

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; Pirotta 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

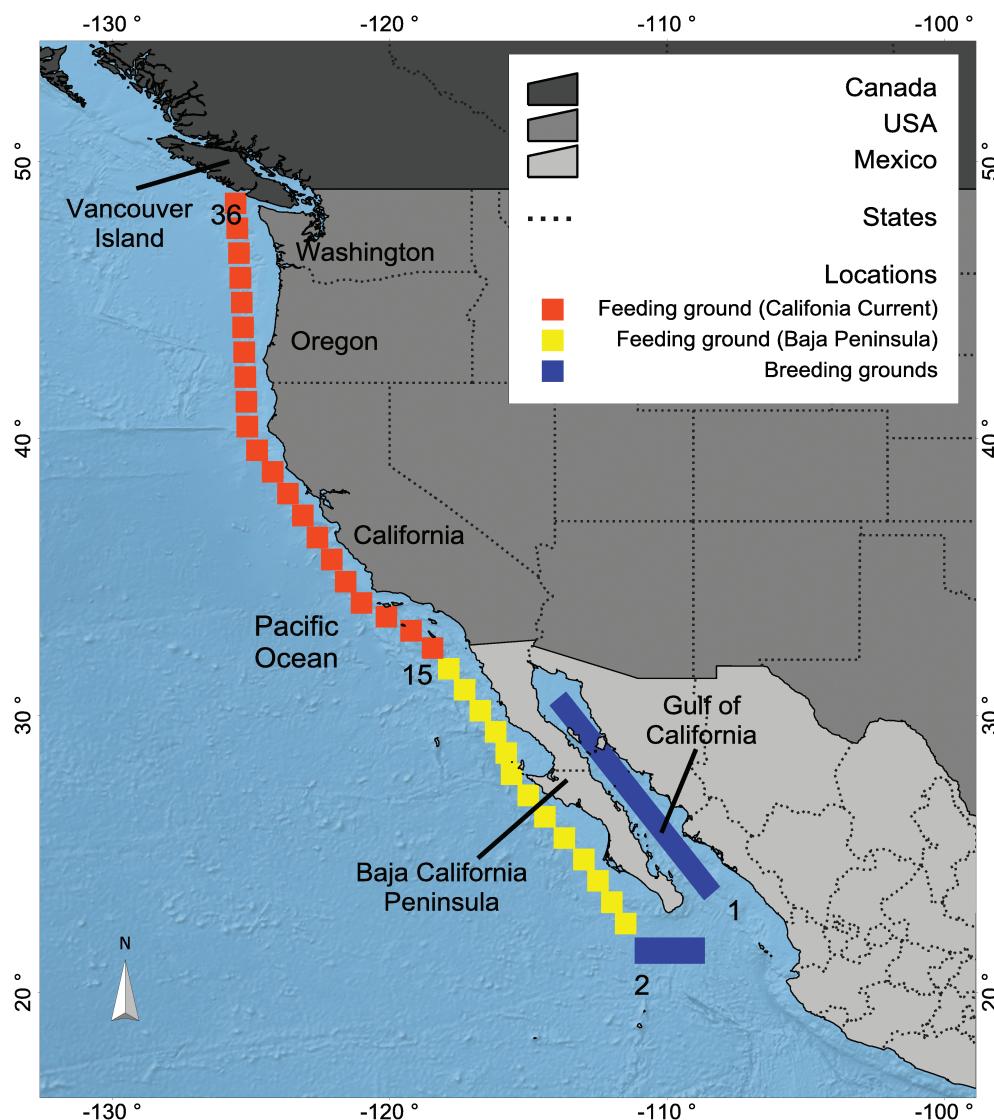


Figure 1: Map of the study area, showing the 36 100 × 100-km locations used in the model. Relevant locations are numbered for reference. Larger boxes for the breeding grounds indicate whales' ability to roam within those areas.

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., McMahon 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_l 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,

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

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 unprecedeted 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_d , 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> (Pirotta 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

