either 1 or 2 (the breeding grounds). We used Monte Carlo simulations to account for the environmental stochasticity encountered at each time step (Mangel and Clark 1988; Clark and Mangel 2000), which was determined by $\lambda(l, i)$ and $p(i, l, t, j)$. We accounted for the degradation of a food patch using the mean time spent in area-restricted search behavior (Bailey et al. 2010). Specifically, after 21 days of daytime feeding in the same patch (Bailey et al. 2010), patches with food (patch types 1 and 2) became patches without food (patch type 3). Decisions regarding abortion, starvation, and calf survival followed the same rules described above. Females that aborted their fetus were counted and removed from future time steps in the simulation.

Simulated Scenarios

We employed a series of forward MC simulations to show how the model could be used to assess changes in vital rates due to both environmental and anthropogenic disturbances. Specifically, we considered five scenarios.

Natural Disturbance. Scenario 1: El Niño (ENSO) conditions. This climatic oscillation results in a northward shift in the distribution of *N. simplex* and an overall reduction in upwelling intensity in the southern and central California Current, where productivity is reduced and confined to coastal pockets (Chavez et al. 2002; Marinovic et al. 2002). ENSO is a periodic climatic event, so it is expected to be part of the whales' evolutionary history.

Scenario 2: A sudden and unprecedented change in the whales' environment. As an example, we used the anomalous conditions observed in 2005, when upwelling in the

California Current was delayed by 2–3 months, causing a reduction in productivity at an intensity comparable to an El Niño event (Brodeur et al. 2005; Schwing et al. 2006).

Anthropogenic Disturbance. Anthropogenic scenarios represented extreme disturbances, and we used them to illustrate possible applications of the model. We simulated disturbance as occurring at given locations with specified daily probability. When in a disturbed location, a whale had the option to change her behavior and select the second-best alternative. Each individual had a probability r_w of moving away from a disturbed location (McHuron et al. 2017). When a whale chose to stay in the disturbed location, her feeding activity was partially impaired (Goldbogen et al. 2013; DeRuiter et al. 2016; Friedlaender et al. 2016). To do this, we reduced the amount of time available to feed on that day by a proportion, s_{ab} , which could indicate the severity or duration of the disturbance or the whale's response. We considered three scenarios for disturbance.

Scenario 3: An intense, localized disturbance source, that is, operating at one location, with a daily probability of 1 and reducing available foraging time to 0. This could correspond to a naval sonar exercise, a seismic survey for oil and gas exploration, or the construction of an offshore wind farm. All whales were assumed to remain in disturbed locations; that is, all $r_w = 0$.

Scenario 4: As scenario 3, but all whales were assumed to move to an undisturbed location; that is, all $r_w = 1$.

Scenario 5: Weak disturbance over a large scale. Half of the locations (selected at random) were disturbed with a 50% daily probability, causing a 50% reduction in available time to feed if females remained in the disturbed location. A whale's tendency to move away from disturbance was drawn from a beta distribution, that is, $r_w \sim \beta(5, 5)$. This scenario could exemplify shipping traffic or whale watching, that is, regular, low-intensity disturbance covering a large portion of the species' range.

Additional details of simulated scenarios are reported in appendix D. Since ENSO events are part of the whales' evolutionary history, we reran the backward iteration to estimate optimal behavioral decisions under the altered environment defined in scenario 1. For the remaining scenarios, we used the SDP results under normal conditions and perturbed the environment in the forward simulations. We ran each MC simulation 100 times and recorded mean recruitment probability, mean number of abortions, mean number of calf starvations, and mean number of female starvations for all undisturbed and disturbed conditions. To compare recruitment probability among scenarios, we computed the value of Cohen's d for each simulation (Cohen 1977; McHuron et al. 2017) and averaged it over the 100 replicates. Cohen's d is the difference between mean recruitment probabilities scaled by the pooled standard deviation, with values of 0.2, 0.5, and

0.8 indicating small, intermediate, and large effect sizes, respectively (Cohen 1977).

Sensitivity Analysis

We used a sensitivity analysis to identify the parameters that had the largest influence on simulation results. We individually varied each parameter by $\pm 10\%$, $\pm 20\%$, and $\pm 40\%$ from the original value, while holding all others constant. We tested model sensitivity to 41 parameters, resulting in 246 investigations of sensitivity (full list in the supplementary material, available online in a PDF). For each investigation, we reran the SDP backward iteration and 100 replicates of the forward iteration. We calculated mean recruitment probability in the undisturbed scenario for the baseline and for each sensitivity combination, as well as the value of Cohen's d for disturbed scenarios.

The code and associated data to run the SDP model, Monte Carlo simulations, and sensitivity analysis are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.md416> (Pirota et al. 2017).

Results

The forward MC simulations (based on the matrix of optimal behavioral decisions) generated results that are consistent with observations of ENP blue whales' natural behavior. Individual blubber mass oscillated in the first phase of migration (fig. 2A), when the whales stopped to feed in the lower-quality patches along the coast of the Baja California Peninsula (fig. 2B, 2C). As females' blubber mass improved, they progressively moved northward into the waters of California, which most whales reached around June (fig. 2C). In these locations and those farther north (fig. 2C), females could feed on high-density patches of larger krill, allowing them to obtain the maximum blubber mass defined by their physiological limitations (fig. 2B). With the approach of autumn, the best strategy for the simulated whales consisted of staying in prey-rich Californian waters as long as possible to maintain their blubber stores before starting their migration back south to give birth to the calf (fig. 2C). This last stage was completed quickly, without stopping for food (fig. 2A). During the winter, female blubber mass declined dramatically, primarily as a result of the milk delivered to the dependent calf (fig. 2A, 2D). As female blubber mass declined, calf condition increased concomitantly (fig. 2D). Females and their calves moved within the breeding grounds until spring (fig. 2A, 2C), when they could start profiting from the enhanced productivity of the low-quality patches in the breeding grounds and along the Baja California Peninsula in order to recover their energy stores (fig. 2B). As environmental productivity increased, whales quickly traveled toward the richer patches of California to support the final

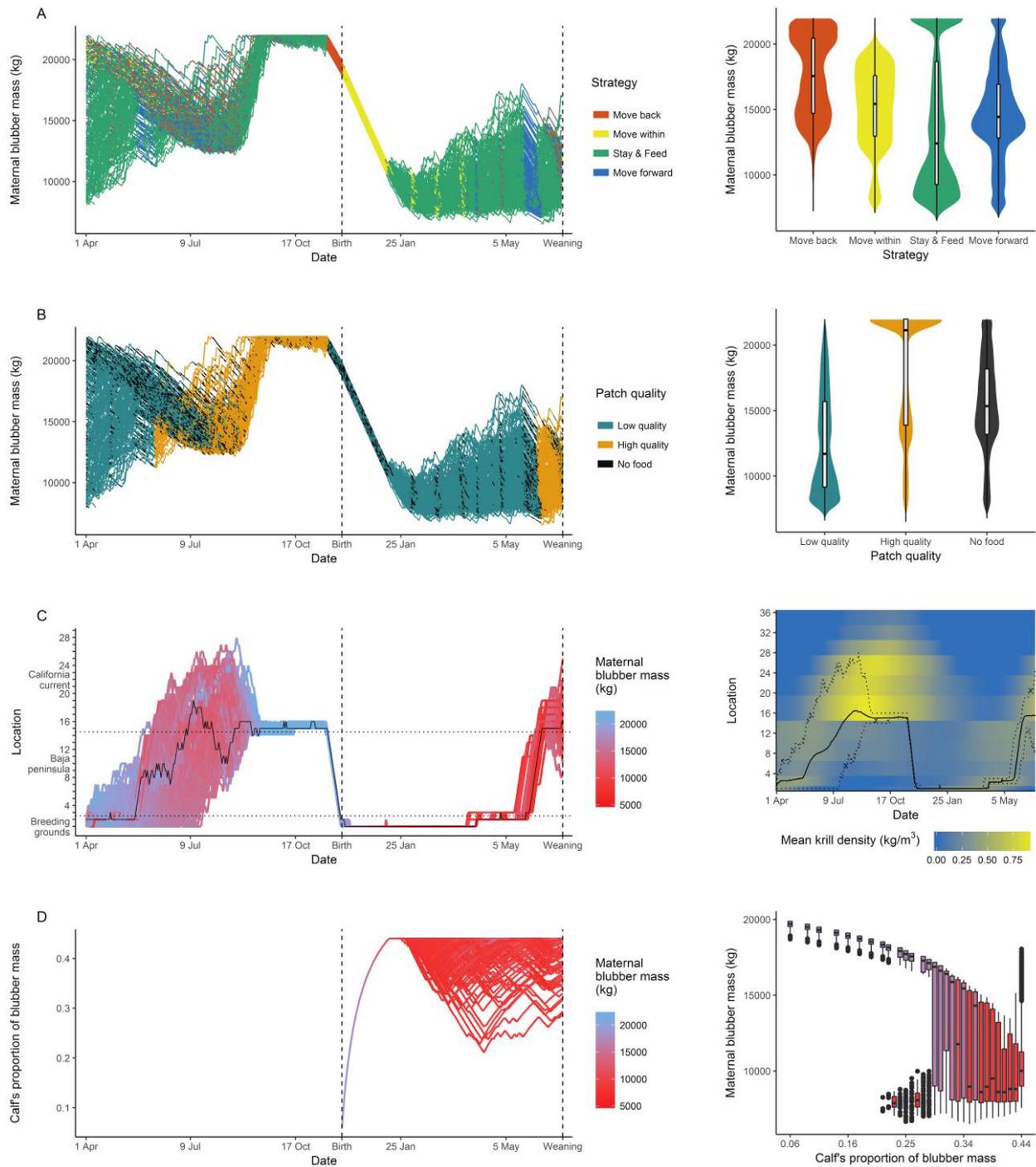


Figure 2: Model results. *A*, Variation in blubber mass over time for 200 females in one run of the forward iteration, colored by behavioral decision at each time step. Birth and weaning are indicated by vertical dashed lines. *Right*, a violin plot of blubber mass under different behavioral decisions. *B*, A similar plot for the variation in blubber mass over time, but colored by encountered patch quality; *right*, the blubber mass in patches of different quality. *C*, Changes in location over time for 200 females over one run of the forward iteration, colored by the corresponding blubber mass and an individual example (black line). Location number varies from 1 (breeding ground) to 36 (northernmost extent of the migration). Horizontal dotted lines represent transitions between geographical regions. *Right*, a heat map of mean krill density in each location over time, varying between 0 kg/m³ (blue) and 0.93 kg/m³ (yellow). In black, the mean (solid line) and range (dotted lines) of whale locations over one run of the forward iteration. *D*, Changes in calf's proportion of blubber mass over time for one run of the forward iteration, colored by maternal blubber mass. The calf starts accumulating blubber mass after it is born at $t = 244$. *Right*, relationship between female and calf condition.

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part of lactation (fig. 2C), although this was not sufficient to regain high blubber reserves (fig. 2D).

Overall, when females were in poor condition or aiming to maintain high reserves, they remained in a patch to feed (fig. 2A). Traveling occurred when a female’s condition improved or when constrained by reproductive needs. Patches with no food were mostly used for transit, and females moved away or within them (fig. 2A, 2B). Female condition matched food availability, so blubber mass was higher in richer patches (fig. 2B) and more productive locations (fig. 2C). During pregnancy, most metabolic expenditure could be ascribed to feeding, especially as the fetus grew, while gestation costs were comparatively low (fig. 3). During lactation, milk delivery became the critical energy cost (fig. 3). In both stages, traveling was relatively inexpensive and exceeded resting costs by only a small amount (fig. 3).

A female’s condition at the start of the simulation affected her initial behavioral decisions and blubber dynamics (fig. 2A). Low initial state also resulted in a few early abortions (2%, on average, over 100 replicates). However, initial conditions became irrelevant as whales reached California waters in summer, where they could fully replenish their blubber stores in good years (fig. 2A). At the end of 100 iterations of the forward simulation, the mean proportion of the calf’s mass that was blubber was 0.43 (standard deviation: 0.03). Combining state-dependent calf recruitment to the population and initial abortions resulted in a 95% mean calf recruitment probability (fig. 4).

Under scenario 1 (El Niño environmental conditions), recruitment probability declined to 92%, on average (fig. 4),

with an increase in mean number of calf starvations during lactation from 0 to 0.2%. However, based on Cohen’s $d = 0.24$, the effect size was small. An unprecedented change in the environment (scenario 2) resulted in a more dramatic decline in mean recruitment (from 95% to 69%) and a large effect size (Cohen’s $d = 0.84$), mostly driven by a steep rise in the number of abortions (from 2% to 25.5%; fig. 4). The effects of an intense, but localized anthropogenic source of disturbance depended strongly on the whales’ response: when the whales stayed and fed in the disturbed patches (scenario 3), mean abortion rate rose to 12.5% and mean percentage of calf starvations rose to 18.5%. In this scenario, females were unable to support lactation, and mean recruitment fell to 63%, a large effect size (Cohen’s $d = 0.99$; fig. 4). However, when all whales moved away from the localized disturbance (scenario 4), there was no detectable change (Cohen’s $d = -0.01$) in mean recruitment probability (95%; fig. 4). Finally, a weak but diffuse disturbance (scenario 5) caused a small decrease (Cohen’s $d = 0.08$) in mean recruitment probability to 94%, which included a small increase in calf starvations (0.2%, on average; fig. 4).

The sensitivity analysis highlighted that the most influential parameters were the morphology of the female and calf (e.g., her energy storage abilities and the allometric relationships), the metabolic rates in different activity states, the characteristics of the environment and prey, and the scaling parameter of the calf survival function (m_{50}). Other aspects of whale physiology, such as costs of pregnancy (with the partial exception of fetus size and heat increment of gestation), costs of lactation (with the exception of the

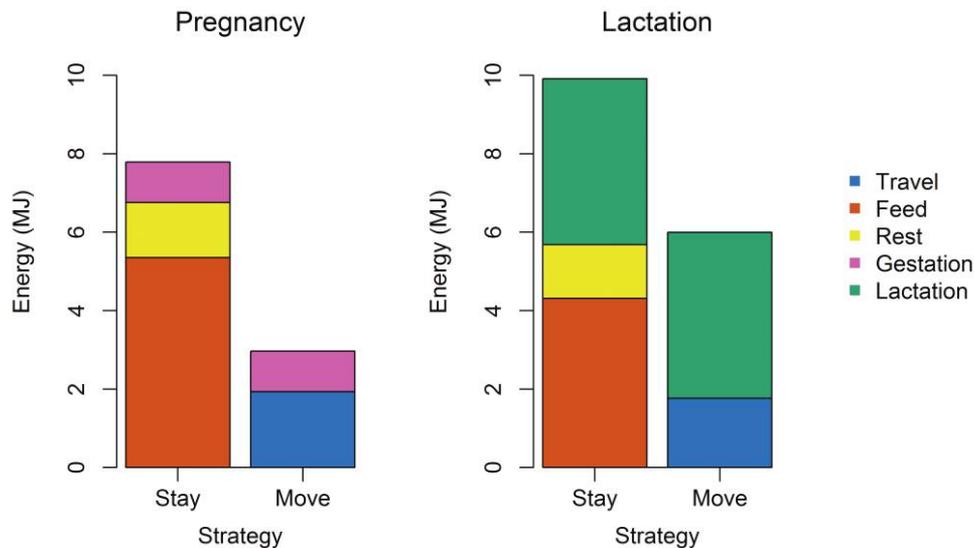


Figure 3: Metabolic costs of different activities (megajoules [MJ]) during pregnancy and lactation. Energy expenditure was averaged across 200 females and across the days that constitute each phase. Feeding and resting costs were calculated assuming a fixed krill density corresponding to 12 h per day of active feeding. Lactation costs correspond to maximum milk delivery rate.

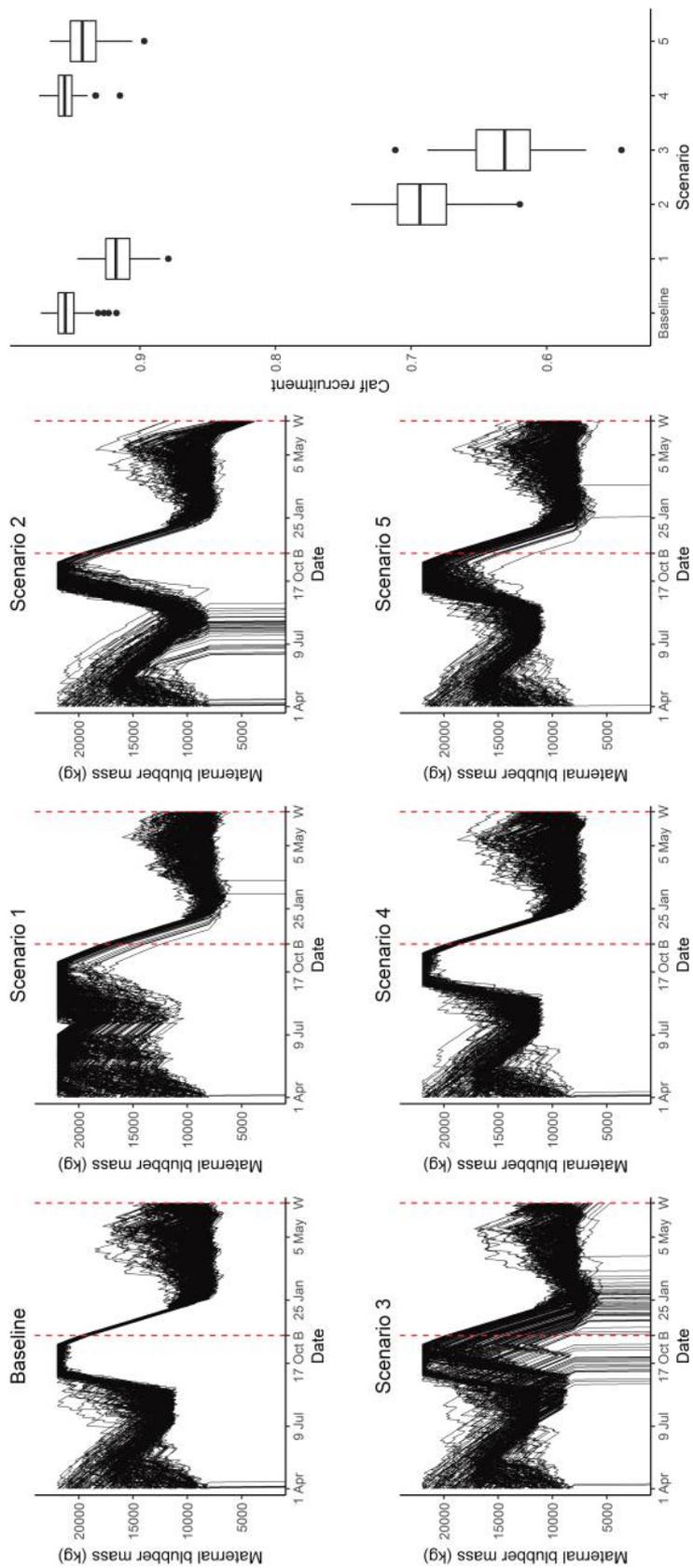


Figure 4: Variation in maternal blubber mass over time under environmental and anthropogenic disturbance scenarios and corresponding changes in calf recruitment probability (boxplot). Vertical dashed lines indicate time of birth (B) and weaning (W). Vertical black lines indicate abortions or starvations.

relative threshold), energy requirements of the growing calf, and the dynamics of digestion, were comparatively less important. Overall, the results of the first three disturbance scenarios showed higher sensitivity to model parameters, while conclusions from scenario 4 and 5 were largely unchanged. A full description of the results is provided in the supplementary material.

Discussion

We developed a dynamic state variable model that synthesizes the behavioral, physiological, and environmental constraints shaping the ecology of migratory populations. We used the model to investigate the complex interaction between a female's energy budget and her ability to exploit dynamic environmental resources to successfully reproduce. By characterizing the physiological mechanisms and challenges that an individual experiences through migration, the model can be used to understand the processes that drive the evolution of life-history strategies and behavioral patterns. This enables us to predict the consequences of behavioral changes caused by environmental or anthropogenic disturbances on population dynamics (Wiedenmann et al. 2011; McHuron et al. 2017). We applied the framework to migratory baleen whales, choosing the ENP blue whale population as an example of how the model could be parameterized. Model results provide practical guidance for identifying the critical data required to inform such an approach and suggest ways to assess knowledge gaps and uncertainty, making it applicable to other populations of migratory animals.

Our approach accounts for behavioral decisions resulting from the trade-off between an individual's condition, the metabolic costs of different activities, the characteristics of the external environment, and the moment in time (Mangel and Clark 1988). Although behavioral decisions were simplified to either staying in a patch or moving, the model captured the dramatic fluctuations in body conditions experienced by a pregnant female throughout a reproductive cycle (Lockyer 1986; fig. 2). Because of the large variation in where and when females could accumulate energy for survival and reproduction, the local dynamics of productivity drove their behavior. This gave rise to the emergence of the migratory behavior, as whales tracked the south-to-north seasonal wave of productivity along the coast in order to support their high energetic requirements (Croll et al. 2005; fig. 2). Our model, therefore, provides support for the hypothesis that migration evolved to exploit temporally productive, spatially explicit regions, while meeting the demands of reproduction (Alerstam et al. 2003; Lennox et al. 2016).

The timing of the various stages of migration resulting from our forward simulations broadly matches the information provided by observational studies and telemetry

data (Mate et al. 1999; Calambokidis et al. 2009; Bailey et al. 2010). Although individual migratory strategies varied, the forward simulations also highlighted a whale's ability to trade off the distance to reach a patch against its quality, so that some individuals used northern, high-quality patches, while others focused on closer, but lower-quality patches along the Baja California Peninsula. This plasticity arose because optimal behavior was determined by current fat reserves, future reproductive needs, and time constraints (fig. 2; Mangel and Clark 1988). However, at certain stages of migration, there were some areas that appeared to be critical to all individuals for maintaining good condition (e.g., the waters off California in late summer). That is, different parts of a migratory species' range have different contributions to fitness (Alerstam et al. 2003). The highly variable metabolic costs of different activities and how these combined in the two phases of the reproductive cycle also contributed to predicted behavior (fig. 3).

