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# OIKOS

## Research

# Anthropogenic disturbance in a changing environment: modelling lifetime reproductive success to predict the consequences of multiple stressors on a migratory population

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Animals make behavioural and reproductive decisions that maximise their lifetime reproductive success, and thus their fitness, in light of periodic and stochastic variability of the environment. Modelling the variation of an individual's energy levels formalises this tradeoff and helps to quantify the population-level consequences of stressors (e.g. disturbance from human activities and environmental change) that can affect behaviour or physiology. In this study, we develop a dynamic state variable model for the spatially explicit behaviour, physiology and reproduction of a female, long-lived, migratory marine vertebrate. The model can be used to investigate the spatio-temporal patterns of behaviour and reproduction that allow an individual to maximise its overall reproductive output. We parametrised the model for eastern North Pacific blue whales *Balaenoptera musculus*, and used it to predict the effects of changing environmental conditions and increasing human disturbance on the population's vital rates. In baseline conditions, the model output had high fidelity to observed energy dynamics, movement patterns and reproductive strategies. Simulated scenarios suggested that environmental changes could have severe consequences on the population's vital rates, but that individuals could tolerate high levels of anthropogenic disturbance. However, this ability depended on where, when and how often disturbance occurred. In scenarios with both environmental change and anthropogenic disturbance, synergistic interactions caused stronger effects than in isolation. In general, larger body size offered a buffer against stochasticity and disturbance, and, consequently, we predicted juveniles to be more susceptible to disturbance. We also predicted that females prioritise their own survival at the

expense of the current reproductive attempt, presumably the result of their long lifespan. Our approach provides a general framework to make predictions of the cumulative and synergistic effects of human disturbance and climate change on migratory populations, which can inform effective management and conservation efforts.

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## Introduction

The reproductive output of animals over the course of their lifetime (hereafter, their reproductive success) is central to their fitness (Stearns 1992), and has important implications for the viability of a population, as well as, more generally, the evolutionary dynamics of a species. Individuals must balance reproductive effort (e.g. whether to initiate reproduction, or abandon a dependent offspring) with their own survival (and thus future reproduction), in light of the features of the environment they inhabit (Hirshfield and Tinkle 1975) relative to their body condition (McNamara and Houston 1996). In long-lived organisms this tradeoff, together with the high amount of energy they generally invest in parental care, means that an individual might choose to abandon the current reproductive attempt and compensate reproductive success over subsequent attempts. However, as the reproductive potential of an individual changes over the course of its life, these decisions may also change (Stearns 1992, Roff 1993, Eberhardt 2002). For migratory species, reproductive decisions are further complicated by the seasonal nature of their environment. This seasonality constrains the timing of reproduction and implies the recurrence of periods when food resources are scarce or absent (Alerstam et al. 2003, Bårdsen et al. 2011). Stochastic and seasonal environmental variability may be buffered by a larger body size, which ensures a greater ability to accumulate energy reserves to sustain an individual during periods of fasting or decreased food availability (Lindstedt and Boyce 1985, Millar and Hickling 1990, Costa 1993) and to support reproduction. Investigating the spatio–temporal dynamics of individual behaviour given the physiological state and the state of the environment could therefore shed light on the evolution of different behavioural and life-history strategies (Boyce 1979, Stearns 1992).

Understanding individual reproductive decisions over their entire life can be used to assess the consequences of disturbance from human activities on wildlife populations (Pirotta et al. 2018a). Anthropogenic disturbance can have nonlethal effects on the vital rates (e.g. survival and reproductive success) of exposed individuals, mediated by behavioural and physiological changes that can alter an individual's health status, defined by New et al. (2014) as all internal factors that affect fitness or homeostasis. Quantifying the long-term, population consequences of these changes is challenging (Pirotta et al. 2018a). Populations of long-lived, wide-ranging species are difficult to monitor at appropriate scales. As a result, when we are able to detect changes in the population's status empirically, it is generally too late to implement suitable management and conservation measures (Taylor et al. 2007). Modelling tools are therefore needed to put these changes into the context of the fitness of an individual and predict any potential population-level repercussions (New et al. 2014, King et al. 2015, McHuron et al. 2017, 2018, Nabe-Nielsen et al. 2018, Pirotta et al. 2018a). In addition, wildlife populations are subject to pressures from an environment that is also changing (Poloczanska et al. 2013). While it is difficult to predict how climate change will affect ecosystems, environmental changes will likely interact with human disturbances to affect the viability of a population (Maxwell et al. 2013). Multiple stressors may act in synergy, so that the resulting consequences will be more severe than the mere summation of the single stressors' effects (Crain et al. 2008), but a way to disentangle these processes in empirical data has yet to be achieved.