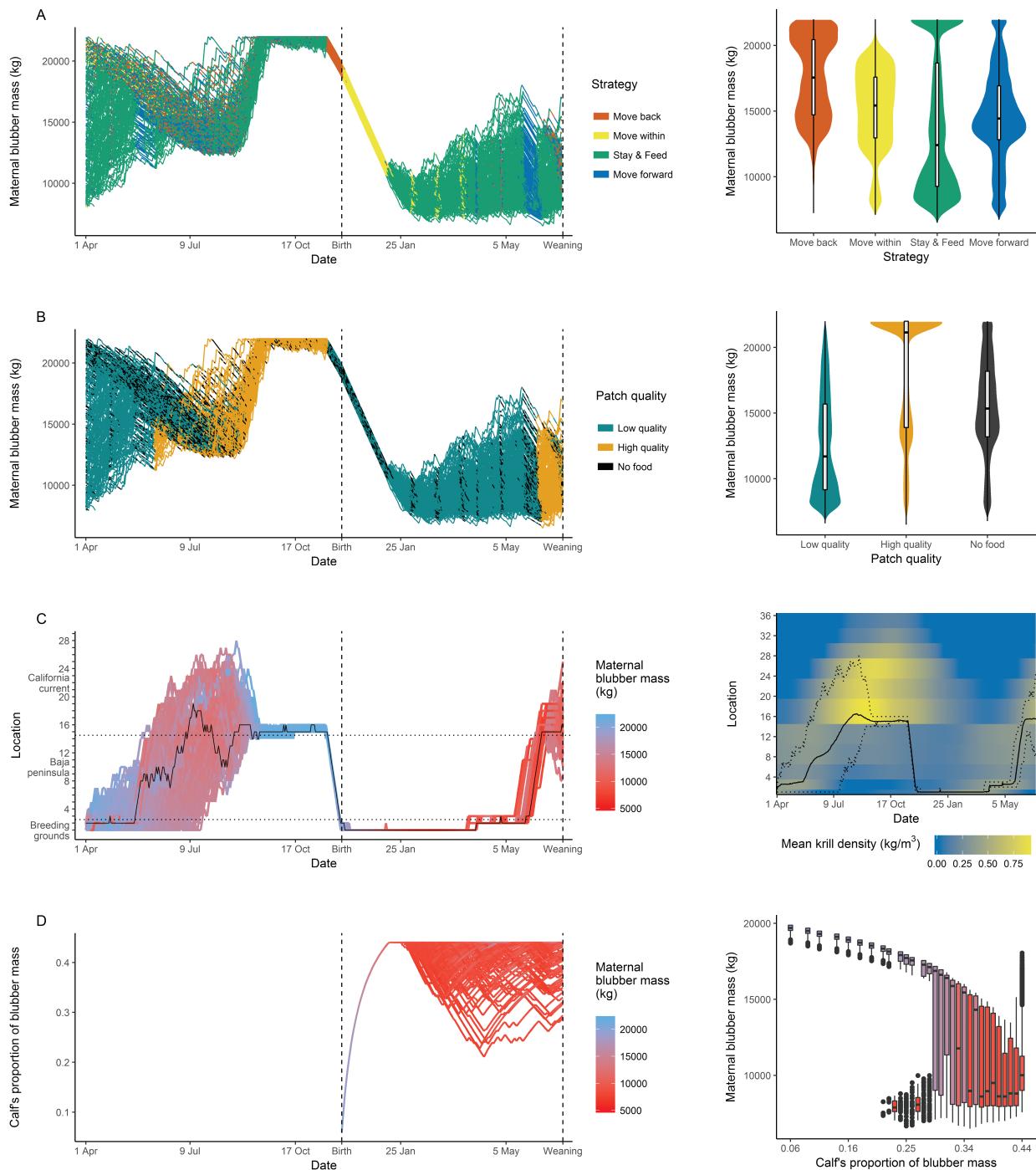


Figure 2: Model results. *A*, Variation in blubber mass over time for 200 females in one run of the forward iteration, colored by behavioral decision at each time step. Birth and weaning are indicated by vertical dashed lines. *Right*, a violin plot of blubber mass under different behavioral decisions. *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/m^3 (blue) and 0.93 kg/m^3 (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.