Lactation was the costliest phase of a whale's reproduction, leaving a female in a state of extreme energy depletion at her calf's weaning (figs. 2, 3; cf. Lockyer 1981; Oftedal 1997). In terms of energy transfer from mother to calf, females maximized milk delivery in the first weeks of the calf's life when their condition was high, relying on body reserves accumulated in the feeding grounds. In this phase, females behaved as stereotypical capital breeders. However, nursing activity became more irregular as blubber reserves were depleted and females had to start feeding to supplement their energy stores (fig. 2). This suggests that females need to feed during winter to survive through lactation. The flexibility of their reproductive strategy reinforces the idea that there is a continuum between pure capital and pure income breeding and that the interplay between morphology, physiology, and food availability drives the observed provisioning strategy (Stephens et al. 2014). The initial condition of pregnant whales only affected behavioral decisions and expected reproductive success in the first phase of the reproductive cycle. Whales in poor condition could lose the fetus before reaching foraging patches productive enough to replenish their blubber stores. However, they were not at a disadvantage once they made it through the summer feeding season in good years (fig. 2). As a result, carrying a fetus to term may not represent a physiological bottleneck, which is confirmed by the low abortion rate in historical whaling records (Ichihara 1962). Under the modeled environmental conditions, whales appeared to be able to fully replenish their body reserves in summer (fig. 2). Natural interannual resource variability may compromise such good performance and have cascading effects on reproductive success, as our environmental perturbation simulations suggest (fig. 4).

Little is known about baleen whale energy dynamics during pregnancy and lactation (Oftedal 1997; Williams et al. 2013; Christiansen et al. 2014), and our results could be

used as testable hypotheses to drive future research efforts. For example, it will be critical to verify whether weaning time is flexible so that females can respond to variable feeding conditions, whether females abandon calves when consistently unable to provide milk and whether calf births can occur outside the breeding grounds, since these assumptions can have large effects on model construction and results. Calf recruitment rate in the baseline scenario (95%) was higher than first-year survival rates estimated for other species (e.g., 87.5% in humpback whales; Barlow and Clapham 1997), but our estimate does not include mortality after weaning. This result is another hypothesis to test with future empirical studies.

Simulating environmental change over a short temporal scale, such as caused by El Niño (e.g., Chavez et al. 2002), led to a reduction in calf recruitment probability, consistent with studies on pinnipeds (e.g., Le Boeuf and Crocker 2005). The reduction was small, since we assumed whales' behavior is adapted to cope with such periodic variation in their environment. Telemetry studies have shown whales in good condition using northern waters unaffected by El Niño in the relevant years (Bailey et al. 2010). Migratory species, which have evolved to track variations in their habitat, are expected to show some plasticity in their movement strategies (Lennox et al. 2016). The ability of whales to compensate for lower food availability in Californian waters during El Niño years is possible due to the low mass-specific cost of transport associated with their large size (Williams 1999). This corresponded with the lower metabolic expense assumed in our model (fig. 3), allowing individuals to travel between alternative patches and reach those with higher productivity at little cost. In contrast, unprecedented environmental change strongly affected reproductive success, particularly in the first phase of the cycle, when failure to compensate resulted in a large number of abortions (fig. 4). These results, although only illustrative and simulated, raise concern regarding the whales' ability to respond to the unpredictable environmental shifts that are anticipated due to global climate changes (e.g., Hazen et al. 2012; IPCC 2014). Although whales may use strategies developed in their evolutionary history to address periodic declines in environmental productivity, these new features of the environment may be sufficiently different from previously experienced scenarios that responses could be difficult or maladaptive.

When considering the potential consequences of extreme responses to anthropogenic disturbance, the effect of a low-intensity disturbance over a diffuse area (e.g., from shipping traffic or whale watching) on reproductive success was minimal. However, the effect of intense, continuous, but confined disturbance in the main summer feeding ground (e.g., a seismic survey or the construction of a wind farm) depended on the behavioral response. When whales stayed in the disturbed environment, they could not compensate for the re-

duction in available foraging time. As a result, their condition deteriorated and the probability of calf recruitment declined following increased abortions and starvation. In contrast, when whales moved away from disturbed locations and fed elsewhere, there was no detectable long-term effect. It is therefore important to investigate whales' behavioral responses to disturbance and, particularly, the context in which these responses may change. The interruption of feeding activity can depend on patch quality (Hazen et al. 2015; Friedlaender et al. 2016) and on the whale's behavioral state (Goldbogen et al. 2013). Other contextual factors, such as body condition, time of year, availability of alternative feeding areas, and individual differences, may also play an important role (Beale and Monaghan 2004; Ellison et al. 2012). The extent of the disturbance, the distance traveled to avoid it, and the intensity of feeding impairment should also be considered, instead of the fixed 100% or 50% reduction in feeding we used here for illustration. Moreover, a whale's responsiveness may evolve over time (Bejder et al. 2009; McHuron et al. 2017). Because of the difficulties associated with data collection, there is limited empirical evidence on the impacts of anthropogenic disturbance on vital rates in cetacean populations (National Research Council 2005). However, a decline in first-year calf survival by 56% was detected in the bottlenose dolphin population of Doubtful Sound, New Zealand, following anthropogenic and environmental perturbations (Currey et al. 2009), which is even larger than the predicted decline under our extreme scenario 3.

These results highlight the need for careful planning of acute anthropogenic disturbances, in order to avoid locations and times critical to the focal species (Foley et al. 2010). However, a weak but long-term disturbance (e.g., noise resulting from regular shipping traffic) may have chronic consequences on whale physiology, leading to a less dramatic but progressive population decline (Ellison et al. 2012). Our model estimates the effects of disturbance on important vital rates, such as successful weaning of a calf and female survival. Evaluation of the population consequences of disturbance will require that the results of these effects be integrated over a longer time horizon, either via SDP extended to a female's reproductive lifetime or by incorporating these effects into a population model (New et al. 2014; Villegas-Amtmann et al. 2015).

Our work shows how to integrate studies on the fine-scale energetics of lunge feeding and swimming dynamics (Goldbogen et al. 2011; Wiedenmann et al. 2011; Potvin et al. 2012; Hazen et al. 2015) with large-scale information on movement patterns and migratory strategies (Mate et al. 1999; Bailey et al. 2010; apps. A, B). We modeled the environment with intermediate complexity (Plagányi et al. 2014), capturing the seasonal, spatial, and stochastic variation driving the availability and distribution of prey resources (Fiedler

et al. 1998; Croll et al. 2005). By treating behavior as an evolutionary trait, state-dependent life-history theory naturally integrates internal and external factors that are influencing individuals' decisions at multiple scales, while explicitly modeling their energetic and long-term fitness implications (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). As such, it has potentially wide applications to other species of migratory marine animals that depend on similarly dynamic environmental resources and are subject to comparable reproductive constraints. In addition to many other cetacean species, some species of pinnipeds, seabirds, elasmobranch, large teleosts, and turtles rely on restricted areas to reproduce, show plastic behavioral traits, and are highly affected by fluctuations in prey availability (Alerstam et al. 2003; Lennox et al. 2016). Our understanding of their feeding, reproductive, and migratory ecology may thus benefit from simulations grounded on energetic and behavioral principles, such as the ones achieved via our model.

Many parameters are required to build SDP models, and their estimation can be problematic for long-lived, large animals such as marine mammals (McHuron et al. 2017). We extracted information from the whaling literature, but this often involved data from different regions or species and may suffer from unknown sampling biases. Moreover, some parameters remain impossible to measure given logistical and ethical restrictions in large vertebrate research (Gales et al. 2009). Most approaches aiming to link behavior to population dynamics face similar difficulties. Dynamic state variable modeling allows for an explicit investigation of the effects of model assumptions, providing a robust way to explore the results' sensitivity to parameter variation, which can direct data collection efforts to efficiently tackle the most crucial uncertainties (Mangel and Clark 1988; Clark and Mangel 2000).

From the sensitivity analysis (supplementary material), we found that the scenarios for environmental change and extreme response to anthropogenic disturbance were the ones most affected by parameter uncertainty. We also confirmed the need for a better understanding of adult and calf morphology, characteristics of the environment, food resource dynamics, movement mechanics, metabolic rates in different activity states, and the whales' ranging pattern and migratory behaviors. These gaps in our knowledge could be filled using (1) further photogrammetry studies as well as ultrasound blubber measurements (Gilpatrick and Perryman 2008; Miller et al. 2011); (2) prey sampling across a wider spatiotemporal range or indirect assessment from long-term monitoring of whales' foraging behavior in different contexts (Nabe-Nielsen et al. 2014; Goldbogen et al. 2015; Hazen et al. 2015) and in response to sound exposure (Friedlaender et al. 2016); (3) hydrodynamic modeling using fine-scale tag data paired with bioenergetic studies (Goldbogen et al. 2011;

Potvin et al. 2012; Villegas-Amtmann et al. 2015); and (4) additional studies using long-term telemetry data, particularly of individuals wintering near the Costa Rica Dome and in feeding areas during years with anomalous productivity (Mate et al. 1999; Bailey et al. 2010).

Conclusion

We developed an effective predictive approach to explore baleen whale migratory ecology and assess the consequences of human and environmental disturbance on their reproductive success. The model highlights trade-offs individuals face between condition, reproductive needs, and the environment, resulting in large fluctuations in energy reserves and the emergence of migration. This tool could be used to support management decisions regarding proposed activities in a population's range, while identifying important knowledge gaps that should be targeted by future research. Our work aligns with efforts to combine behavioral and physiological research to support wildlife conservation (Cooke et al. 2014) and is thus firmly in Pasteur's quadrant, in which fundamental understanding is sought in the resolution of an important applied problem (Stokes 1997; Clark et al. 2016). We demonstrated how context, in both the nature of disturbance and whale behavioral responses, can drastically change conclusions regarding the long-term effects of disturbance (Ellison et al. 2012). Moreover, we showed how environmental changes can disproportionately affect reproductive success depending on how whales react and adjust to a perturbed environment. The approach outlined here could be adapted to other marine migratory species for which information on morphology, feeding and swimming energetics, ranging behavior, and reproductive physiology is available. Although extensive prior knowledge is required to inform the parameters of the model, its structure is flexible and data from comparable species could be used in the interim, while providing an indication of how the associated uncertainties influence the results.

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Appendix A from E. Pirotta et al., “A Dynamic State Model of Migratory Behavior and Physiology to Assess the Consequences of Environmental Variation and Anthropogenic Disturbance on Marine Vertebrates” (Am. Nat., vol. 191, no. 2, p. E000)

State Variables

Female Blubber Mass

We assumed that a whale stores most of its energy reserves in the form of blubber mass and that changes in mass occur only through changes in blubber (Nordøy and Blix 1985; Pond and Mattacks 1988; Miller et al. 2011). This is supported by empirical evidence showing a correlation between blubber thickness of baleen whales and their reproductive status, as well as changes in blubber thickness associated with environmental fluctuations (Reeves et al. 2001; Miller et al. 2011; Williams et al. 2013; Braithwaite et al. 2015*b*; George et al. 2015; Seyboth et al. 2016). Using blubber thickness as a health metric ignores that low nutritional status might also affect blubber composition, in terms of the type and density of lipids that are stored (Lockyer 1986, 1987), but the two are thought to vary in parallel (Miller et al. 2011). Our measure of blubber mass can be interpreted as the overall amount of lipids available to the animal.

Given length $a = 22$ m (Gilpatrick and Perryman 2008), the average expected total mass of a blue whale is $W_a = 4.6 \times a^{3.05}$ (Lockyer 1976), that is, 57,000 kg. Based on the values of blubber mass reported in Lockyer (1976, 1981), we assumed blubber constituted 27% of the total mass, on average, leading to 73% average nonblubber mass (hereafter, “lean mass,” albeit encompassing ash and water). Lean mass remains constant throughout the reproductive cycle. In the absence of information on the minimum amount of energy stores required to support reproduction, we used the lower extreme of the recorded range of percentages (16%) to inform x_{abo} and x_{lac} , that is, the values of blubber mass below which the female aborts the fetus (when pregnant) and does not deliver milk (when lactating); $x_{\text{abo}} = x_{\text{lac}} = 8,000$ kg. This also agrees with the minimum preferred percentage of blubber used for bioenergetics modeling in pinnipeds and matches estimates of ideal fat content (Baxter 1989). We used the upper extreme of percentage blubber (35%) as the maximum amount of blubber a female can accumulate $x_{\text{max}} = 22,000$ kg. We also set a minimum percentage of blubber mass (5%) at which a female is believed to die of starvation, $x_{\text{min}} = 2,000$ kg. Although this is well below the lower observed percentage of blubber mass reported in whaling data (Lockyer 1976, 1981), it allowed us to explore behavioral decisions under conditions of extreme leanness (Wiedenmann et al. 2011). It also corresponds to the minimum blubber percentage that has been used for pinniped bioenergetic modeling (e.g., Malavear 2002), which refers to the percentage of essential fat estimated in studies on pigs (Whittemore 1998). For ease of derivation of the stochastic dynamic programming equations, female blubber mass varies in increments of 500 kg.

Location

Assuming that the whales overwinter in the waters off the west coast of Baja California and in the Gulf of California, Mexico (Bailey et al. 2010), for the purposes of this study the migration range can be schematically subdivided into 36 locations. Locations 1 and 2 represent the breeding grounds in the Gulf of California and off Baja California, respectively, location 15 marks the beginning of the summer feeding ground in Californian waters, and location 36 is the maximum northward extent of the migration, reaching the waters south of Vancouver Island, Canada.

Each location along the migratory route corresponds to a square patch of size 100 km, which was chosen based on the distribution of observed transiting speeds from telemetry data (see following section). This patch size also matches the blue whale patch size reported by Bailey et al. (2010) and previously used by Wiedenmann et al. (2011), as well as the distance that a humpback whale can cover on average during a day of traveling at the optimal migration speed of 1.1 m/s (Braithwaite et al. 2015*a*). When traveling, the whales are assumed to move from one location to the next without foraging. When foraging and resting, the whales are assumed to stay within a patch. The activity budget (i.e., the amount of time a whale feeds and rests in a day) emerges as the result of prey availability, whale morphology, and digestion

constraints, as detailed in appendix B. We acknowledge that there will be some movement within the patch, but we assume this movement involves low energy expenditure comparable to resting. The breeding grounds at locations 1 and 2 can be thought to cover a larger area than other locations along the migratory route. When on the breeding ground, whales have an additional available behavioral choice, which is to move within the location, in order to capture the roaming behavior in these grounds during the winter months (Bailey et al. 2010). Therefore, the whale can travel for a day, but her location does not change.

Patch Type

The environment in which the whales move is assumed to have a hierarchical structure (Fauchald 1999). There are two macroareas that the whales can enter and exit when they move: the waters of the Gulf of California and along the west coast of Baja California (locations 1–14) and the California current spanning between California and Washington (locations 15–36; Bailey et al. 2010). The two macroareas are characterized by a different availability of food resources. This availability is defined by $\lambda(l)$, a vector of the probabilities of encountering each patch type, so that when traveling to location l , the probability of encountering a patch of type i is $\Pr(I(l) = i) = \lambda(l, i)$. There are two patch types with food: patches with swarms of the subtropical euphausiid species *Nyctiphanes simplex* (patch type 1) available in the Gulf of California and along the west coast of the Baja California Peninsula (Brinton and Townsend 1980; Gendron 1992; Gómez-Gutiérrez 1995; Gómez-Gutiérrez et al. 1995; Gómez-Gutiérrez and Robinson 1997) and patches where whales can find the larger temperate euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* (patch type 2) available in the California Current (Brinton 1962; Smith and Adams 1988; Schoenherr 1991; Croll et al. 2005; Gómez-Gutiérrez et al. 2005). Patches without any available krill (patch type 3) occur in both macroareas with probability $1 - \lambda(l, 1) - \lambda(l, 2)$.

We used a long-term existing Argos satellite tracking data set collected on eastern North Pacific (ENP) blue whales by Oregon State University (Mate et al. 1999; Bailey et al. 2010; Irvine et al. 2014) to inform the probability $\lambda(l, i)$ of encountering a patch with food (patch type 1 or 2) as opposed to a patch without food (patch type 3) when moving in each macroarea. Details of the data collection can be found in Mate et al. (1999) and Bailey et al. (2010). These data are available via the Integrated Ocean Observing System's Animal Telemetry Network website (<http://oceanview.pfeg.noaa.gov/ATN/>). Tracking data were analyzed using a Bayesian hierarchical switching state space model with a daily time step, fitted with package *bsam* (Jonsen et al. 2013) in R (R Development Core Team 2016). This modeling approach allows the identification of periods during which the tagged individual engaged in one of two behavioral modes, namely, area restricted search (ARS, characterized by low autocorrelation in speed and large angle between consecutive locations, leading to a convoluted track) and transit (high autocorrelation and small angle between consecutive locations, leading to directed movement), while accounting for the error in the Argos location system (Jonsen et al. 2005). ARS behavior is generally assumed to represent periods spent in a profitable area searching for food (Kareiva and Odell 1987). We calculated the proportion of daily transitions from transit behavior to ARS behavior and from ARS behavior to ARS behavior over the total number of transitions in each macroarea (applying a cut-off value of 1.5 to the posterior behavioral state estimates) and used it as an estimate of the probability of encountering a patch with food on a given day ($\lambda(l, 1)$ and $\lambda(l, 2)$, depending on the macroarea). Since the whales are absent or not feeding in the California Current macroarea in winter months, we calculated $\lambda(l, 2)$ using transitions from May onward.

Each patch type offers a distribution of krill densities that varies in space and time. Patches of type 1, characterized by *N. simplex* and available in the breeding grounds and along the west coast of Baja California, are less seasonal than patches in temperate and polar waters, since *N. simplex* is a subtropical species and tends to reproduce year round (Fernández-Álamo and Färber-Lorda 2006). Nonetheless, several authors have recorded some seasonal fluctuations in abundance and availability of this species in the area, suggesting that it peaks in correspondence with the highest levels of upwelling (Brinton and Townsend 1980; Gendron 1992; Gómez-Gutiérrez 1995; Gómez-Gutiérrez et al. 1996, 2010; De Silva-Dávila et al. 2002; Ladrón de Guevara P. et al. 2008). *Nyctiphanes simplex* has been documented to reach its highest levels in the Gulf of California in winter and early spring (February–June, peaking in mid-March; Brinton and Townsend 1980; Gendron 1992; Ladrón de Guevara P. et al. 2008; Gómez-Gutiérrez et al. 2010), while along the west coast of Baja California it is abundant in spring and early summer, although it remains available in later months (Gómez-Gutiérrez 1995; Gómez-Gutiérrez et al. 1996; De Silva-Dávila et al. 2002). Patches of type 2, characterized by *T. spinifera* and *E. pacifica*, undergo dramatic seasonal fluctuations following the patterns of upwelling, which promotes blooms in productivity in the California Current (Brinton 1962; Smith and Adams 1988; Schoenherr 1991; Croll et al. 2005; Gómez-Gutiérrez et al. 2005). Croll et al. (2005) reported that extremely high peaks in krill abundance and

availability occur in Central California from midsummer to early autumn (July-October), at least 3 months after the highest upwelling rates. The upwelling peak intensity (and, hence, the krill bloom) shifts further into the season as latitude increases (Schwing et al. 1996). The upwelling range also becomes progressively less marked, until the waters of British Columbia where seasonal upwelling is virtually absent (Schwing et al. 1996). Croll et al. (2005) suggested that blue whales might track these seasonal changes in productivity by migrating to different portions of their range at different times of the year.

In order to capture and simplify this complex and dynamic environment, we used a measure of upwelling rate along the coast as a proxy for krill availability and abundance. The coastal upwelling index has been computed at 15 sites along the west coast of North America since 1967 by the Pacific Fisheries Environmental Laboratory (PFEL; now the Environmental Research Division of NOAA/NMFS's Southwest Fisheries Science Center; Schwing et al. 1996). We downloaded the daily values up to May 2016 from the PFEL website (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html) and fitted a cyclic cubic spline at each sampling site in a generalized additive modeling framework, using the package *mgcv* (Wood 2006) in R. The mean estimated values of the index on each day of the year at each site were divided by the maximum upwelling observed in the waters of Southern California in summer, in order to obtain a relative index scaled by the highest recorded value. The scaled upwelling index was then lagged by 90 days in the California Current to represent the documented lag between the upwelling and the peak in zooplankton abundance (Croll et al. 2005). No information on the levels of upwelling was provided by PFEL for the Gulf of California. Given the published timing of krill peaks in this region (Brinton and Townsend 1980; Gendron 1992; Ladrón de Guevara P. et al. 2008; Gómez-Gutiérrez et al. 2010), we used the scaled upwelling for the sampling site off the west coast of Baja California and shifted it toward the winter so that the maximum value corresponded to the time of the maximum reported krill abundance (mid-March). Negative values of the index were set to 0. The resulting scaled and lagged upwelling index is hereafter referred to as the krill index (fig. A2).

The distribution of krill densities per patch in Southern California was derived from published data of krill densities in the patches targeted by blue whales in summer in this region (Croll et al. 2005; Goldbogen et al. 2011, 2015; Hazen et al. 2015) and was drawn from a gamma distribution, $\Gamma(\text{shape} = 2.5, \text{rate} = 5.5)$ (fig. A3). We assumed this represented the highest possible krill availability over the entire range, since it corresponds with the location and time of the highest upwelling intensity. Each of the 36 locations along the migratory range was then assigned to the nearest PFEL sampling site, and the original density distribution was scaled by the corresponding krill index on each day of the year.

In addition, the distribution of krill density was scaled to account for prey differences among patch types. In the absence of information on the calorific content of *N. simplex*, we used the ratio between the length of the smaller species and the mean length of the two larger species as an indication of the relative difference in quality of these food sources. *Thysanoessa spinifera* and *E. pacifica* are bigger (on average, 23 and 18 mm, respectively) than *N. simplex* (12 mm, on average; Scripps Institution of Oceanography Zooplankton Guide, available at <https://scripps.ucsd.edu/zooplankton/guide/>), with a size ratio $r_s = 0.6$. As a result, patches of type 1 (available in the Gulf of California and along Baja California) show a krill density distribution that is scaled by both the krill index and the size ratio, while the krill distribution in patches of type 2 (available in the California Current) is only scaled by the krill index.

We discretized krill densities into 30 bins. When staying in a patch of type i to forage at location l on a given day t , the probability of finding krill density j is $\Pr(K(i, l, t) = j) = p(i, l, t, j)$. To mimic the ephemeral nature of krill swarms in this region, krill density is assumed to vary on each day that a whale spends in a given patch. The expected temporal autocorrelation in krill densities in a given location is accounted for by fixing patch type (with vs. without food) as long as the whale stays in a location, up to a maximum of 21 days. This corresponds to the mean time spent in an ARS patch estimated from blue whale telemetry data (Bailey et al. 2010), after which a patch with food was assumed to degrade to patch type 3 (without food).

One potential limitation with our use of the upwelling index to characterize krill availability is that the seasonal cycle of upwelling and productivity decouples in winter months due to insufficient solar radiance and surface stratification to sustain biological production (Foukal and Thomas 2014). This could explain why we had to impose a size threshold on the calf to avoid females leaving the breeding grounds early after birth to access food resources at other locations.

Calf's Proportion of Blubber Mass

On any day, the proportion of blubber mass of a calf lies between 0.05 (5%) and 0.44 (44%), varying in increments of 0.01. The upper range of this state variable is higher than the maximum percentage defined for the adult female, since a

calf needs to store proportionally more fat reserves than an adult to support its higher energetic demands for growth (Miller et al. 2011). The maximum was chosen based on the maximum blubber proportion recorded in recently weaned phocid seal pups (Reilly and Fedak 1990; Noren and Mangel 2004). Weaning fat masses larger than this maximum are expected to impair the calf's swimming performance (Adachi et al. 2014). A calf with a proportion of blubber mass ≤ 0.05 dies. Calf survival probability after 7 months of lactation is modeled as a function of its proportion of blubber mass at the end of the modeled period (the terminal fitness function; Cairns 1987; McMahon et al. 2003; New et al. 2014). The terminal fitness function is $\varphi_s(m) = m^\gamma / (m^\gamma + m_{50}^\gamma)$, defined by parameters: m_{50} , representing a 50% chance of survival and set to 0.27 (since 27% is the average blubber percentage observed in adults; Lockyer 1976); and γ , set to a value of 8, so that the probability of calf survival is approximately 0 when the proportion of blubber mass is 0.05 and 1 when it is 0.44 (fig. A1).

Unlike the adult female (assumed to be at asymptotic length), a calf invests a large portion of its daily energy intake in growth, which can be simplified as the progressive accumulation of lean mass (Lockyer 1981). Following the fetus's growth curve during gestation, the weight of a calf at birth is taken to be 2,500 kg (Huggett and Widdas 1950 in Lockyer 1981). We assume that, at birth, a calf's mass is mainly constituted of lean tissue, that is, that the blubber mass is at the minimum proportion allowing survival (0.06, or 6%). Estimates by Mackintosh and Wheeler (1929) and Tomilin (1946), reported in Lockyer (1981), suggested that during lactation, the calf linearly grows by around 17,000 kg, therefore reaching an average total mass of 19,500 kg at weaning. This weaning mass agrees with available information on calf length at weaning (Mackintosh and Wheeler 1929; Huang et al. 2009). In the absence of information on the body composition of weaned calves, we assume that, on average, they have the same percentage of lean mass as the adults, that is, 73% (Lockyer 1976). Therefore, the lean mass of the calf increases from $0.94 \times 2,500 = 2,350$ kg at birth to $0.73 \times 19,500 = 14,235$ kg at weaning, that is, a linear increase of $(14,235 - 2,350)/211 \sim 56$ kg/d. Following Lockyer (1981), we used the reported calorific content of lean meat ($1,500 \times 4.184$ kJ/kg) and estimated the energy required to support such daily growth as $56 \times 1,500 \times 4.184 \sim 351,000$ kJ/d. In addition, a calf needs energy to cover its daily metabolic costs, which we take to be $200,000 \times 4.184 \sim 837,000$ kJ/d (Lockyer 1981). While basal metabolic rate is likely to vary as the calf grows, it is unknown how it scales with size compared to adults. Therefore, we used the only available estimate from Lockyer (1981), who assumed a fixed calf metabolic rate in the calculation of lactation costs. As a result, the calf requires a minimum of approximately 1,190,000 kJ/d to survive and grow, while any surplus of energy received from the mother can be stored as fat reserves in the blubber, increasing its proportion of blubber mass. On days when the calf receives less energy than its daily requirements to survive and grow, it will use the stored reserves to sustain such costs, and its proportion of blubber mass will be consequently decreased. All calculations of a calf's proportion of blubber mass take into account the calf's growth in lean mass over the course of lactation.

The female transfers energy to the calf in the form of milk. Whenever her blubber mass is greater than the threshold to begin lactation, x_{lac} , this surplus energy is transformed into milk and delivered to the calf. Following the midpoint of two sets of estimates provided by Oftedal (1997), we set a maximum amount of milk that can be delivered per day of 220 kg/d. When the calf has reached its maximum storage capabilities (i.e., its proportion of blubber mass on that day is already 0.44), the female will only deliver the milk required to sustain the calf's costs on that day and save the extra energy as blubber. If the female's blubber mass falls below the threshold of starvation x_{min} , she dies, but her calf can survive with a probability that depends on its current proportion of blubber mass and the time left before autonomous feeding at 7 months. Specifically, the total energy required to survive and grow until that date is subtracted from the current mass, and the resulting mass at 7 months is calculated. Calf survival probability is then extracted from the terminal fitness function using this final proportion of blubber mass.

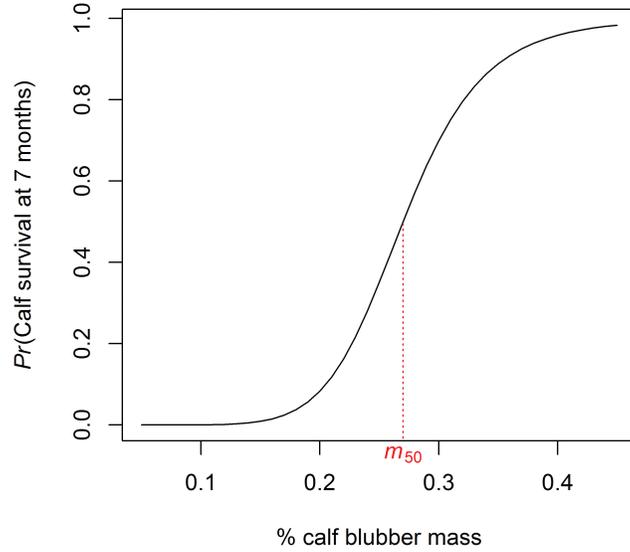


Figure A1: Fitness function for the lactation phase, relating the proportion of blubber mass of the calf at weaning (i.e., after 7 months of lactation, on average) and its probability of survival. In red, m_{50} , that is, the value of the proportion of blubber at which the calf has a 50% chance of survival.

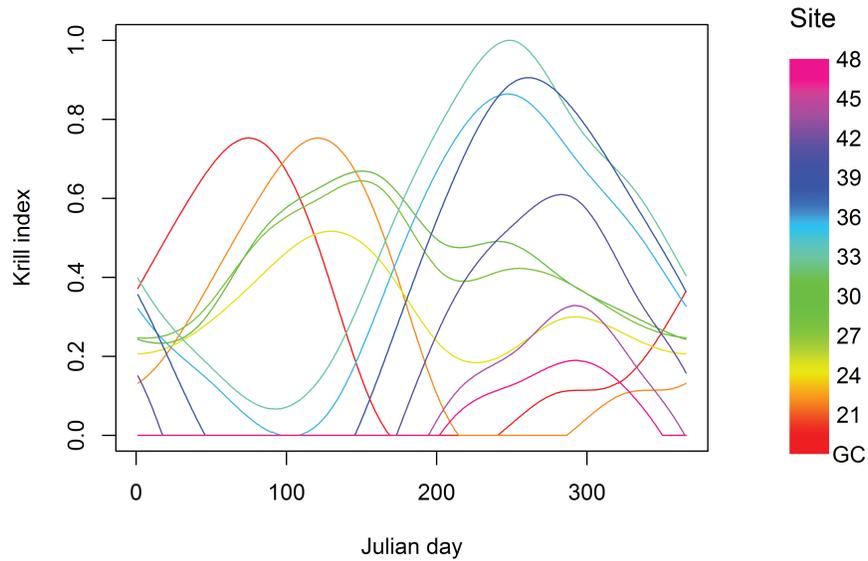


Figure A2: Seasonal and spatial variability of the krill index. This was derived from the daily coastal upwelling index provided by the Pacific Fisheries Environmental Laboratory (now the Environmental Research Division of NOAA/NMFS Southwest Fisheries Science Center) for 10 sampling sites along the west coast of North America. The curve for the Gulf of California (GC) was derived from the curve available at the southernmost location as described in the text. The labels for all other sites correspond to their latitude (in degrees north).

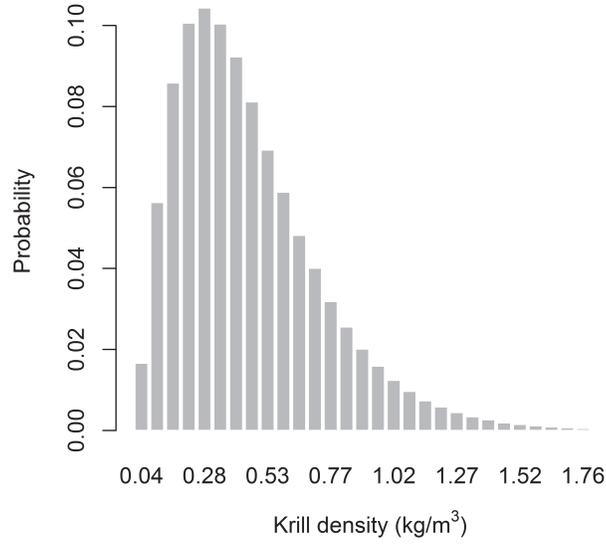


Figure A3: Distribution of krill densities in the waters off Southern California (lat. 33°N) in summer ($l = 17, i = 2, t = 159$). Krill densities were discretized into 30 bins (j) for ease of derivation of the stochastic dynamic programming equations. On the Y -axis, the probability of finding krill density j , $\Pr(K(2, 17, 159) = j) = p(2, 17, 159, j)$. This distribution represents the maximum achievable krill density and was used as the baseline distribution to derive krill density distributions at each of the 36 locations on each day of the year.

Appendix B from E. Pirotta et al., “A Dynamic State Model of Migratory Behavior and Physiology to Assess the Consequences of Environmental Variation and Anthropogenic Disturbance on Marine Vertebrates” (Am. Nat., vol. 191, no. 2, p. E000)

State Dynamics

See table B1 and table 1 in the main text for a summary of the parameters and their definitions.

Pregnant Female

At model time $t = 1$, a 90-day pregnant female can begin her northbound migration, starting from the breeding ground ($L(t = 1) = 1$ or $L(t = 1) = 2$). At each time step, she can make one of three decisions (b_p): leave the current location to travel forward, leave the current location and travel backward, or stay in the current location to feed and rest. If $L(t) = 1$ or $L(t) = 2$ (i.e., in the breeding ground), she can also decide to travel within the same location. The time spent feeding and resting in a day when she stays in the current location emerges from the characteristics of the environment and the constraints of her morphology and physiology, as detailed below. We let $g = 0.73 \times 4.6 \times a^{3.05}$ denote the lean mass (invariant, 73% of the average weight for length a), summed to the blubber mass $X(t)$, to give the total mass $W(t)$; that is, $W(t) = X(t) + g = X(t) + 42,000$ kg, if length $a = 22$ m. We let $w_f(t) = [0.52 \times (t + 90 - 73)]^3 / 1,000$, from Huggett and Widdas (1950) in Lockyer (1981), denote the mass of the fetus at time t . Then the cost of transport (COT) is described as $\text{COT}(t) = 7.79 \times [W(t) + w_f(t)]^{0.29}$ (in kJ/km/kg; Williams 1999).

When the female decides to leave her current location and travel forward,

$$X(t + 1) = X(t) - \frac{\text{COT}(t) \times d \times [W(t) + w_f(t)] + \alpha_g(t)}{u},$$

$$L(t + 1) = L(t) + 1,$$

$$I(t + 1) \sim \text{multinomial}(\lambda(l + 1)),$$

where d is 100 km, that is, the distance covered in a day of traveling (Wiedenmann et al. 2011; Braithwaite et al. 2015a); $\alpha_g(t) = \Delta w_f(t) \times c_f + h(t)$ is the daily cost of gestation (Lockyer 1981, 2007), which depends on $\Delta w_f(t) = w_f(t) - w_f(t - 1)$ (change in weight of the fetus from the previous day), c_f (cost of pregnancy per unit of fetus weight), and $h(t) = p(t) \times (4,400 \times 4.184 \times w_b^{1.2})$ (heat of gestation, given $p(t) = \Delta w_f(t) / w_b$, the proportional change in fetus weight on that day with respect to the weight at birth w_b); u is the amount of utilizable energy in a kilogram of blubber, that is, 31,798 kJ/kg (Lockyer 1981); and $\lambda(l + 1)$ is the vector of probabilities of encountering different patch types when moving to the new location. This varies depending on the macroarea to which location $l + 1$ belongs (app. A).

When she decides to leave her current location and travel backward,

$$X(t + 1) = X(t) - \frac{\text{COT}(t) \times d \times [W(t) + w_f(t)] + \alpha_g(t)}{u},$$

$$L(t + 1) = L(t) - 1,$$

$$I(t + 1) \sim \text{multinomial}(\lambda(l - 1)).$$

When she is in the breeding ground and decides to travel within the same location,

$$X(t+1) = X(t) - \frac{\text{COT}(t) \times d \times [W(t) + w_f(t)] + \alpha_g(t)}{u},$$

$$L(t+1) = L(t),$$

$$I(t+1) \sim \text{multinomial}(\lambda(I)).$$

When she decides to stay in the current location to feed and rest,

$$X(t+1) = X(t) - \frac{C_f(t) + C_r(t) + \alpha_g(t) - y_j}{u},$$

$$L(t+1) = L(t),$$

$$I(t+1) = I(t),$$

where $C_f(t) = R \times (3,600 \times t_f) \times [W(t) + w_f(t)]$ is the cost of feeding (kJ); $R = 26.23 \times a^{-0.809}$ is the mass-specific rorqual average active metabolic rate (W/kg; from Potvin et al. 2012), and $t_f = t_j \times n_j$ is the time spent feeding in hours (see below); $C_r(t) = t_r/24 \times \text{MR}_r(t)$ is the cost of resting (kJ); $\text{MR}_r(t) = 2 \times \text{BMR}(t)$ is the resting metabolic rate (Potvin et al. 2012); $\text{BMR}(t) = 4 \times [W(t) + w_f(t)]^{0.75} \times 86,400/1,000$ is the daily basal metabolic rate (kJ/d; Kleiber 1975 in Potvin et al. 2012), and $t_r = 24 - t_f$ is the time spent resting; $y_j = n_j \times \Psi \times \rho \times A$ is the gain in energy in patch type i with density j (kJ); n_j is the number of times the forestomach can be filled; $\Psi = 0.47 \times a^{2.88}$ is the forestomach capacity (adjusted from the value reported by Vikingsson [1997] for fin whales as in Wiedenmann et al. [2011]); $A = 0.84$ is the assimilation efficiency (Goldbogen et al. 2011); $\rho = 4,184$ kJ is the energy density of krill (Lockyer 1981); $t_j = \Psi/(\omega_j \times j \times \beta)$ is the time it takes to fill the forestomach, which depends on forestomach capacity Ψ , the number of lunges per hour ω , the krill density j in patch i , location l and time t , and the volume that can be engulfed in a lunge $\beta = 0.0011 \times a^{3.56}$ (Goldbogen et al. 2009); $n_j = h_i(l, t)/t_j$ if t_j (see below) is greater than $t_c = 4$ h, the time required to clear the forestomach (Vikingsson 1997), otherwise $n_j = h_i(l, t)/t_c$. Here, $h_i(l, t)$ is the maximum number of hours available for feeding at location l on day t and corresponds to the hours of daylight, since most blue whale feeding activity is thought to concentrate between dawn and dusk (Croll et al. 1998; Fiedler et al. 1998). We used the astronomical twilight times provided by the Astronomical Applications Department of the US Naval Observatory (downloaded from http://aa.usno.navy.mil/data/docs/RS_OneYear.php), calculated at the center of each of the 36 modeled locations on each day of the year; ω_j is the number of lunges per hour given krill density j ; $\omega_j = 10$ when $j < 0.2$ kg/m³, $\omega_j = 20$ when $0.2 \leq j \leq 0.4$ kg/m³, and $\omega_j = 30$ when $j > 0.4$ kg/m³ (Goldbogen et al. 2015; Hazen et al. 2015).

Sequential Coupling Step: Calf Birth

On December 1 ($t = 244$), the female gives birth and becomes a lactating female. Therefore, in the preceding time step, she only rests in the breeding ground ($L(t = 243) = 1$ or $L(t = 243) = 2$):

$$X(t+1) = X(t) - \frac{C_r(t) + \alpha_g(t)}{u},$$

$$L(t+1) = L(t),$$

$$I(t+1) = I(t).$$

Lactating Female

A lactating female has the same three possible behavioral choices (or four, if in the breeding ground) at each time step.

When she decides to leave her current location and travel forward,

$$\begin{aligned}
 X(t+1) &= X(t) - \frac{\text{COT}(t) \times d \times W(t) + D(t) \times e/E}{u}, \\
 M(t+1) &= \frac{B(c, t+1)}{N(c, t+1) + B(c, t+1)}, \\
 L(t+1) &= L(t) + 1, \\
 I(t+1) &\sim \text{multinomial}(\lambda(l+1)),
 \end{aligned}$$

where $D(t)$ is the amount of milk delivered on that day (see below), $e = 17,309$ kJ/kg is the energy content per unit weight of milk (Lockyer 1981), and $E = 0.9$ is the mammary gland efficiency (Brody 1968 in Lockyer 1981); $N(c, t+1)$ is the calf's lean mass at time $t+1$, assuming a linear growth between 2,350 and 14,235 kg from birth to weaning (Lockyer 1981); $B(c, t+1) = B(c, t) + (D(t) \times e - E_r)/u$, where $B(c, t) = N(c, t) \times M(t)/[1 - M(t)]$ and $E_r \sim 1,190,000$ kJ is the daily energy requirement of the growing calf (see app. A); $D(t) = 0$ if $[X(t) - \text{COT}(t) \times d \times W(t)/u] \leq x_{\text{lac}}$. That is, when a whale does not have lipid reserves in excess of x_{lac} , she will not deliver any milk; $D(t) = [(X(t) - x_{\text{lac}}) \times u - \text{COT}(t) \times d \times W(t)] \times E/e$, if $[X(t) - \text{COT}(t) \times d \times W(t)/u] > x_{\text{lac}}$ and $[(X(t) - x_{\text{lac}}) \times u - \text{COT}(t) \times d \times W(t)] < M_{\text{max}} \times e/E$, where M_{max} is the maximum amount of milk that can be delivered on a given day (Ofteidal 1997). That is, if she does have excess reserves to deliver as milk, and this excess is not greater than the maximum milk she can deliver, she will deliver it all as milk; $D(t) = M_{\text{max}}$, if $[X(t) - \text{COT}(t) \times d \times W(t)/u] > x_{\text{lac}}$ and $[(X(t) - x_{\text{lac}}) \times u - \text{COT}(t) \times d \times W(t)] \geq M_{\text{max}} \times e/E$. That is, if the excess reserves are greater than the milk she can physically deliver, she will deliver the maximum amount of milk possible and store the rest as blubber.

If, with a delivery of $D(t)$, $M(t+1) > m_{\text{max}}$, then

$$\begin{aligned}
 M(t+1) &= m_{\text{max}}, \\
 X(t+1) &= X(t) - \frac{\text{COT}(t) \times d \times W(t) + D(t) \times e/E}{u} + \frac{B(c, t+1) - b_{\text{max}}}{E},
 \end{aligned}$$

where $b_{\text{max}} = N(c, t+1) \times m_{\text{max}}/(1 - m_{\text{max}})$ is the maximum blubber the calf can carry on that day. That is, the mother does not waste the extra energy that the calf cannot store but retains it in her own blubber mass.