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

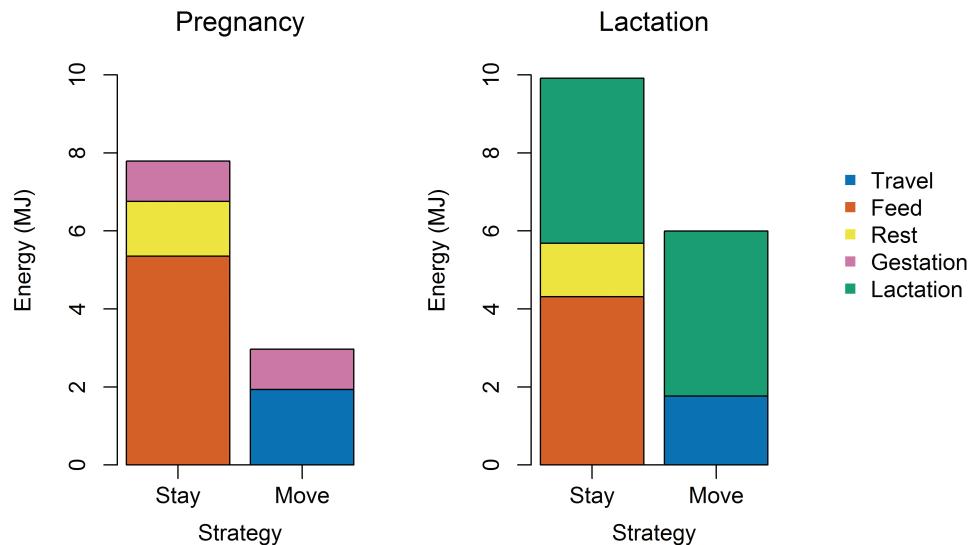


Figure 3: Metabolic costs of different activities (megajoules [MJ]) during pregnancy and lactation. Energy expenditure was averaged across 200 females and across the days that constitute each phase. Feeding and resting costs were calculated assuming a fixed krill density corresponding to 12 h per day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

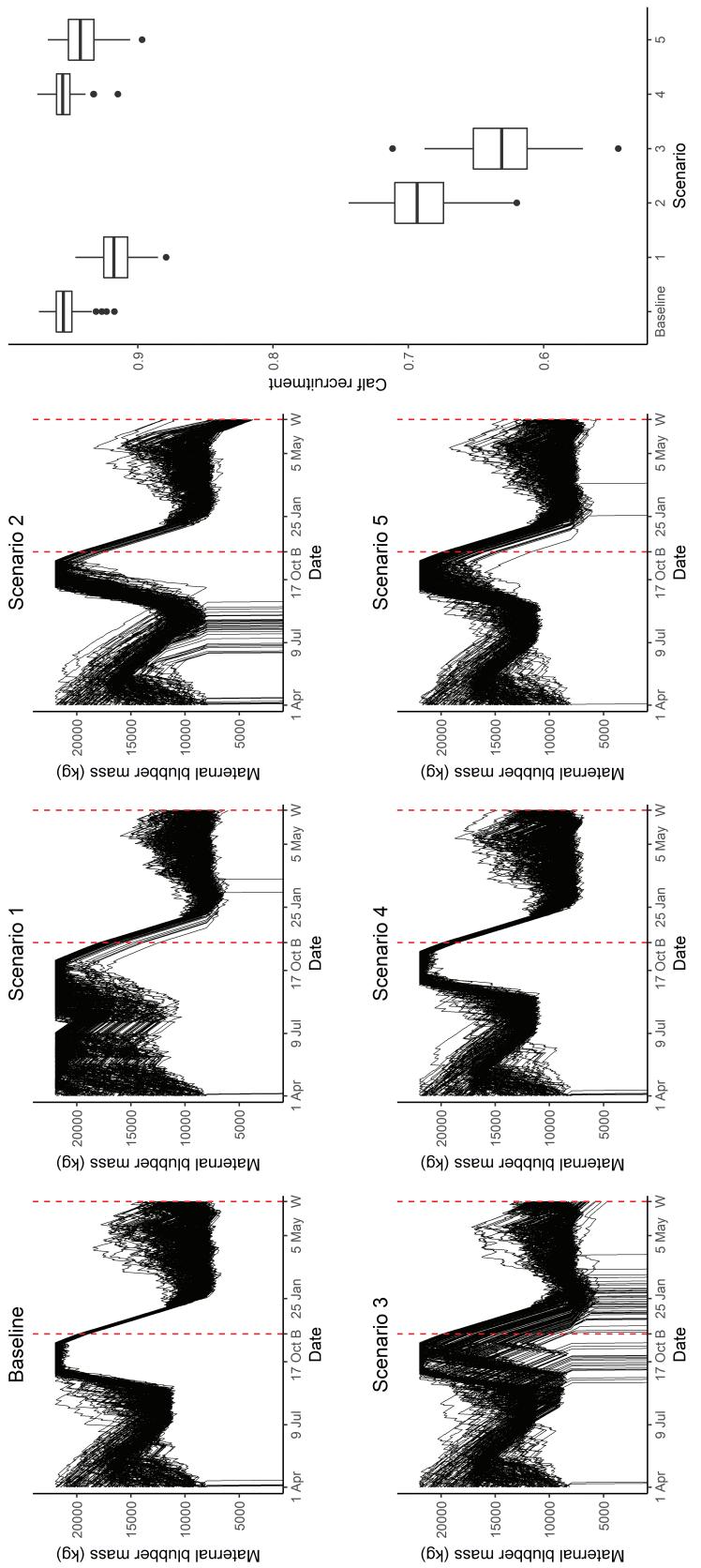


Figure 4: Variation in maternal blubber mass over time under environmental and anthropogenic disturbance scenarios and corresponding changes in calf recruitment probability (boxplot). Vertical dashed lines indicate time of birth (B) and weaning (W). Vertical black lines indicate abortions or starvations.

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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