When she decides to leave her current location and travel backward,

$$\begin{aligned}
 X(t+1) &= X(t) - \frac{\text{COT}(t) \times d \times W(t) + D(t) \times e/E}{u}, \\
 M(t+1) &= \frac{B(c, t+1)}{N(c, t+1) + B(c, t+1)}, \\
 L(t+1) &= L(t) - 1 \\
 I(t+1) &\sim \text{multinomial}(\lambda(l-1)).
 \end{aligned}$$

If $M(t + 1) > m_{\max}$,

$$M(t + 1) = m_{\max},$$

$$X(t + 1) = X(t) - \frac{\text{COT}(t) \times d \times W(t) + D(t) \times e/E}{u} + \frac{B(c, t + 1) - b_{\max}}{E}.$$

When she is in the breeding ground and decides to travel within the same location,

$$X(t + 1) = X(t) - \frac{\text{COT}(t) \times d \times W(t) - D(t) \times e/E}{u},$$

$$M(t + 1) = \frac{B(c, t + 1)}{N(c, t + 1) + B(c, t + 1)},$$

$$L(t + 1) = L(t),$$

$$I(t + 1) \sim \text{multinomial}(\lambda(\mathbf{I})).$$

If $M(t + 1) > m_{\max}$, then

$$M(t + 1) = m_{\max},$$

$$X(t + 1) = X(t) - \frac{\text{COT}(t) \times d \times W(t) + D(t) \times e/E}{u} + \frac{B(c, t + 1) - b_{\max}}{E}.$$

When she decides to stay in the current location to feed and rest,

$$X(t + 1) = X(t) - \frac{C_f(t) + C_r(t) - y_j + D(t) \times e/E}{u},$$

$$M(t + 1) = \frac{B(c, t + 1)}{N(c, t + 1) + B(c, t + 1)},$$

$$L(t + 1) = L(t),$$

$$I(t + 1) = I(t),$$

where $D(t) = 0$, if $[X(t) - (C_f(t) + C_r(t) - y_j)/u] \leq x_{\text{lac}}$; $D(t) = [(X(t) - x_{\text{lac}}) \times u - C_f(t) - C_r(t) + y_j] \times E/e$, if $[X(t) - (C_f(t) + C_r(t) - y_j)/u] > x_{\text{lac}}$ and $[(X(t) - x_{\text{lac}}) \times u - C_f(t) - C_r(t) + y_j] < M_{\max} \times e/E$; and $D(t) = M_{\max}$, if $[X(t) - (C_f(t) + C_r(t) - y_j)/u] > x_{\text{lac}}$ and $[(X(t) - x_{\text{lac}}) \times u - C_f(t) - C_r(t) + y_j] \geq M_{\max} \times e/E$.

If $M(t + 1) > m_{\max}$, then

$$M(t + 1) = m_{\max},$$

$$X(t + 1) = X(t) - \frac{C_f(t) + C_r(t) - y_j + D(t) \times e/E}{u} + \frac{B(c, t + 1) - b_{\max}}{E}.$$

Table B1: Parameters of the equations of the state dynamics

Parameter	Description	Value	Unit	Reference
a	Whale asymptotic length	22	m	Gilpatrick and Perryman 2008
W_a	Mean weight of an adult female	57,000	kg	Lockyer 1976
g	Whale mean lean (nonblubber) mass, given a	42,000	kg	Lockyer 1976
$COT(t)$	Cost of transport	$7.79 \times [W(t) + w_f(t)]^{0.29}$	kJ/kg/km	Williams 1999
$W(t)$	Whale mass at time t	$g + X(t)$	kg	Lockyer 1976
$w_f(t)$	Weight of fetus at time t	$[0.52 \times (t + 90 - 73)]^3/1,000$	kg	Huggett and Widdas 1950
$h(t)$	Heat of gestation at time t	$p(t) \times (4,400 \times 4.184 \times w_b^{1.2})$	kJ	Lockyer 1981, 2007
$p(t)$	Proportional daily growth of fetus	$\Delta w_f(t)/w_b^\dagger$...	Huggett and Widdas 1950
c_f	Energetic cost per kg of fetus weight	$2,940 \times 4.184$	kJ/kg	Lockyer 1981, 1987, 2007
w_b	Final weight of fetus and weight of calf at birth	2,500	kg	Huggett and Widdas 1950
u	Utilizable energy in blubber	$4,137 \times 4.184 = 31,798$	kJ/kg	Lockyer 1981
R	Rorqual average active metabolic rate	2.15	W/kg	Potvin et al. 2012
$BMR(t)$	Basal daily metabolic rate	$4 \times W(t)^{0.75} \times 86,400/1,000$	kJ/d	Kleiber 1975
$MR_r(t)$	Resting daily metabolic rate	$2 \times BMR(t)$	kJ/d	Potvin et al. 2012
ψ	Forestomach capacity	$0.47 \times a^{2.88}$	kg	Vikingsson 1997; Wiedenmann et al. 2011
A	Assimilation efficiency	0.84	...	Goldbogen et al. 2011
ρ	Energy density of krill	4,184	kJ	Lockyer 1981
β	Volume of water ingested per lunge	$0.0011 \times a^{3.56}$	m ³	Goldbogen et al. 2009
t_c	Time required to empty forestomach	4	h	Vikingsson 1997
ω_j	No. lunges per hour, given food density j	10 for $j < 0.2$ kg/m ³ ; 20 for $0.2 \leq j \leq 0.4$ kg/m ³ ; 30 for $j > 0.4$ kg/m ³	n/h	Goldbogen et al. 2015; Hazen et al. 2015
$h_f(l, t)$	Max. no. hours available for feeding at location l on day t	Astronomical twilight times (Astronomical Applications Department of the US Naval Observatory)	h	Croll et al. 1998; Fiedler et al. 1998
M_{max}	Max. amount of milk delivered per day	220	kg/d	Oftedal 1997
e	Milk energy content	$4,137 \times 4.184 = 17,309$	kJ/kg	Lockyer 1981
E	Mammary gland efficiency	0.9	...	Brody 1968
w_{cal}	Calorific content of lean whale meat	$1,500 \times 4.184$	kJ/kg	Lockyer 1981
MR_c	Calf daily metabolic rate	$200,000 \times 4.184 \sim 837,000$	kJ/d	Lockyer 1981
g_c	Total growth of calf during lactation	17,000	kg	Lockyer 1981
$N(c, t = 244)$	Lean mass of calf at birth	2,350 [†]	kg	Huggett and Widdas 1950
$N(c, T)$	Lean mass of calf at weaning time T	14,235 [†]	kg	Lockyer 1981
d_i	Time after which a patch degrades	21 [†]	d	Bailey et al. 2010
s	Age threshold for calf to be able to leave breeding ground with mother	40	d	...

Note: When the value changes over time, the corresponding time-dependent equation is reported, where t indicates model time (i.e., $t = 1$ corresponds to April 1). Where the values from the original reference were transformed from kcal to kJ, the calculation is reported explicitly.

[†] These values were derived from the cited source following calculations described in the text.

Appendix C from E. Pirotta et al., “A Dynamic State Model of Migratory Behavior and Physiology to Assess the Consequences of Environmental Variation and Anthropogenic Disturbance on Marine Vertebrates” (Am. Nat., vol. 191, no. 2, p. E000)

Stochastic Dynamic Programming Equations

Terminal Fitness Function

$$\varphi_s(m) = \frac{m^\gamma}{m^\gamma + m_{50}^\gamma}$$

Lactating Female ($t > 243$)

Given $X(t) = x, M(t) = m, L(t) = l = 1, I(t) = i$:

$$\begin{aligned} F_{\text{lac}}(x, m, l, i, t) = & \max\{\sum_j p(i, l, t, j) F_{\text{lac}}(x', m', l, i, t + 1); H(t - (s + 244)) \\ & \times \sum_k \lambda(l + 1, k) F_{\text{lac}}(x'', m'', l + 1, k, t + 1); \\ & \sum_k \lambda(l, k) F_{\text{lac}}(x'', m'', l, k, t + 1)\} \end{aligned}$$

Given $X(t) = x, M(t) = m, L(t) = l = 2, I(t) = i$:

$$\begin{aligned} F_{\text{lac}}(x, m, l, i, t) = & \max\{\sum_j p(i, l, t, j) F_{\text{lac}}(x', m', l, i, t + 1); H(t - (s + 244)) \\ & \times \sum_k \lambda(l + 1, k) F_{\text{lac}}(x'', m'', l + 1, k, t + 1); \\ & \sum_k \lambda(l - 1, k) F_{\text{lac}}(x'', m'', l - 1, k, t + 1); \\ & \sum_k \lambda(l, k) F_{\text{lac}}(x'', m'', l, k, t + 1)\} \end{aligned}$$

Given $X(t) = x, M(t) = m, L(t) = l > 2, I(t) = i$:

$$\begin{aligned} F_{\text{lac}}(x, m, l, i, t) = & \max\{\sum_j p(i, l, t, j) F_{\text{lac}}(x', m', l, i, t + 1); \sum_k \lambda(l + 1, k) F_{\text{lac}}(x'', m'', l + 1, k, t + 1); \\ & \sum_k \lambda(l - 1, k) F_{\text{lac}}(x'', m'', l - 1, k, t + 1)\} \\ x' = & [1 - H(x - (C_f(t) + C_r(t) - y_j)/u - x_{\text{lac}})] \times \{x - [C_f(t) + C_r(t) - y_j]/u\} \\ & + H(x - (C_f(t) + C_r(t) - y_j)/u - x_{\text{lac}}) \times [1 - S((x - x_{\text{lac}}) \times u - C_f(t) - C_r(t) \\ & + y_j - M_{\text{max}} \times e/E)] \times x_{\text{lac}} + H(x - (C_f(t) + C_r(t) - y_j)/u - x_{\text{lac}}) \times S((x - x_{\text{lac}}) \times u - C_f(t) - C_r(t) \\ & + y_j - M_{\text{max}} \times e/E) \times \{x - [C_f(t) + C_r(t) - y_j - M_{\text{max}} \times e/E]/u\} \\ x'' = & [1 - H(x - \text{COT}(t) \times d \times (x + g)/u - x_{\text{lac}})] \times [x - \text{COT}(t) \times d \times (x + g)/u] + H(x - \text{COT}(t) \\ & \times d \times (x + g)/u - x_{\text{lac}}) \times [1 - S((x - x_{\text{lac}}) \times u - \text{COT}(t) \times d \times (x + g) - M_{\text{max}} \times e/E)] \times x_{\text{lac}} \\ & + H(x - \text{COT}(t) \times d \times (x + g)/u - x_{\text{lac}}) \times S((x - x_{\text{lac}}) \times u - \text{COT}(t) \times d \times (x + g) - M_{\text{max}} \\ & \times e/E) \times \{x + [-\text{COT}(t) \times d \times (x + g) - M_{\text{max}} \times e/E]/u\} \end{aligned}$$

$$\begin{aligned}
 m' = & [1 - H(x - (C_f(t) + C_r(t) - y_j)/u - x_{lac})] \times [N(c, t) \times m/(1 - m) + (0 - E_r)/u] / \{N(c, t + 1) \\
 & + [N(c, t) \times m/(1 - m) + (0 - E_r)/u] + H(x - (C_f(t) + C_r(t) - y_j)/u - x_{lac}) \times [1 - S((x - x_{lac}) \\
 & \times u - C_f(t) - C_r(t) + y_j - M_{max} \times e/E)] \times [N(c, t) \times m/(1 - m) + [(x - x_{lac}) \times u - C_f(t) - C_r(t) + y_j] \\
 & \times E - E_r)/u] / \{N(c, t + 1) + [N(c, t) \times m/(1 - m) + [(x - x_{lac}) \times u - C_f(t) - C_r(t) + y_j] \times E - E_r)/u]\} \\
 & + H(x - (C_f(t) + C_r(t) - y_j)/u - x_{lac}) \times S((x - x_{lac}) \times u - C_f(t) - C_r(t) + y_j - M_{max} \times e/E) \\
 & \times [N(c, t) \times m/(1 - m) + (M_{max} \times e - E_r)/u] / \{N(c, t + 1) + [N(c, t) \times m/(1 - m) \\
 & + (M_{max} \times e - E_r)/u]\}
 \end{aligned}$$

$$\begin{aligned}
 m'' = & [1 - H(x - COT(t) \times d \times (x + g)/u - x_{lac})] \times [N(c, t) \times m/(1 - m) + (0 - E_r)/u] / \{N(c, t + 1) \\
 & + N(c, t) \times m/(1 - m) + (0 - E_r)/u\} + H(x - COT(t) \times d \times (x + g)/u - x_{lac}) \\
 & \times [1 - S((x - x_{lac}) \times u - COT(t) \times d \times (x + g) - M_{max} \times e/E)] \times [N(c, t) \times m/(1 - m) \\
 & + [(x - x_{lac}) \times u - COT(t) \times d \times (x + g)] \times E - E_r)/u] / \{N(c, t + 1) + [N(c, t) \times m/(1 - m) \\
 & + [(x - x_{lac}) \times u - COT(t) \times d \times (x + g)] \times E - E_r)/u\} + H(x - COT(t) \times d \times (x + g)/u - x_{lac}) \\
 & \times S((x - x_{lac}) \times u - COT(t) \times d \times (x + g) - M_{max} \times e/E) \times [N(c, t) \times m/(1 - m) \\
 & + (M_{max} \times e - E_r)/u] / \{N(c, t + 1) + [N(c, t) \times m/(1 - m) + (M_{max} \times e - E_r)/u]\}
 \end{aligned}$$

If $m' > m_{max}$: $x' = x' + [N(c, t + 1) \times m'/(1 - m') - N(c, t + 1) \times m_{max}/(1 - m_{max})]/E$; $m' = m_{max}$
 If $m'' > m_{max}$: $x'' = x'' + [N(c, t + 1) \times m''/(1 - m'') - N(c, t + 1) \times m_{max}/(1 - m_{max})]/E$; $m'' = m_{max}$

$$H(z) = 1 \text{ if } z > 0, \text{ and } H(z) = 0 \text{ if } z \leq 0$$

$$S(z) = 1 \text{ if } z \geq 0, \text{ and } S(z) = 0 \text{ if } z < 0$$

$$F_{lac}(x, m, l, i, t) = 0 \quad \text{if } m \leq m_{min}$$

$$F_{lac}(x, m, l, i, t) = \varphi_s(m_f) \text{ if } x \leq x_{min}$$

where $m_f = (B(c, t) - E_{rem})/[N(c, T) + (B(c, t) - E_{rem})]$; $E_{rem} = E_r \times (T - t)/u$.

Pregnant Female (t < 243)

Given $X(t) = x$, $L(t) = l = 1$, $I(t) = i$:

$$F_{preg}(x, l, i, t) = \max\{\sum_j p(i, l, t, j) F_{preg}(x', l, i, t + 1); \sum_k \lambda(l + 1, k)$$

$$F_{preg}(x'', l + 1, k, t + 1); \sum_k \lambda(l, k)$$

$$F_{preg}(x'', l, k, t + 1)\}$$

Given $X(t) = x$, $L(t) = l = 2$, $I(t) = i$:

$$F_{preg}(x, l, i, t) = \max\{\sum_j p(i, l, t, j) F_{preg}(x', l, i, t + 1); \sum_k \lambda(l + 1, k)$$

$$F_{preg}(x'', l + 1, k, t + 1); \sum_k \lambda(l - 1, k)$$

$$F_{preg}(x'', l - 1, k, t + 1); \sum_k \lambda(l, k)$$

$$F_{preg}(x'', l, k, t + 1)\}$$

Given $X(t) = x$, $L(t) = l > 2$, $I(t) = i$:

$$F_{\text{preg}}(x, l, i, t) = \max\{\sum_j p(i, l, t, j) F_{\text{preg}}(x', l, i, t + 1); \sum_k \lambda(l + 1, k) F_{\text{preg}}(x'', l + 1, k, t + 1); \sum_k \lambda(l - 1, k) F_{\text{preg}}(x'', l - 1, k, t + 1)\}$$

$$x' = x - [C_f(t) + C_r(t) + \alpha_g(t) - y_j]/u$$

$$x'' = x - \{\text{COT}(t) \times d \times [x + g + w_f(t)] + \alpha_g(t)\}/u$$

$$F_{\text{preg}}(x, l, i, t) = 0 \text{ if } x < x_{\text{abo}}$$

Transition between Pregnancy and Lactation (t = 243; Sequential Coupling)

Given $X(t) = x$, $L(t) = l$, $I(t) = i$:

$$F_{\text{preg}}(x, l, i, t) = F_{\text{lac}}(x', m_0, l, i, t + 1)$$

$$x' = x - [C_r(t) + \alpha_g(t)]/u$$

$$m_0 = 0.06$$

$$F_{\text{preg}}(x, l, i, t) = 0 \text{ if } l > 2 \text{ or } x < x_{\text{abo}}$$

For the backward iteration of the stochastic dynamic programming equations, we used linear interpolation when the values of the state variables were not integers. When the fitness values corresponding to different behavioral decisions were the same, we recorded these behavioral decisions and picked one at random in the forward iteration.

Appendix D from E. Pirotta et al., “A Dynamic State Model of Migratory Behavior and Physiology to Assess the Consequences of Environmental Variation and Anthropogenic Disturbance on Marine Vertebrates”

(Am. Nat., vol. 191, no. 2, p. E000)

Details of Simulated Scenarios

Scenario 1: El Niño Conditions

Nyctiphanes simplex extends to the waters of North California ($l = 28$) at the expense of *Thysanoessa spinifera* and *Euphausia pacifica* (Benson et al. 2002; Chavez et al. 2002; Marinovic et al. 2002). Specifically, we simulate a reduction by 70% in the two temperate species, following a corresponding increase in *N. simplex* in the southern and central California Current; that is, $\lambda(l = 15:28, i = 1:3) = (0.49, 0.21, 0.3)$. Productivity in this region is also reduced by 70% overall (Chavez et al. 2002); that is, the upwelling index is multiplied by an additional scaling factor $eN = 0.3$.

Scenario 2: Unprecedented Change in the Environment (2005-Like)

The 2–3 month delay in upwelling in the southern and central California Current (Brodeur et al. 2005; Schwing et al. 2006) is simulated by adding an additional lag of 75 days between the upwelling and the krill index in this region. The resulting reduction in productivity is simulated by increasing the probability of encountering patches without food by 70%, that is, $\lambda(l = 15:28, i = 1:3) = (0, 0.21, 0.79)$.

Scenario 3: Intense, Localized Disturbance, Staying Response

Location 16 (Southern California) is disturbed every day (i.e., with a daily probability of 1) for the entire duration of the reproductive cycle. For all whales, $r_k = 0$; that is, all whales stay in the disturbed location, but feeding time is reduced to 0 on disturbed days (i.e., every day). This scenario exemplifies a source of intense disturbance operating continuously at a small spatial scale, such as a seismic survey for oil and gas exploration, a naval exercise, or pile-driving associated with the construction of an offshore wind farm.

Scenario 4: Intense, Localized Disturbance, Moving Away Response

Location 16 (Southern California) is disturbed every day (i.e., with a daily probability of 1) for the entire duration of the reproductive cycle. For all whales, $r_k = 1$; that is, all whales respond by moving away from the disturbed location.

Scenario 5: Weak, Diffuse Disturbance, Mixed Response

Half of the locations along the migratory range (selected at random at the beginning of the simulation) are disturbed with a 50% daily probability. The time available for feeding at these locations (and, hence, feeding performance) is reduced to 50% of the original time on disturbed days. Whales' tendency to move away from disturbed locations is drawn from a beta distribution at the start of the simulation; that is, $r_k \sim \beta(5, 5)$. This scenario could simulate the disturbance resulting from activities such as shipping traffic or whale watching, which can operate over a large portion of the whales' range but are weaker in intensity.

A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates

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The American Naturalist

Supplementary material: Sensitivity analysis

Table S1. List of parameters tested in the sensitivity analysis. Some sensitivity combinations could not be tested or the corresponding percentage change had to be adjusted, because they involved impossible values of the parameters.

Parameter	Description	Sensitivity combinations
W_a	Mean weight of an adult female*	$\pm 10, \pm 20$ and $\pm 40\%$
g	Mean lean mass	$\pm 10, \pm 20, -40$ and $+30\%$
x_{max}	Maximum blubber mass	$\pm 10, \pm 20$ and $\pm 40\%$
x_{min}	Minimum blubber mass	$\pm 10, \pm 20$ and $\pm 40\%$
x_{abo}	Threshold blubber mass for abortion	$\pm 10, \pm 20$ and $\pm 40\%$
x_{lac}	Threshold blubber mass for lactation	$\pm 10, \pm 20$ and $\pm 40\%$
m_{max}	Maximum % blubber mass of the calf	$\pm 10, \pm 20$ and $\pm 40\%$
m_{min}	Minimum % blubber mass of the calf	$\pm 10, \pm 20$ and $\pm 40\%$
m_{50}	Scale parameter of the fitness function (% blubber mass of the calf at which calf survival probability is 0.5)	$\pm 10, \pm 20$ and $\pm 40\%$
γ	Shape parameter of the fitness function	$\pm 10, \pm 20$ and $\pm 40\%$
M_{max}	Maximum amount of milk delivered per day	$\pm 10, \pm 20$ and $\pm 40\%$
e	Milk energy content	$\pm 10, \pm 20$ and $\pm 40\%$
E	Mammary gland efficiency	$\pm 10, -20$ and -40%
c_f	Energetic cost per kg of fetus weight	$\pm 10, \pm 20$ and $\pm 40\%$
$w_f(t)$	Weight of the fetus at time t^{**}	$\pm 10, \pm 20$ and $\pm 40\%$
$h(t)$	Heat of gestation at time t	$\pm 10, \pm 20$ and $\pm 40\%$
s	Age threshold for the calf to be able to leave the breeding ground with the mother	$\pm 10, \pm 20$ and $+40\%$
$N(c, t = 244)$	Lean mass of the calf at birth	$-10, -20$ and -40%

g_c	Total growth of the calf during lactation	$\pm 10, \pm 20$ and $\pm 40\%$
$N(c, T)$	Lean mass of the calf at weaning	$\pm 10, \pm 20, -40$ and $+30\%$
w_{cal}	Calorific content of lean whale meat	$\pm 10, \pm 20$ and $\pm 40\%$
MR_c	Calf daily metabolic rate	$\pm 10, \pm 20$ and $\pm 40\%$
u	Utilizable energy in blubber	$\pm 10, \pm 20$ and $\pm 40\%$
ω_1	Number of lunges per hour, given food density $< 0.2 \text{ kg/m}^3$	$\pm 10, \pm 20$ and $\pm 40\%$
ω_2	Number of lunges per hour, given $0.2 \leq \text{food density} \leq 0.4 \text{ kg/m}^3$	$\pm 10, \pm 20$ and $\pm 40\%$
ω_3	Number of lunges per hour, given food density $> 0.4 \text{ kg/m}^3$	$\pm 10, \pm 20$ and $\pm 40\%$
R	Rorqual Average Active Metabolic Rate	$\pm 10, \pm 20$ and $\pm 40\%$
β	Volume of water ingested in a lunge	$\pm 10, \pm 20$ and $\pm 40\%$
t_e	Time required to clear the forestomach	$\pm 10, \pm 20$ and $\pm 40\%$
ψ	Forestomach capacity	$\pm 10, \pm 20$ and $\pm 40\%$
ρ	Energy density of krill	$\pm 10, \pm 20$ and $\pm 40\%$
A	Assimilation efficiency	$\pm 10, \pm 20$ and -40%
$h_f(l, t)$	Maximum number of hours available for feeding at location l on day t	$\pm 10, \pm 20$ and $\pm 40\%$
Shape of $p(2, 17, 159, j)$	Shape parameter for the Gamma distribution of krill densities in in the waters off southern California in summer	$\pm 10, \pm 20$ and $\pm 40\%$
Rate of $p(2, 17, 159, j)$	Rate parameter for the Gamma distribution of krill densities in in the waters off southern California in summer	$\pm 10, \pm 20$ and $\pm 40\%$
r_s	Size ratio between different krill species	$\pm 10, \pm 20$ and $\pm 40\%$
lag	Temporal lag between upwelling and krill peak in California Current	$\pm 10, \pm 20$ and $\pm 40\%$
$\lambda(l)$	Vector of probabilities of encountering different patch types (given location l)	$\pm 10, \pm 20$ and $\pm 40\%$
$BMR(t)$	Basal daily metabolic rate	$\pm 10, \pm 20$ and $\pm 40\%$
$COT(t)$	Cost of transport	$\pm 10, \pm 20$ and $\pm 40\%$
d_t	Days after which a patch degrades	$\pm 10, \pm 20$ and $\pm 40\%$

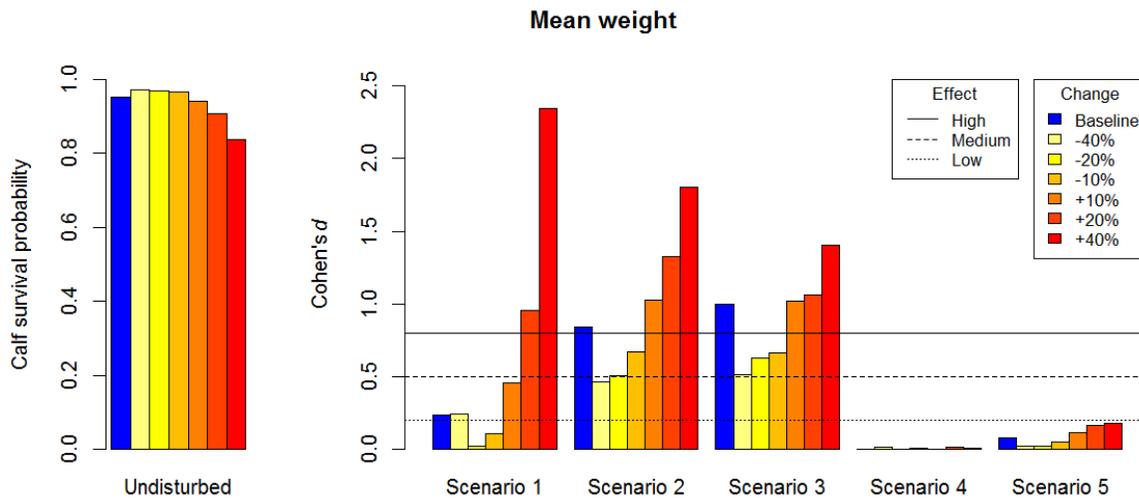
* This includes uncertainty on the average length.

** This also affects the final weight of the fetus (which is equal to the weight of the calf at birth).

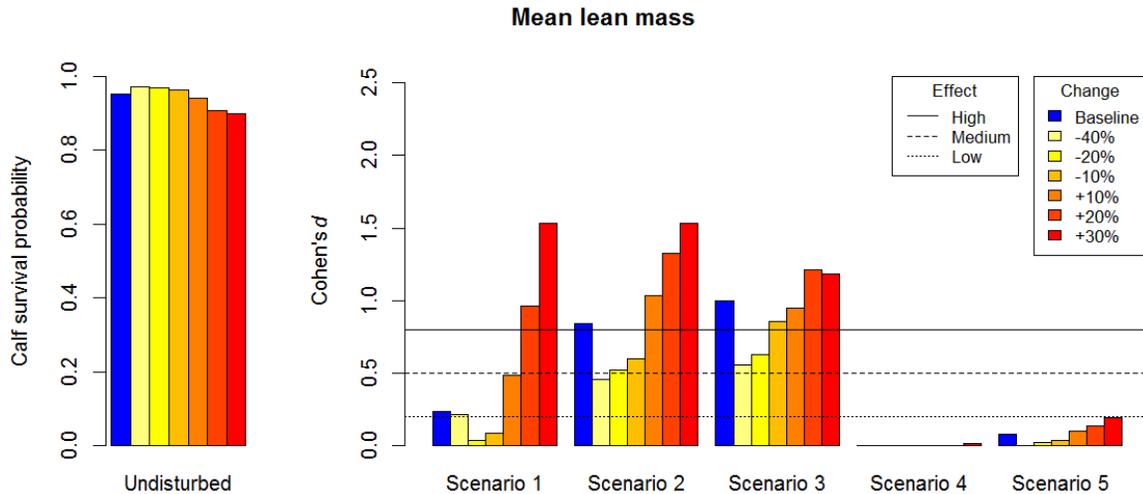
Results of the sensitivity analysis

Details of how each parameter affected model results are reported below, together with summary figures. In each figure, the bar plot on the left shows the survival probability of the calf in baseline conditions and under the sensitivity analysis. On the right, the bar plots summarize the values of Cohen's d for each scenario of environmental or anthropogenic disturbance. The colors indicate the size of the change in the corresponding parameter, while the horizontal lines indicate the threshold for an effect to be considered low, medium or high based on the value of Cohen's d (Cohen 1977).

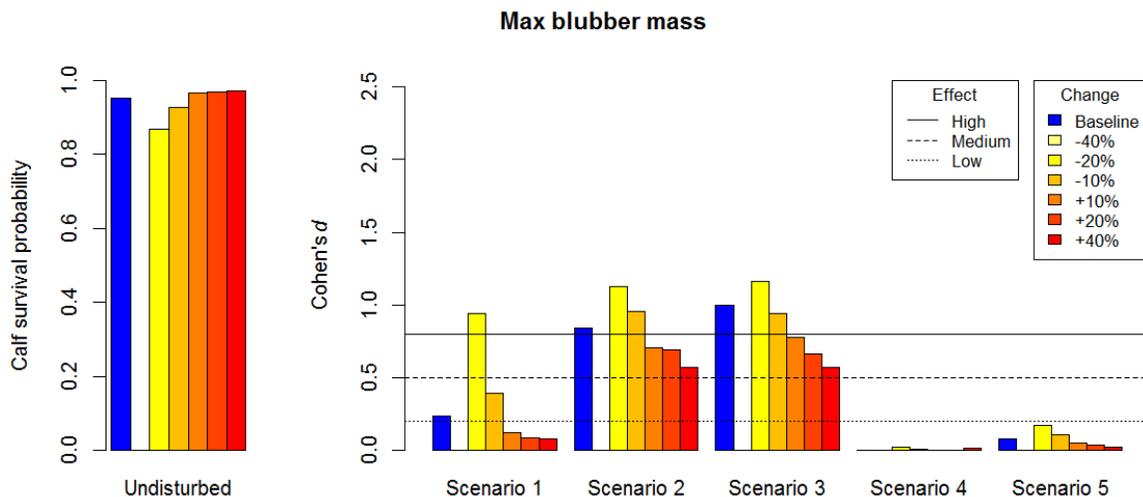
Mean weight of the adult: higher values of this parameter caused a substantial reduction in calf survival probability. This parameter also had a strong influence on the value of Cohen's d , which was lower when the mean weight was decreased, and higher when it was increased. A higher mean weight required females to sustain a larger mass, which resulted in higher metabolic rates, more abortions and a lower ability to nurse the growing calf, causing a higher sensitivity to any perturbation (environmental or anthropogenic).



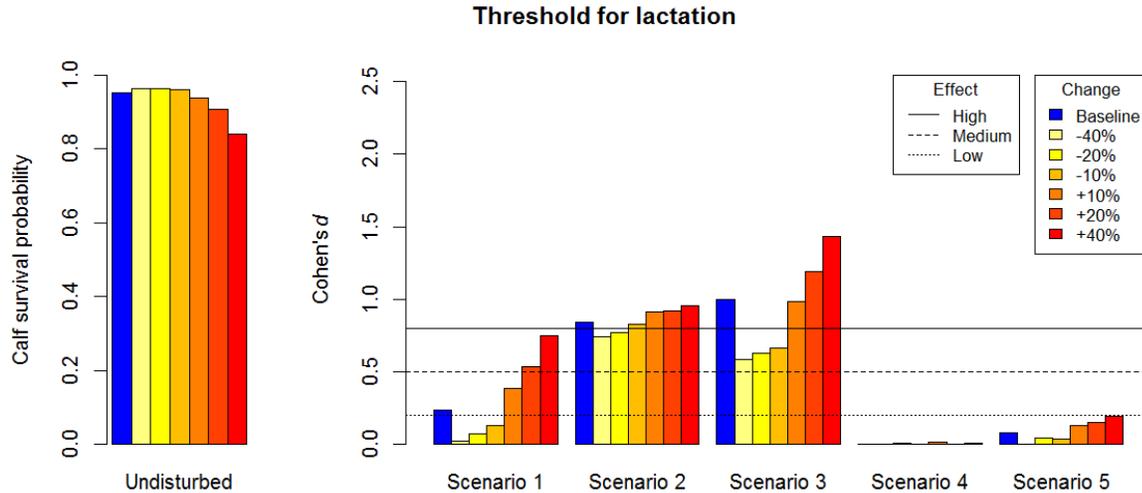
Mean lean mass: the sensitivity results for this parameter were comparable to the ones for total mean weight. Similarly, a higher lean mass caused higher energy requirements while reducing the compensatory abilities of the female. Very low (e.g. -40%, corresponding to 43% lean mass) and very high (e.g. +30%, corresponding to 95% lean mass) mean percentages of lean mass, however, are unlikely to be occurring, since they would imply unrealistic blubber storage capabilities.



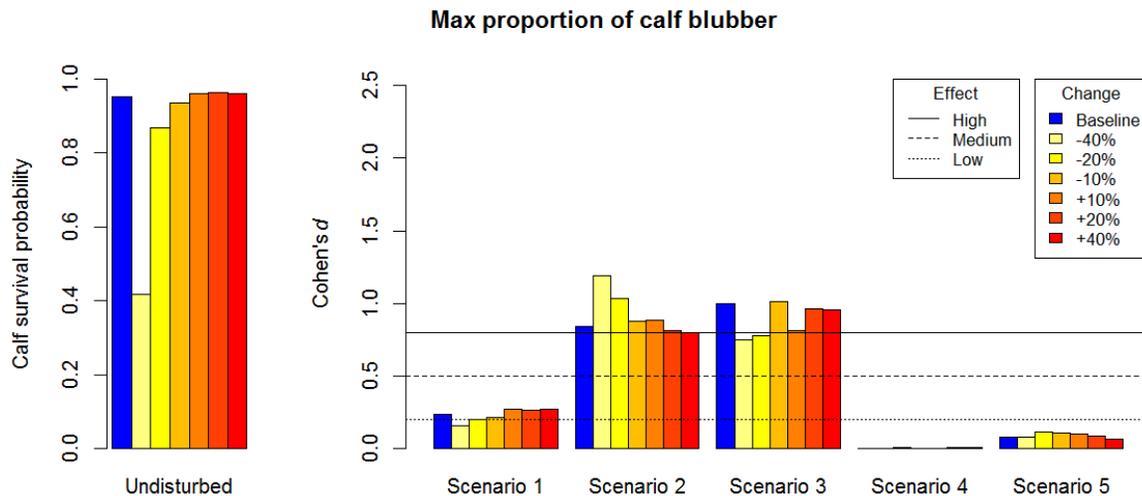
Maximum blubber mass: a reduction in the maximum amount of blubber that a female can store had a strong influence on her reproductive success, which dropped to 0 for a 40% decrease (approximately 13 tons of blubber, as opposed to 22 tons in the baseline scenario). In general, lower blubber stores resulted in a reduced ability of the female to counteract disturbance, which thus had a stronger effect. Vice versa, higher storage abilities resulted in higher calf survival probability and higher resilience to disturbance.



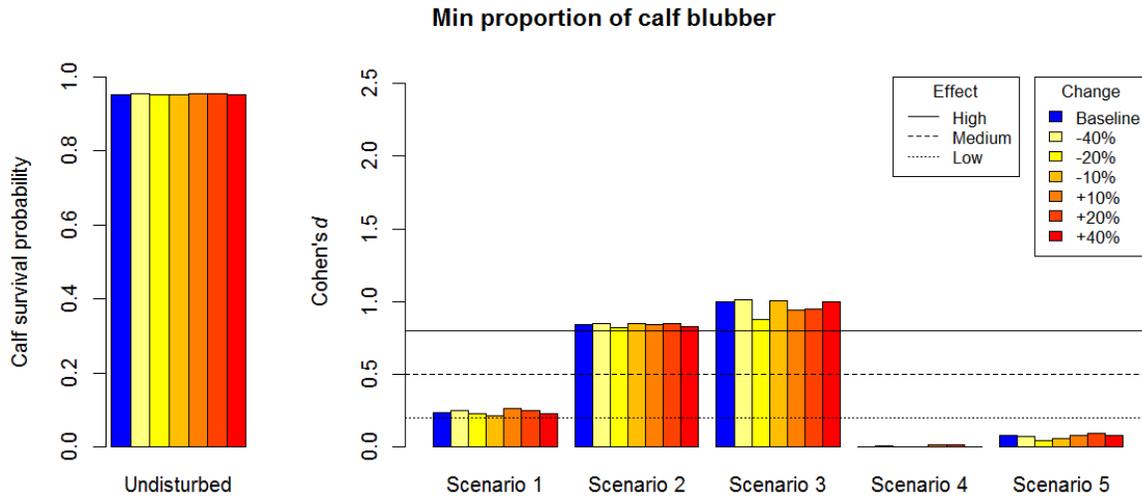
Threshold blubber mass for lactation: this threshold had a stronger effect on the results than the one for abortion. An increased value led to a decrease in calf survival probability and a more dramatic effect of both environmental and anthropogenic disturbances. A higher threshold implied that the whale needed to maintain a higher condition to be able to nurse her calf, and calf condition was therefore affected, reducing its chances to survive when the mother was disturbed. Conversely, a lower threshold had a positive effect on both survival probability and resilience to disturbance.



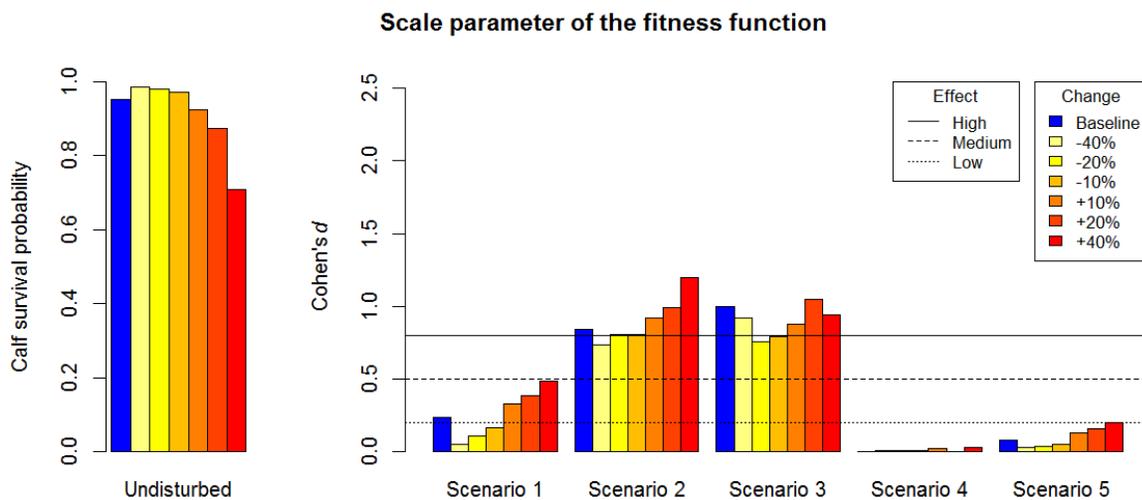
Maximum proportion of blubber mass of the calf: results were not sensitive to the overestimation of the maximum proportion of blubber mass that the calf can accumulate. However, severe underestimation of this parameter (-40% and -20%, corresponding to a percentage of blubber equal to 26% and 35%) had a strong impact on calf survival probability and the effects of disturbance. This was mostly because the fitness function remained unvaried, and a calf was simply unable to reach a condition that would guarantee a higher survival. In reality, the relationship between calf blubber mass and its survival is likely to vary together with the maximum blubber that a calf can accumulate, and the effects of an underestimation would therefore be reduced.



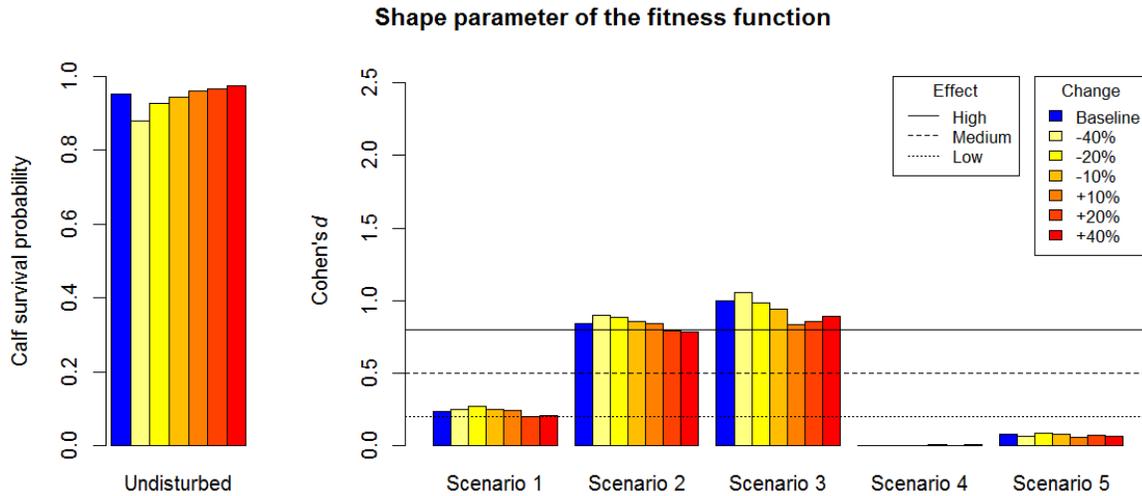
Minimum proportion of blubber mass of the calf: this parameter did not have a large influence on the results of the simulations. Both calf survival probability and the conclusions of the disturbance scenarios remained substantially unchanged in our sensitivity analysis.



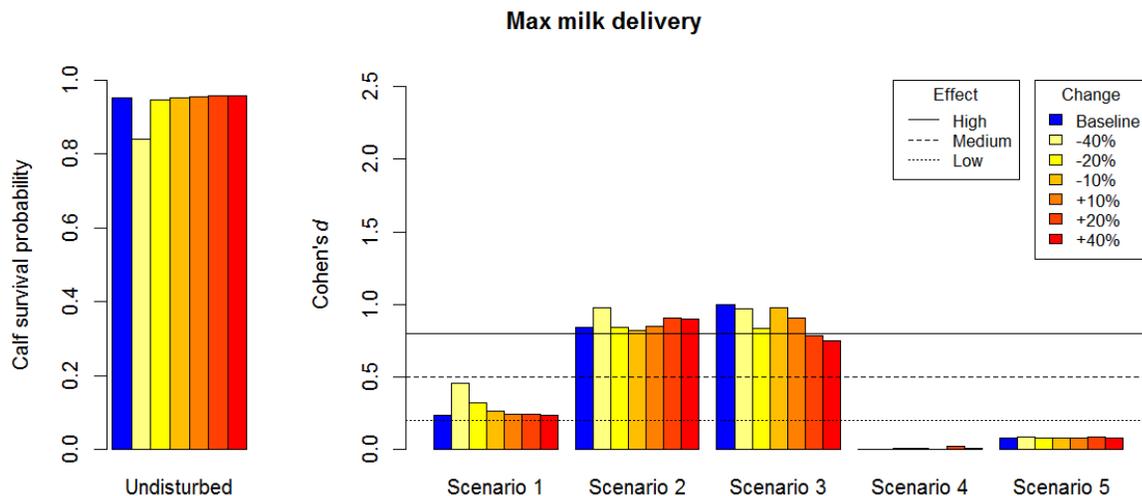
Scale parameter of the fitness function: as predictable, this parameter had a substantial influence on both calf survival probability and the results of the disturbance scenarios. A higher value meant that the calf had to be in better condition at the end of the simulation to be able to have the same survival probability as in the baseline, and vice versa when this value was lower.



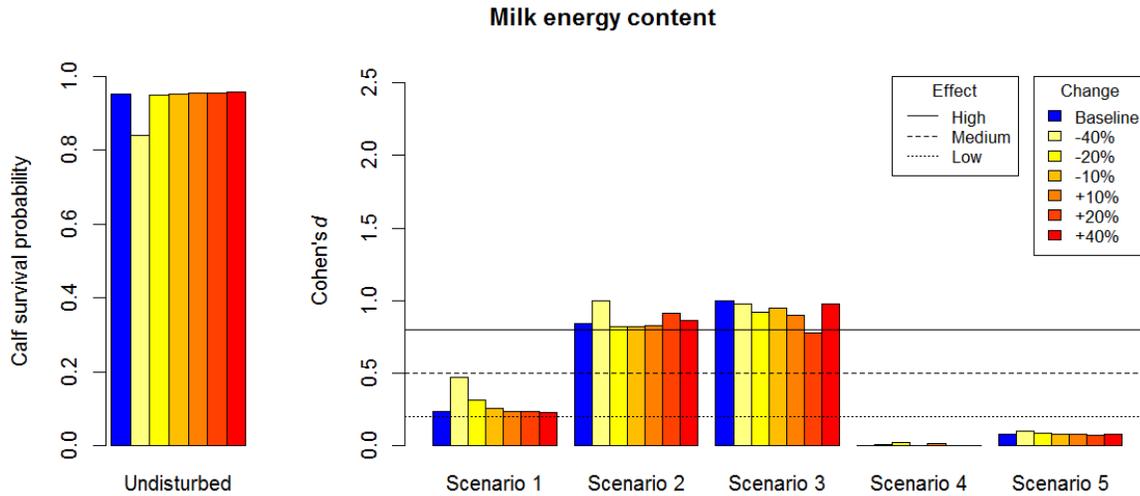
Shape parameter of the fitness function: a smaller value of γ (i.e. lower steepness of the fitness curve) led to lower calf survival probability and higher values improved survival. While affected, the value of Cohen's d for each disturbance scenario did not change dramatically, and conclusions on effect sizes were substantially unchanged. The value of γ appeared to mainly affect the conversion from calf's proportion of blubber mass to survival at the end of the simulations.



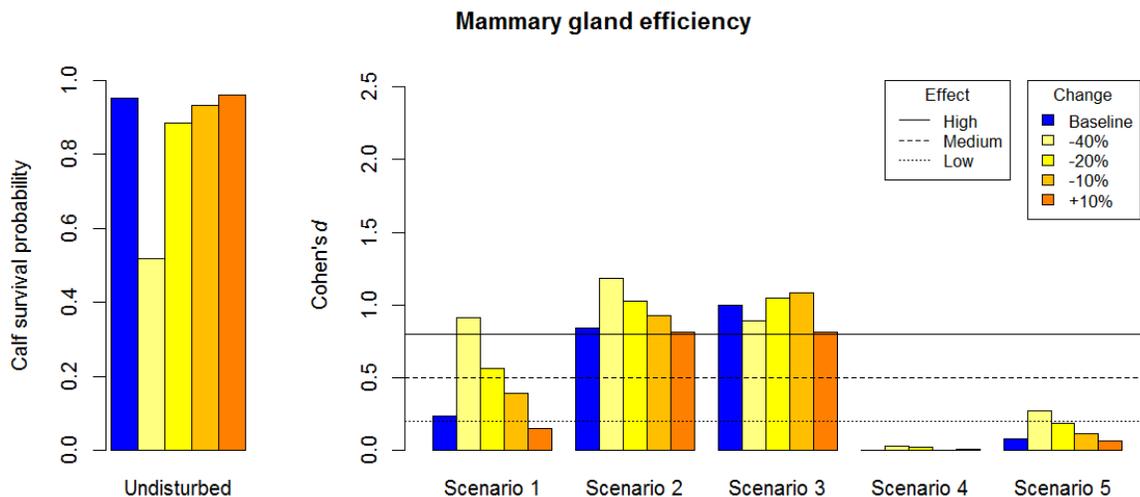
Maximum milk delivery: This parameter was found to affect calf survival probability mainly when its value was severely reduced (-40%). This reduction (132 kg/d) resulted in stronger consequences of the environmental changes. Insufficient milk received by the calf therefore became particularly problematic when the environment was less productive and the mother was less able to compensate for reduced nursing. In contrast, more energy transferable from the mother to the calf appeared to protect the calf against the effects of anthropogenic disturbance, improving the results in Scenario 3. Overall, the sensitivity of the results was lower than for other parameters, even though the range of values was large (132-308 kg/d).



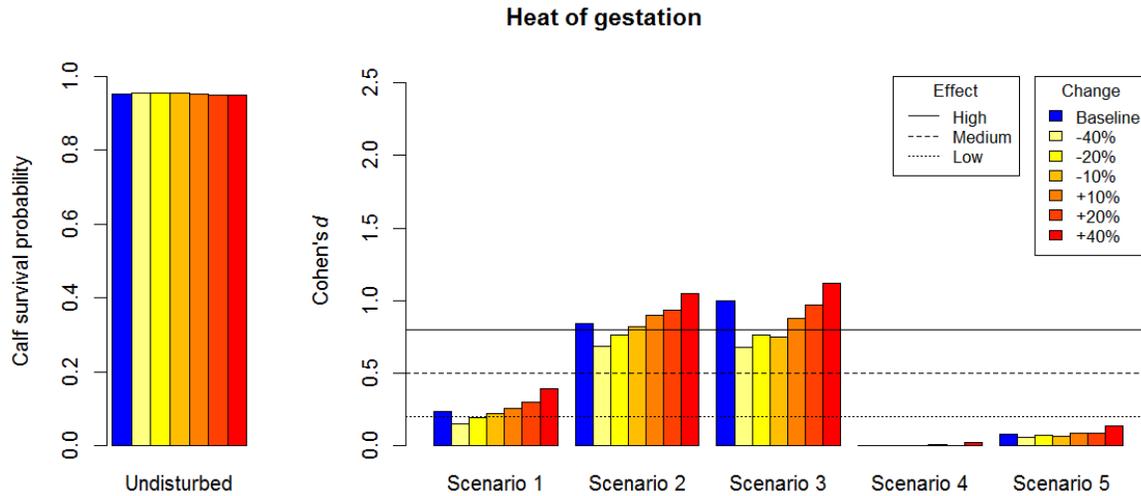
Milk energy content: changes to this parameter had a similar influence on the estimates of survival probability and the values of Cohen's d as the maximum milk delivery. Substantially higher energy content (+40%) appeared to lose the beneficial effect that was observed for the amount of milk delivered under Scenario 3, possibly because of the higher costs of producing milk incurred by the mother. However, extreme under- or overestimation of this parameter is unlikely.



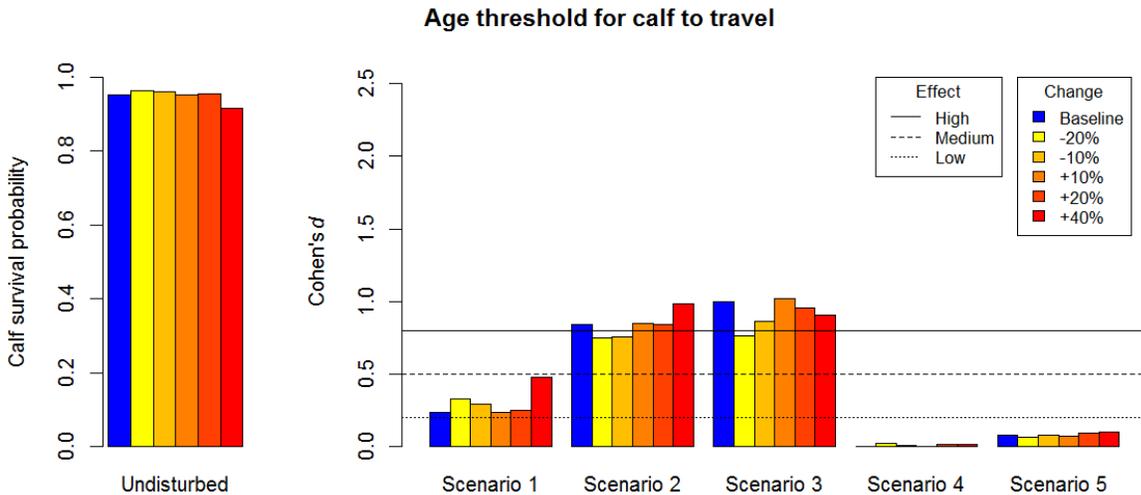
Mammary gland efficiency: low values of this parameter caused calf survival to drop in undisturbed conditions, and decline more dramatically in the disturbed scenarios. However, such low efficiencies (e.g. 0.5, corresponding to a -40% reduction, or 0.8, corresponding to a -10% reduction) are unrealistic for marine mammals (Lockyer 1981; Villegas-Amtmann *et al.* 2015). The sensitivity to +20% and +40% increases could not be tested, since these led to efficiencies greater than 1.



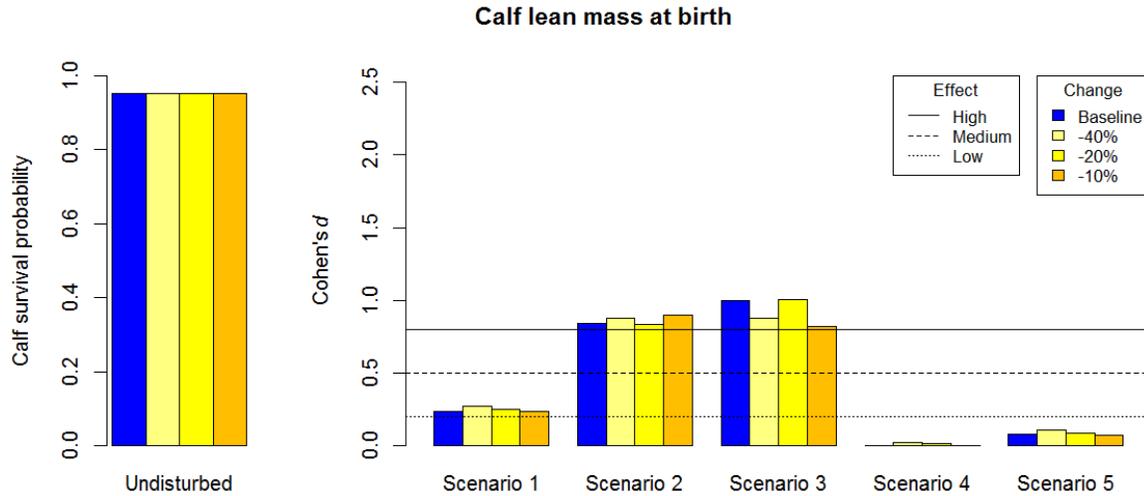
Heat of gestation: changes in the total heat of gestation had a similar effect on the results as observed for the weight of the fetus. In undisturbed conditions, calf survival probability was not affected, but lower costs of sustaining the pregnancy resulted in higher resilience to disturbance and, thus, a reduced effect of both environmental and anthropogenic perturbations. An increase in such costs had the opposite effect on the results. Overall, the sensitivity of simulation results to the value of this parameter was comparatively lower.



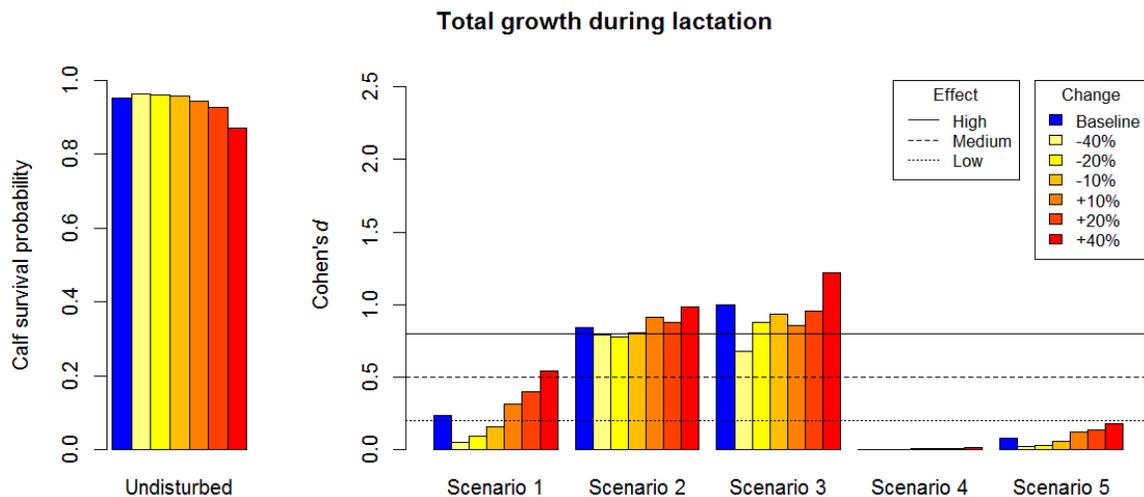
Age threshold for the calf to travel with the mother: a much higher value of this parameter (+40%) prevented mother and calf from leaving the breeding ground before May, and therefore limited their access to food resources as they became available along Baja peninsula. This caused a reduced survival probability and higher effects of environmental and anthropogenic perturbations. In general, however, results showed low sensitivity to the value of this parameter. A reduction of -40% could not be tested as this date fell before the birth of the calf, while a reduction of -20% implied that the calf could immediately travel outside the breeding ground with the mother.



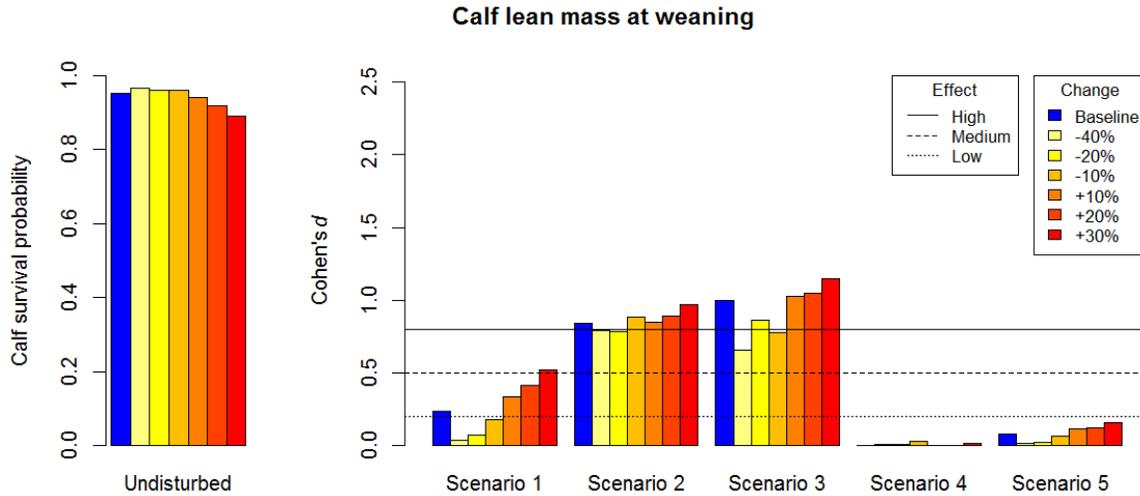
Lean mass of the calf at birth: an underestimation of this parameter did not strongly affect calf's survival probability or the conclusions drawn from the disturbance simulations. Calf lean mass could not be higher than the value we assumed, since this would result in a blubber mass lower than the minimum required for survival.



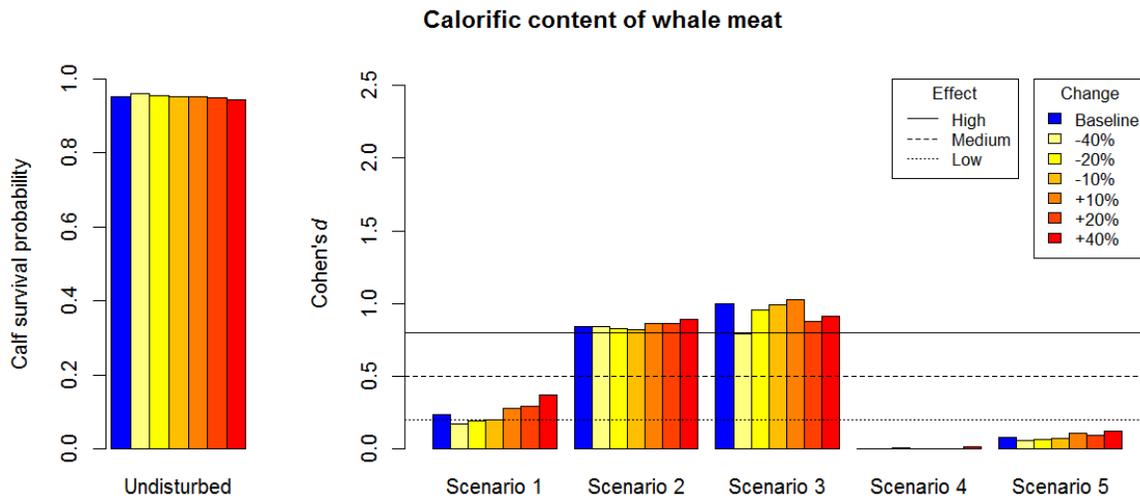
Total growth of the calf during lactation: a reduction of the total growth achieved during lactation resulted in higher calf survival probability and a smaller effect of the disturbance scenarios. An increase in this parameter had the opposite effect. These results are not surprising, since total growth affects daily growth requirements, which increase the energy needs of the calf. The consequences of disturbance were also affected by alterations in this parameter (e.g. effect size went from small to medium under Scenario 1 for a 40% increase in total growth, i.e. from 17 tons to almost 24 tons). However, sensitivity to such changes was high mainly for extreme over and under estimations.



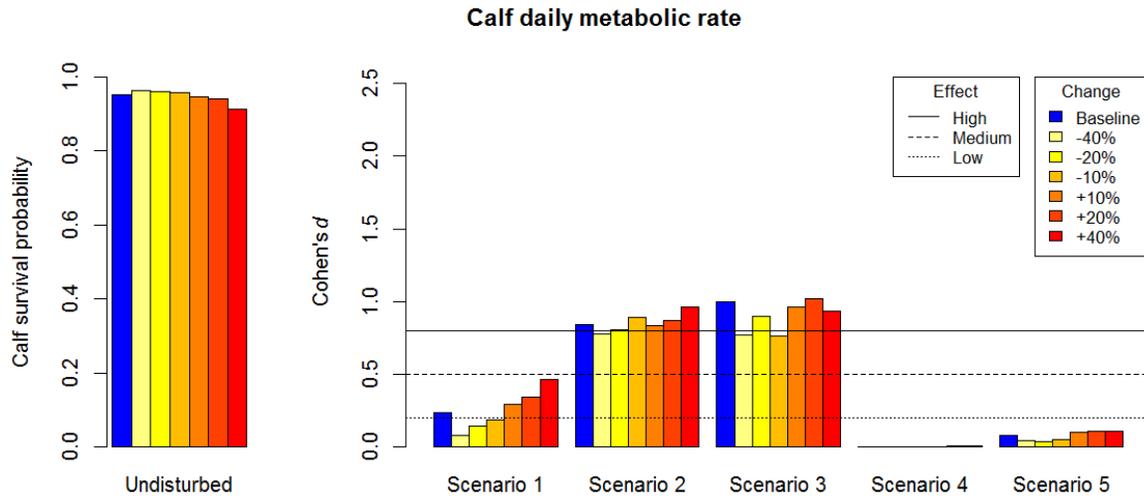
Lean mass of the calf at weaning: changes in this parameter had similar effects as the changes in total growth of the calf. This was expected, given that lean mass at weaning affects a calf's daily energy requirements for growth and the amount of energy that can be stored in the blubber.



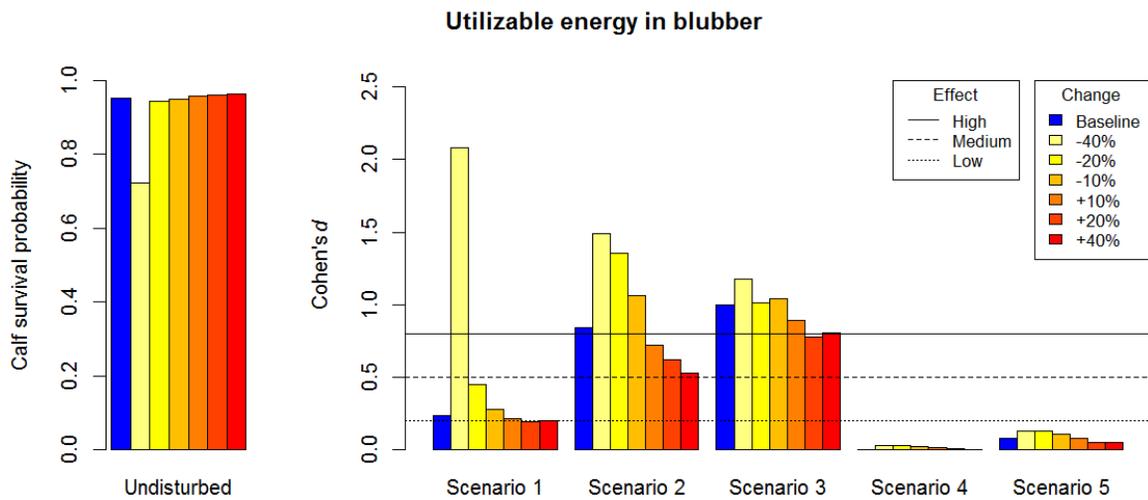
Calorific content of lean whale meat: model results were relatively less sensitive to under or overestimations of this parameter. The energy content of lean meat affected the costs to sustain the daily growth of the calf, but had a smaller influence than the parameters determining the rate of such growth.



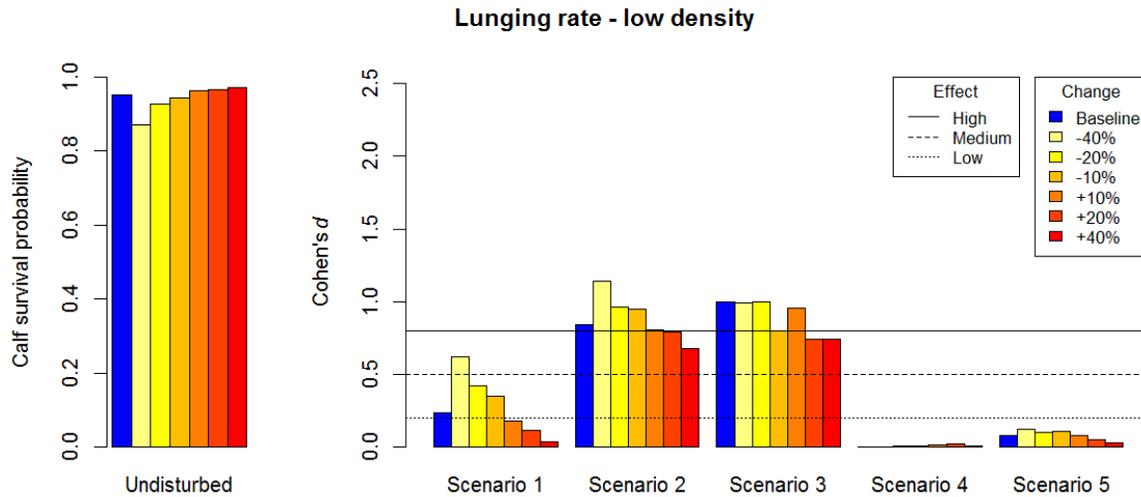
Calf daily metabolic rate: changes in this parameter had a similar effect to changes in the energy required by the calf to accumulate lean mass. By increasing the daily needs for the calf to survive, a higher value led to reduced survival probability and an increased effect of disturbance, but these changes were small.



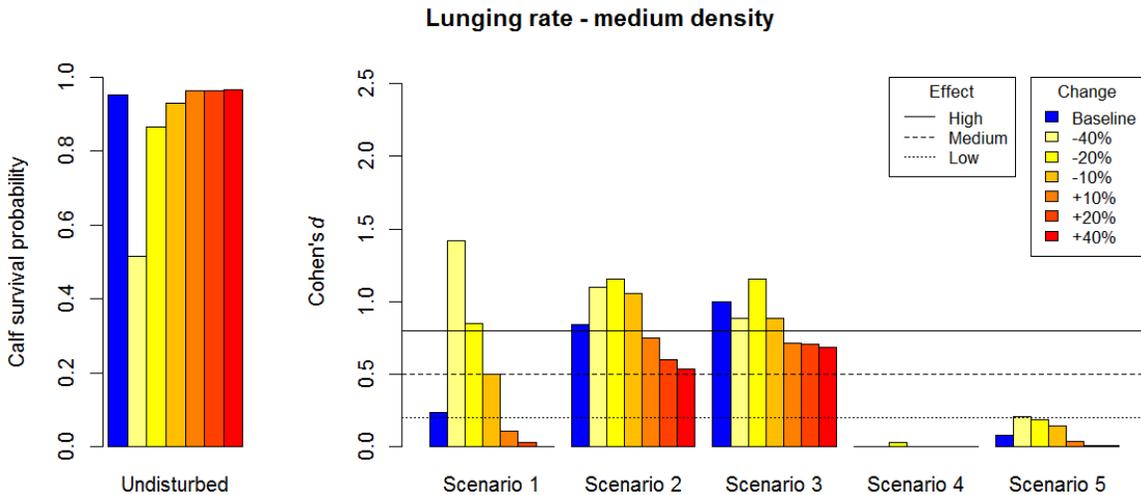
Utilizable energy in blubber: the energy content of the blubber per unit of weight had a predictable influence on the results. When this parameter was lower, calf survival probability was decreased and the effects of disturbances were more severe, because of the limited energy storage capabilities of the whale. On the other hand, an energy-richer blubber meant that, within the same blubber mass, the whale could accumulate more energy reserves, which made her more resilient to disturbance. These effects were particularly evident in the scenarios simulating environmental changes.



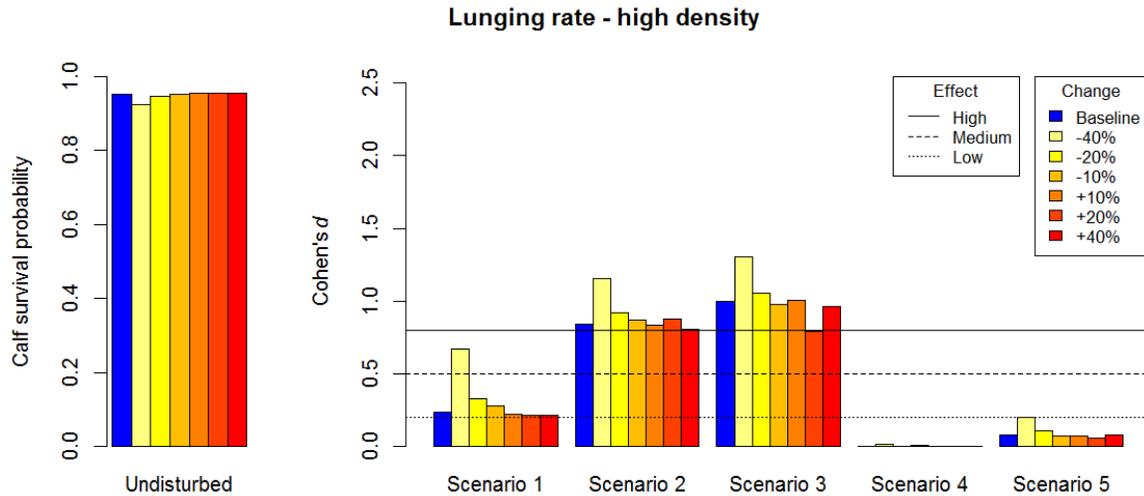
Lunging rate for low krill density: a lower value of this parameter caused a reduction in survival probability and a stronger effect of environmental disturbances, as highlighted by the changes in Cohen's d . In contrast, an increased lunging rate for low food densities had a beneficial effect on the results. This parameter affected the rate at which a whale extracted energy from a poor patch, which was critical when the environment was less productive and these densities were encountered more frequently. Reproductive success also improved under anthropogenic disturbance, because lost feeding time could be counteracted more effectively.



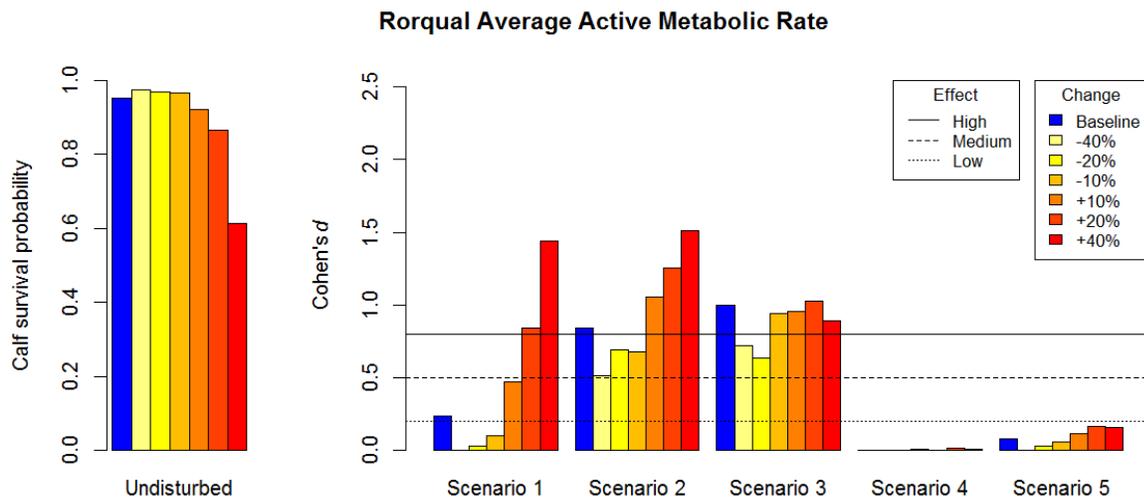
Lunging rate for medium krill density: a lower lunging rate for medium krill densities had severe effects both on calf survival probability and on the values of Cohen's d under disturbance. This had to do with the ability of the whale to access a sufficient amount of food and therefore compensate for the effects of disturbance. An increase in lunging rate had the opposite effect, resulting in an improvement of the effects of disturbance.



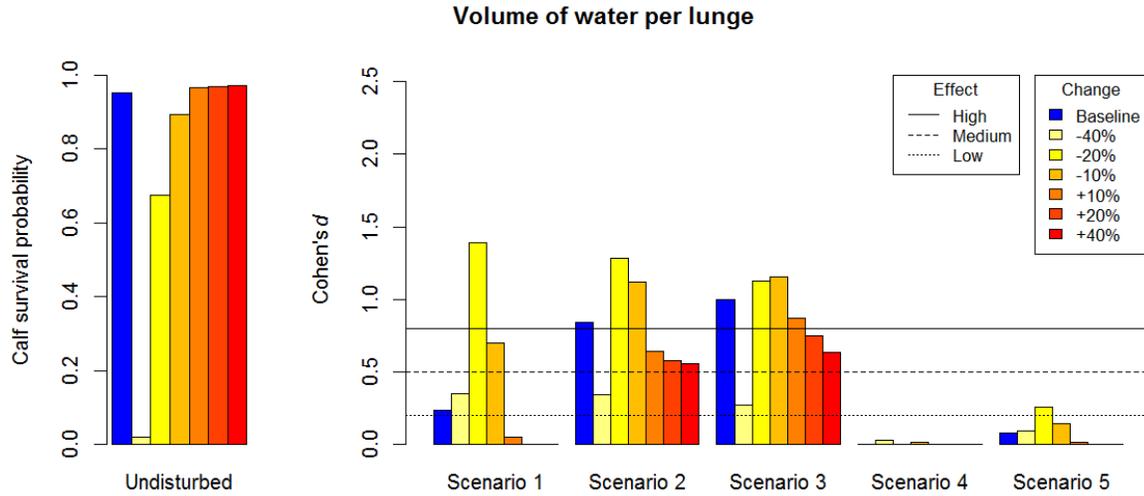
Lunging rate for high krill density: results were less sensitive to the lunging rate for high krill densities. While a severe decrease in the value of this parameter (-40%) still worsened the effects of environmental and anthropogenic perturbations, other alterations were less influential. This suggests that lunging rate when krill is abundant is sufficiently high in the baseline scenario (30 lunges per hour) to allow a whale to exploit these large amounts of food efficiently.



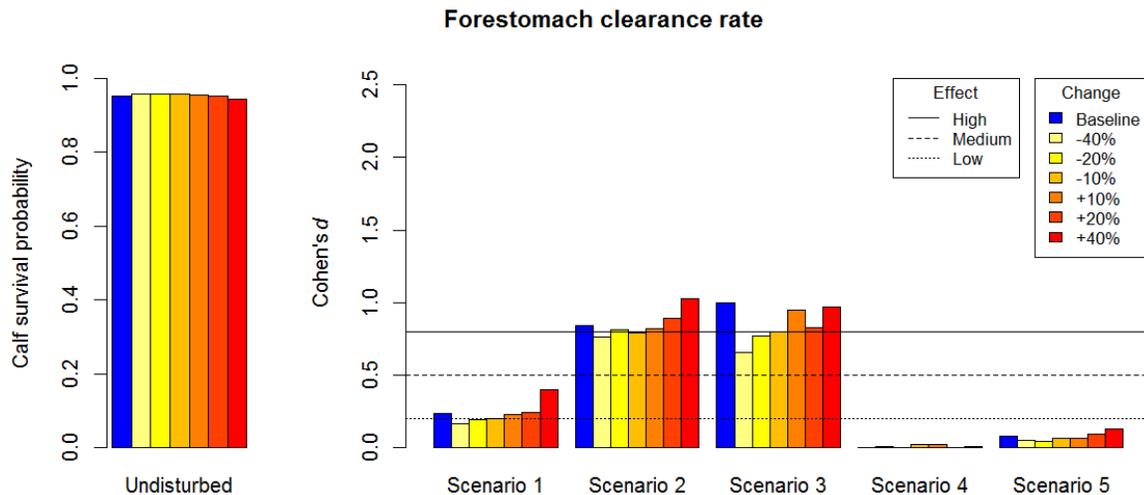
Rorqual Average Active Metabolic Rate: as we would expect, lower metabolic costs while foraging resulted in higher calf survival probability and weaker effects of disturbance. On the other hand, a higher energy expenditure compromised the whale's ability to sustain herself and her calf, and made her more vulnerable to disturbances. Sensitivity was relatively high compared to other parameters, especially when RAAMR increased and the environment was perturbed.



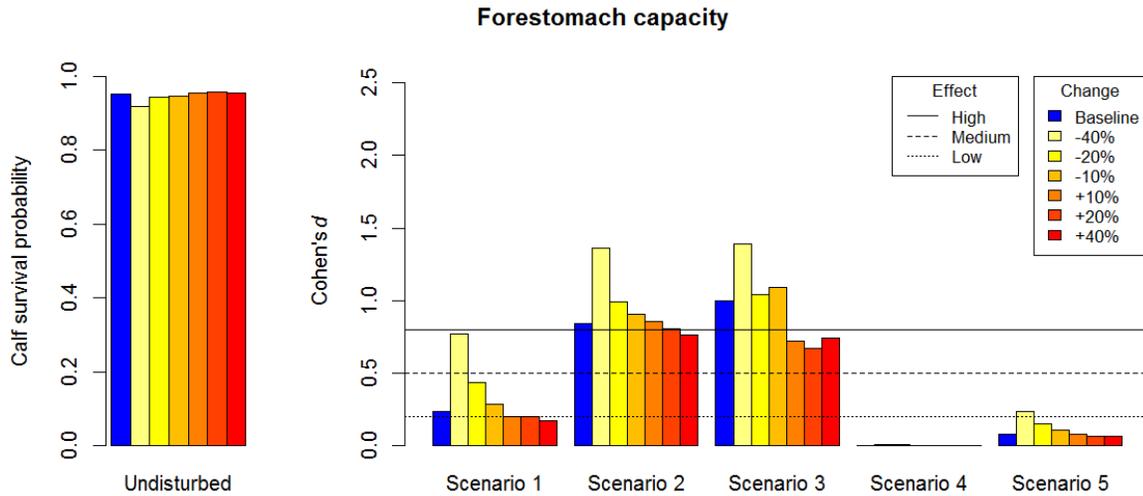
Volume of water ingested in a lunge: when the amount of water engulfed per lunge was reduced, a whale ingested less krill and, as a result, acquired less energy per energy spent foraging. Her calf's survival probability declined and the effects of environmental and anthropogenic perturbations were stronger. The highest decrease in volume (-40%, from 66 to 40 m³ of water) improved Cohen's *d* because calf survival probability almost dropped to zero under both undisturbed and disturbed scenarios. A larger volume ingested per lunge had an opposite effect, as it led to more krill acquired per energy spent.



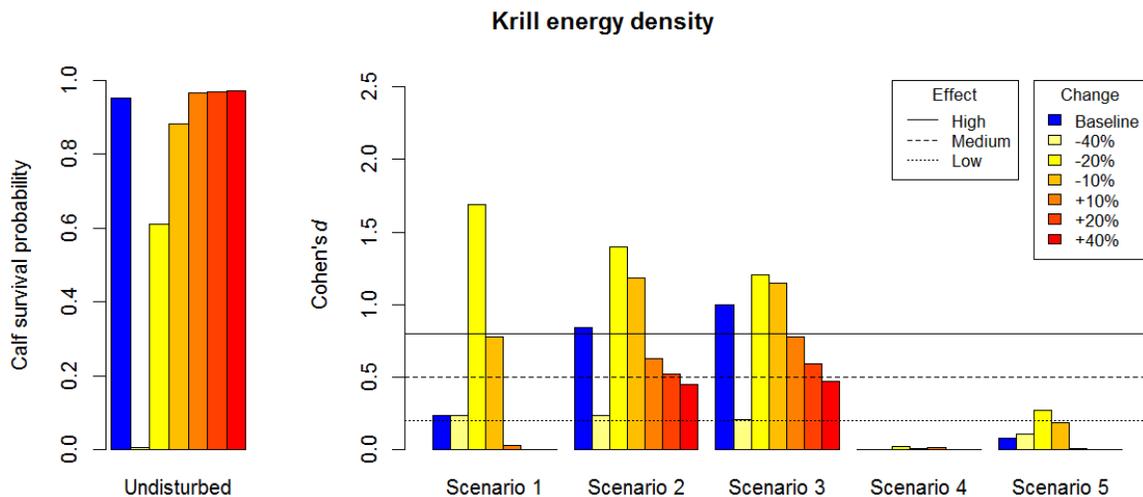
Time required to clear the forestomach: while the average survival probability remained unchanged in undisturbed conditions, extreme values of this parameter influenced the effects of disturbance. Less time needed to empty the forestomach meant that the whales could feed more efficiently and therefore acquire energy more quickly, while more time had the reverse effect. However, simulation results appeared generally less sensitive to this parameter compared to others.



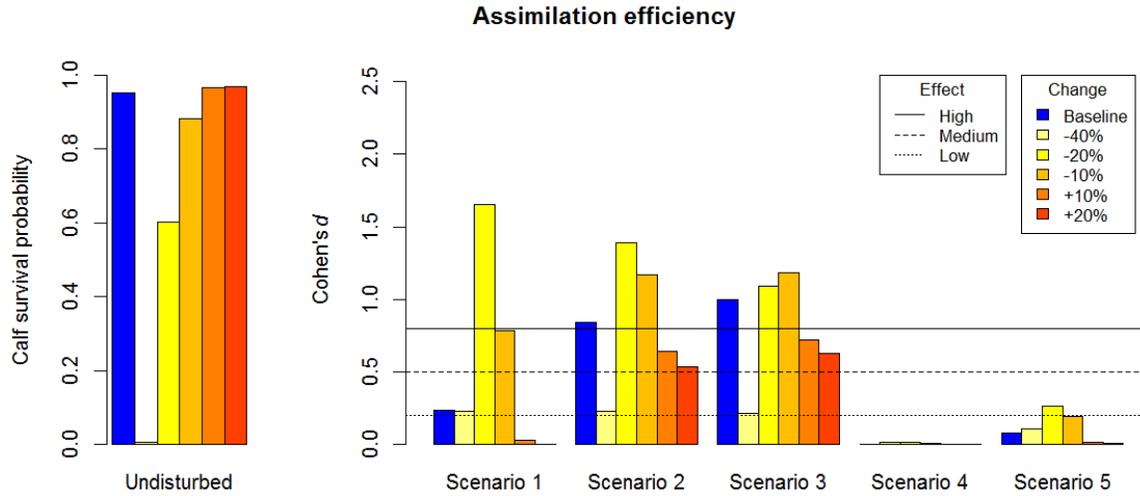
Forestomach capacity: while the effects of changes in this parameter on calf survival probability were small, the conclusions drawn from the disturbance simulations were more sensitive to its value. Specifically, when forestomach capacity was too small (e.g. -40% of the baseline value), the whales were not able to ingest sufficient krill and their compensatory abilities were therefore impaired. Similarly, a larger forestomach allowed a female to exploit the feeding patch more efficiently, improving her resilience to disturbance.



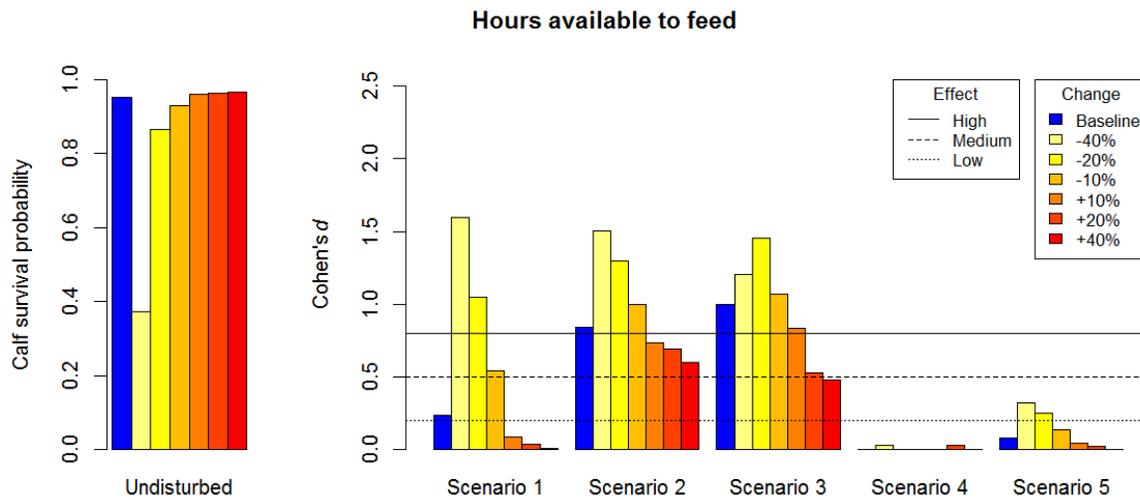
Energy density of krill: predictably, the energy content of the krill had a strong effect on the results, with reductions in this value having severe consequences on survival probability and causing an increased effect of anthropogenic and environmental perturbations. Conversely, increased energy content per unit of krill weight meant higher energy acquisition and an overall improvement of the results. The highest reduction (-40%, corresponding to approximately 2500 kJ/kg) led to a zero probability of calf survival in both undisturbed and disturbed conditions.



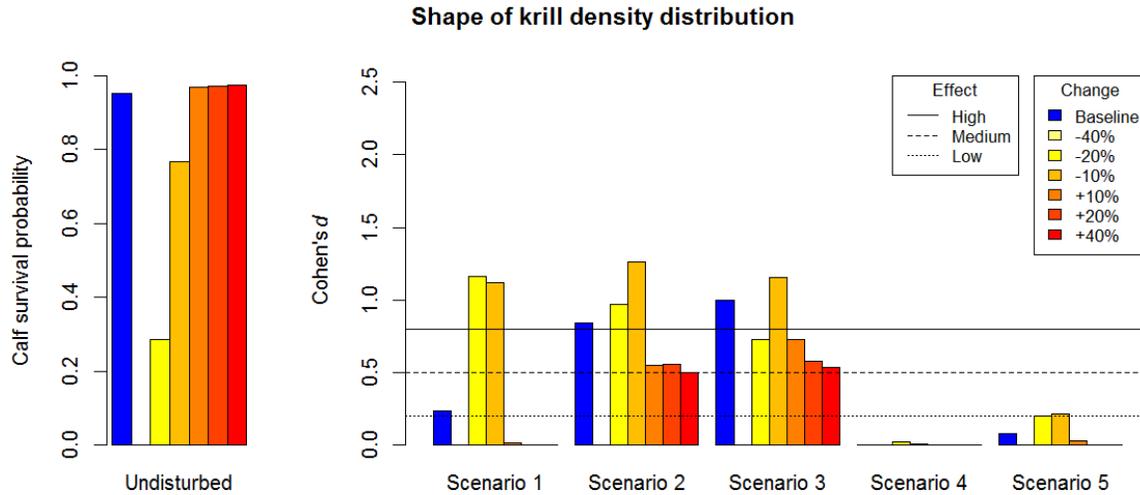
Assimilation efficiency: poor efficiency in extracting energy from the krill resulted in a dramatic reduction in survival probability and an increased effect of disturbance, with the exception of the highest decrease in efficiency (-40%). The -40% reduction (i.e. a 0.5 assimilation efficiency) improved Cohen's d only because calf survival probability was almost zero under both undisturbed and disturbed scenarios. Higher efficiency improved whales' reproductive success and resilience to disturbance, although to a lesser extent. The +40% increase could not be tested since it corresponded to an efficiency higher than 1.



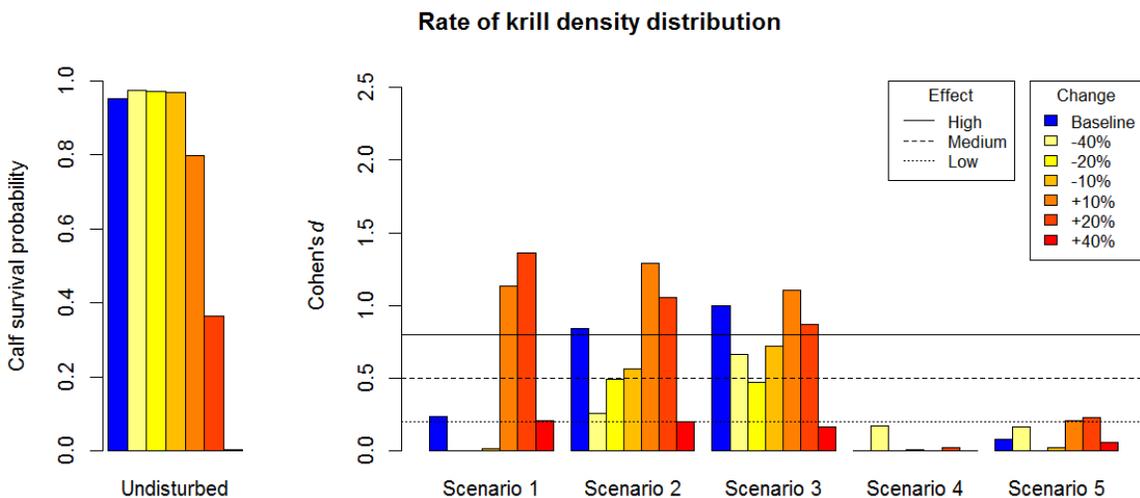
Maximum number of hours available for feeding: the time available for feeding during a day had a comparably strong influence on simulation results as the assimilation efficiency, because it ultimately affected the amount of food that the whale could extract from a given patch.



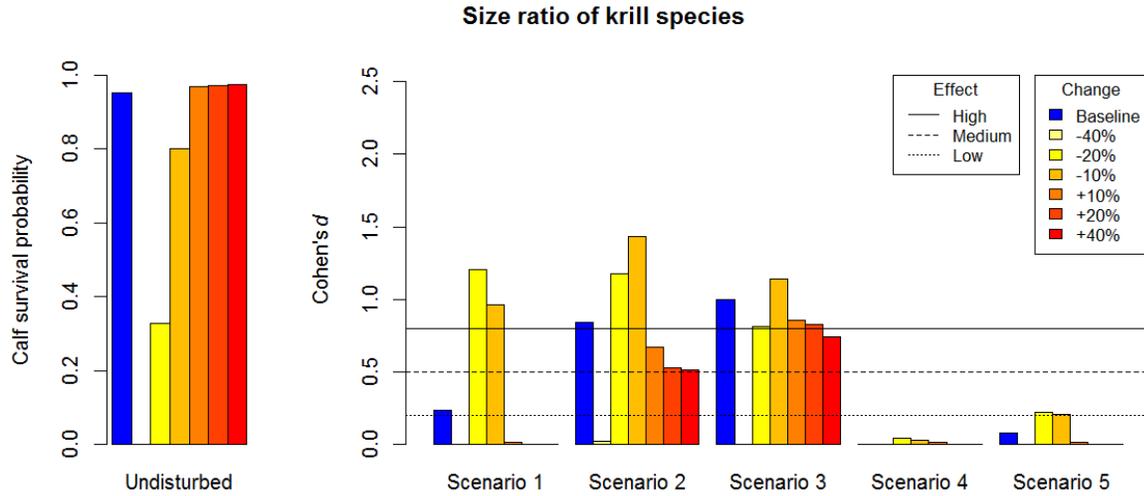
Shape parameter for the Gamma distribution of krill densities: as for the previous two parameters, this parameter affected the overall energy status of the whales and thus calf survival probability. The shape of the Gamma distribution influenced the amount of krill available in the productive waters off California in summer. This distribution was then used to derive the availability of food at other locations based on the krill index, and any change in its shape thus impacted availability throughout the migratory range. When the environment was less productive, compensatory abilities were reduced and the effect of environmental perturbations was enhanced. When this parameter was increased, calf survival and the productivity of the environment were so high that any effect of disturbance was strongly reduced under all scenarios.



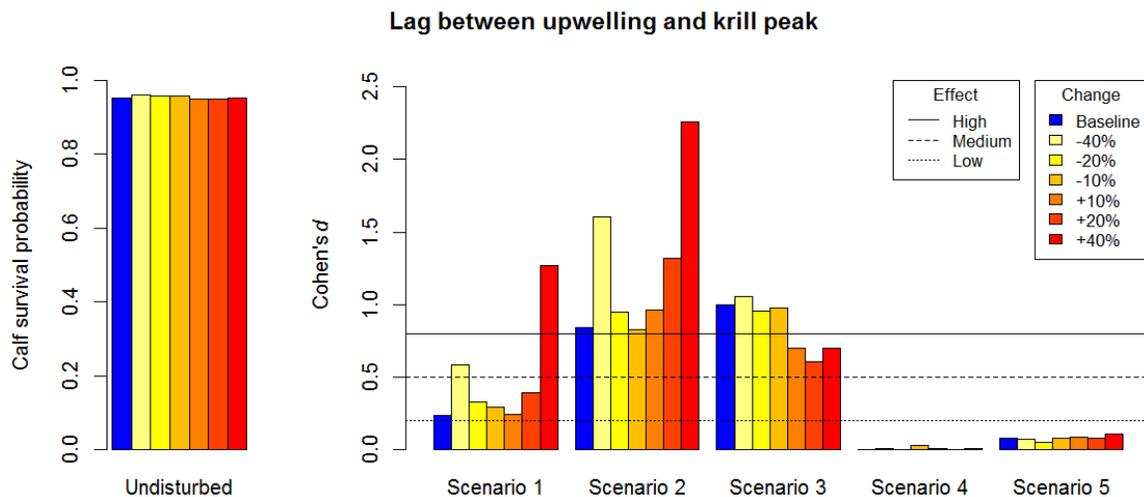
Rate parameter for the Gamma distribution of krill densities: simulation results were highly sensitive to the value of this parameter. A lower rate corresponded to higher krill densities in the original krill distribution for California in summer. This resulted in higher survival and increased abilities to counteract disturbances. On the other hand, an increase in this rate led to a drastic decline in survival probability and an increased effect of disturbance, as indicated by the higher Cohen's d . At the extreme increase (+40%), survival was reduced to almost zero for both undisturbed and disturbed scenarios, hence Cohen's d indicated the lack of an effect.



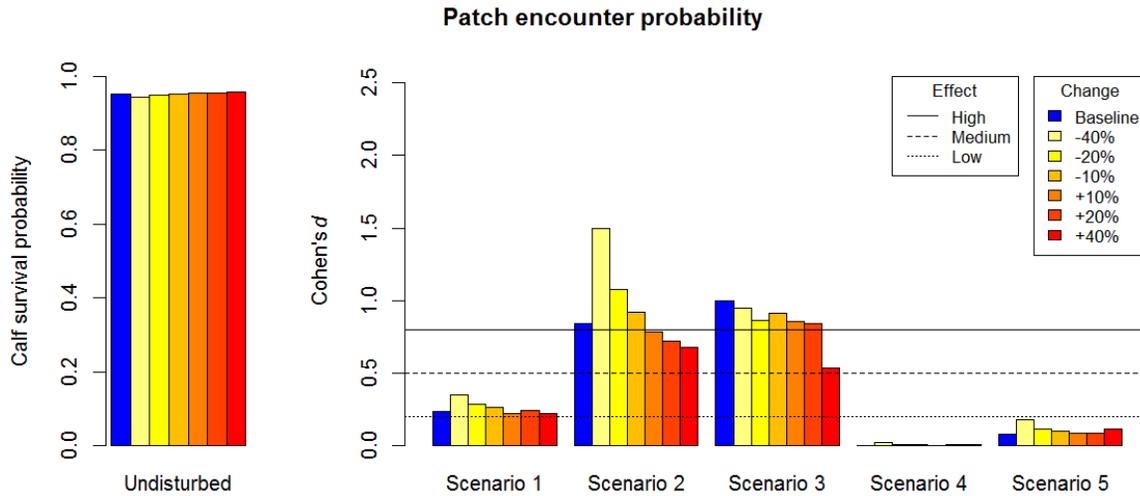
Size ratio between different krill species: the ratio of the sizes of krill found in the southern portion of the migratory range as opposed to the California Current affected a whale's ability to forage efficiently in winter and spring, when exploiting the patches along the coast of Baja California peninsula and in the breeding ground. A smaller ratio implied that these patches did not contain enough energy for the female to survive until upwelling improved productivity in the California Current in summer, while a larger ratio allowed whales to fully sustain their condition throughout the year.



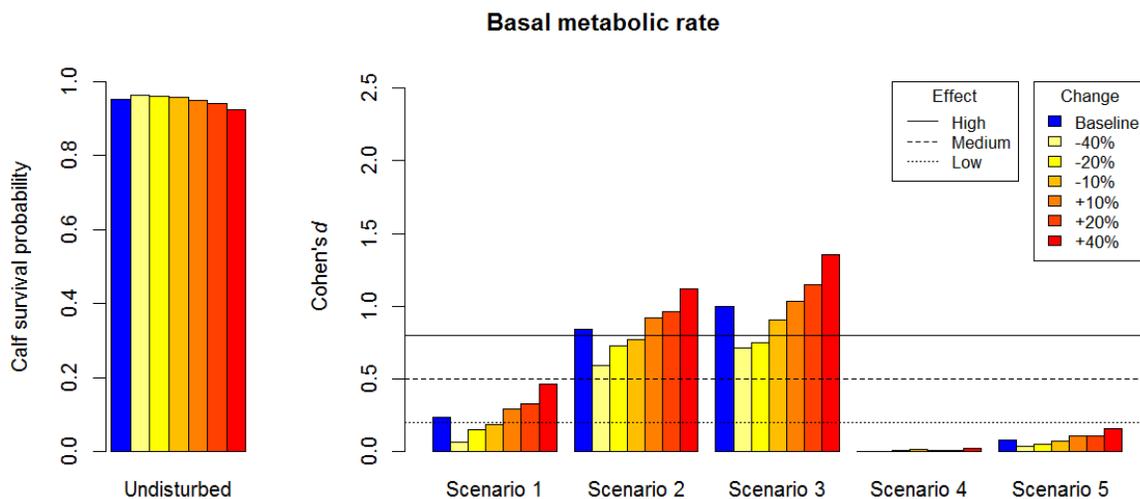
Temporal lag between upwelling and krill peak: the time required for the effects of upwelling to propagate through the trophic web had only a small effect on calf survival probability in undisturbed conditions. However, it did have a strong influence on the results of the disturbance scenarios, particularly in the case of environmental perturbations. The movement patterns were altered when this parameter varied, and extreme values ($\pm 40\%$) disrupted whales' ability to access sufficient resources at different times of the year.



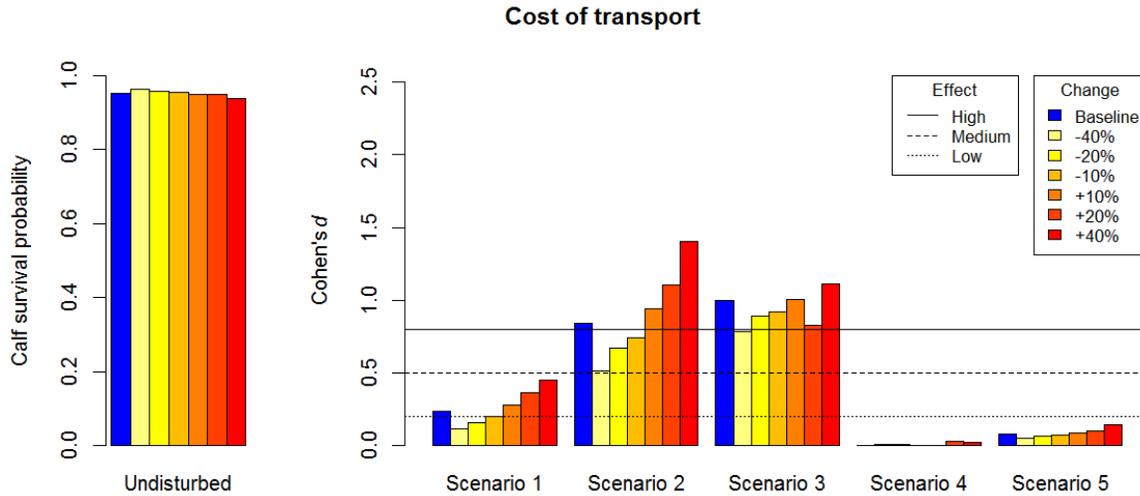
Probability of encountering different patch types: only extreme changes of the probability of encountering a patch with food ($\pm 40\%$) affected the conclusions drawn from the simulated disturbance scenarios, and calf survival probability in undisturbed condition remained mostly unchanged even under such extreme alterations. For intermediate values, the whales appeared to be able to compensate for a lower encounter probability.



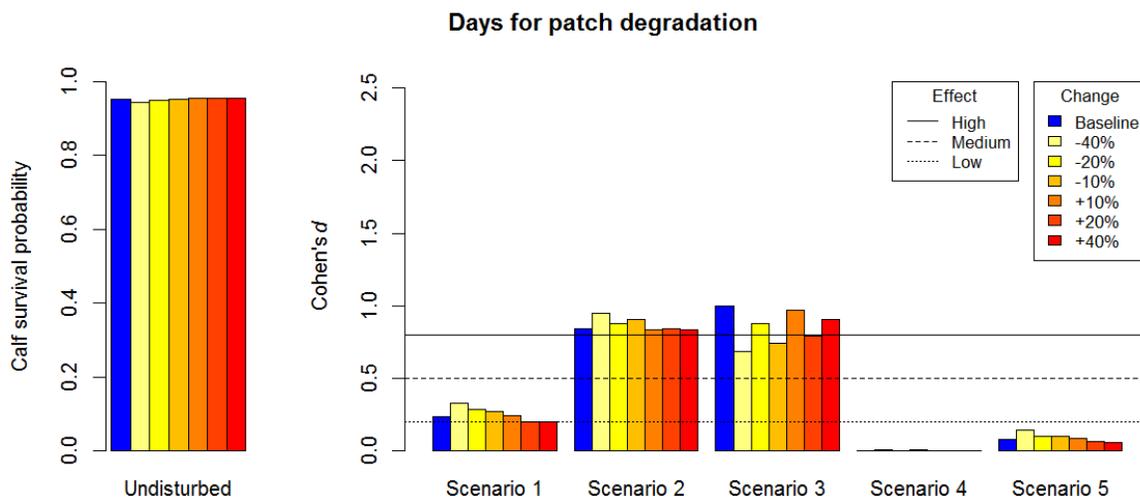
Basal daily metabolic rate: a lower basal metabolic rate reduced female energy expenditure, allowing for more storage and more energy transferred to the calf. It is therefore not surprising that this parameter improved calf survival probability and resilience to disturbance when reduced, and had an opposite effect when increased.



Cost of transport: as for the previous parameter, lower swimming costs improved the results by reducing a whale's energy expenditure, while higher costs reduced calf survival probability and worsened any effect of disturbance.



Days after which a patch degrades: the time after which an exploited patch became empty of food did not have a strong influence on the results. However, when this was reduced to approximately 13 days (-40%), there was a small negative effect on survival probability and Cohen's d , particularly when the environment was perturbed.



Discussion of sensitivity results

In general, the results of the first three scenarios of disturbance showed a higher sensitivity to the values of model parameters. The conclusions from Scenario 4 and 5 were, in most cases, unchanged, and either a negligible or small effect of disturbance on calf survival probability was confirmed.

Simulation results were particularly sensitive to some morphometric characteristics of the female (e.g. the average weight, the amount of blubber that can be carried as energy storage, or the capacity of the buccal cavity and of the forestomach). Extreme under or overestimation of these parameters (e.g. a 40% increase or decrease in mean weight, leading to a 34 ton or 80 ton whale, respectively) are unlikely. However, additional photogrammetry studies and morphometric analysis of stranded carcasses should be carried out to confirm the distribution of adult lengths and allometric relationships in this population (Durban & Parsons 2006; Gilpatrick & Perryman 2008; Fearnbach *et al.* 2011; Christiansen *et al.* 2016). Ultrasound techniques to measure blubber thickness (Miller *et al.* 2011) and subsequent scaling to total amount of blubber (Christiansen *et al.* 2013) could also be used to quantify those parameters that, in the past, were measured with lethal sampling. Other aspects of the morphology (e.g. the minimum blubber at which starvation occurs) were found to be less influential, or at least less important in their range of plausible values (e.g. percentage lean mass).

The growth dynamics of the calf (e.g. total growth, final lean mass) also had an effect on model results, although this was particularly true for severe errors in the estimation of these parameters ($\pm 40\%$). It will therefore be important to quantify a reasonable range of calf sizes at different stages of the lactation for this population, to make sure that such extreme scenarios are unrealistic. Photogrammetry techniques could again be used to this purpose (Rowe *et al.* 2010; Miller *et al.* 2012; Christiansen *et al.* 2016). Other aspects of calf development, such as the energy required to build lean mass, the minimum and maximum proportion of blubber mass that it can accumulate or the number of days before it can travel with the mother outside the breeding ground, had a weaker effect on the simulations.

Some of the costs sustained during pregnancy appeared to have a small influence on our results (e.g. the costs of fetus growth and the ratio of lean mass to blubber at the end of pregnancy). Even the threshold of blubber below which abortion occurred did not affect mean calf survival probability, although extreme changes in this parameter did alter the number of abortions under disturbance. It is challenging to estimate such relationship, but indirect evidence and data from other species remain an option in the *interim* (Williams *et al.* 2013; Christiansen *et al.* 2014). However, the weight of the fetus over the pregnancy and the heat of gestation had a larger impact on the results of the simulations, as they affected the ability of the whale to compensate for disturbance.

The details of lactation (in terms of maximum milk delivery, milk energy content and mammary gland efficiency) were also not strongly influencing the results, although a severe underestimation of these parameters could still affect the conclusions. The controversy regarding the amount of milk delivered per day (Lockyer 1981; Oftedal 1997) should therefore be addressed with further bioenergetic modeling. The value of 90 kg/d proposed by Tomilin (1946) and used by Lockyer (1981) would cause an even stronger effect than the 40% reduction we tested in our simulations. The estimates of milk energy content and mammary gland efficiency are unlikely to have this level of inaccuracy. On the other hand, the threshold of mass at which a female started to nurse her calf was found to affect results substantially. It will remain

difficult to measure this parameter in the field, although a relative measure of condition when whales are actively lactating could be obtained from unmanned aerial vehicles (Miller *et al.* 2012; Christiansen *et al.* 2016).

Metabolic rates (in the form of basal, foraging and swimming costs) and the efficiency in energy absorption were all found to be highly influential on the results. Respirometry studies will probably remain impossible for these large species, but hydrodynamic modeling of the engulfment process (Goldbogen *et al.* 2011; Potvin, Goldbogen & Shadwick 2012) should continue to be refined to ensure that these estimates are realistic, and possibly paired with bioenergetic modeling based on respiration rate data (Villegas-Amtmann *et al.* 2015). The quantity of energy stored in the blubber also had a strong effect, although this parameter is less likely to suffer from severe underestimation. Other physiological parameters (e.g. the rate of forestomach clearance) had a smaller influence on the results.

The dynamics of lunge feeding were found to be particularly important for intermediate values of krill densities, probably because these were the conditions most frequently encountered by the whales. Lunge rate at low krill density became important under a perturbed environment, when poorer patches were more prevalent. These parameters were estimated from fine-scale tag data (Goldbogen *et al.* 2011, 2015; Hazen, Friedlaender & Goldbogen 2015) and are therefore expected to be robust. Additional tag deployments in different environmental contexts could be beneficial to further characterize the variability around these estimates.

The characteristics of the environment in which the whales moved and fed were critical for the results of the simulations. The time available to feed in a patch, the average distribution of krill densities in the study area, the spread of such distribution, the energy content of the krill, its relative geographical variation and the lag between upwelling and krill all had a strong effect both on the average survival probability in undisturbed condition and on the effects of disturbances. Prey sampling across a wide spatiotemporal range of conditions and a close interaction with oceanographers and plankton biologists could improve our understanding of this complex ecological system. Alternatively, these parameters could be informed indirectly from long-term monitoring of whales' foraging behavior in different contexts (Nabe-Nielsen *et al.* 2014; Goldbogen *et al.* 2015). Other environmental parameters (such as the time it takes for whales to use all resources within a foraging patch, or the probability of encountering patches with food) were less influential.

Finally, the characteristics of the fitness function relating calf final condition to its survival probability affected the results, although this influence could be mostly ascribed to the position of the curve (as indicated by the value at which this probability was 50%).

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