State-dependent behavioural and life-history theory, implemented via stochastic dynamic programming (SDP) and Monte Carlo (MC) simulations, provides a framework to investigate animal behavioural and reproductive strategies in these contexts. It integrates the internal (e.g. energy reserves) and external (e.g. the environment) stimuli that affect an individual's decision making, under the assumption that decisions are optimised to maximise fitness over an individual's lifetime (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000). This framework has also proven effective for assessing the consequences of anthropogenic disturbance, which are interpreted as novel stimuli that are not part of a species' evolutionary history (McHuron et al. 2017, 2018, Pirotta et al. 2018b). Pirotta et al. (2018b) demonstrated such models can be used to model the migratory behaviour of baleen whales, and to disentangle the various processes that drive individual decisions as animals move through an environment that may be both disturbed and changing. However, their model was restricted to one reproductive cycle and, as a result, did not account for the ability of a female to compensate for a failed reproductive attempt over her reproductive lifespan. Understanding the consequences of disturbance at a population level requires the non-trivial extension of this model to multiple reproductive cycles.

In this study, we aim to extend the model proposed by Pirotta et al. (2018b) to cover the entire lifetime and overall reproductive history of a female mammal belonging to a migratory population (cf. McHuron et al. 2018 for a non-migratory population). From a fundamental perspective, this model could be used to explore aspects of the movements, feeding ecology and reproductive strategies of a migratory organism with a complex life history. We focus on baleen whales as a case study, because they exemplify the challenges,

at multiple scales, that migratory animals face when making behavioural and reproductive decisions. Particularly, we parameterised the model for eastern North Pacific blue whales *Balaenoptera musculus*, given the relatively large body of work available for this population, their management and conservation relevance, and the existing bioenergetic model for females belonging to this population (Pirotta et al. 2018b). Baleen whales are amongst the largest animals to ever exist, and blue whales are the largest (Goldbogen and Madsen 2018). With such large body sizes, their daily prey intake is enormous and balancing their energy budget is challenging. This is because of the high costs of some of their activities (e.g. lunge feeding) (Goldbogen et al. 2011) and the substantial investment in the production of calves (e.g. during lactation) (Lockyer 1981, 1984). The amount and rate of energy invested in their offspring is well beyond that of most mammals when normalized for body mass (Sibly and Brown 2007, Costa and Shaffer 2012). Moreover, these species are subject to increasing pressures from expanding human activities in the ocean (Crain et al. 2008, Maxwell et al. 2013), including both changing climatic conditions (Hazen et al. 2013, Poloczanska et al. 2013) and acoustic disturbance from anthropogenic activities (Rolland et al. 2012, Goldbogen et al. 2013, Blair et al. 2016), which may have long-term consequences for their populations' status. Our ultimate goal is to develop a predictive tool to investigate the consequences of disturbance from human activities and environmental variability on this, and other, migratory populations of long-lived animals. This approach could be used to evaluate the potential synergistic effects on individuals' vital rates of the multiple stressors operating on a population (National Academies 2017).

## Material and methods

The present study builds on the dynamic state variable model that Pirotta et al. (2018b) developed for one reproductive cycle of a female blue whale. The original model covered the period from pregnancy to weaning, and was used to investigate the female's strategy that maximised the survival probability of her calf. The female's decision to move or feed was a function of her state and the features of the environment; the resulting dynamics of her energy reserves were captured by an underlying bioenergetic model. Disturbance was simulated as an additional feature of the whale's environment, to assess the effects of disturbance on the probability of successfully raising a calf. Here, the model of Pirotta et al. (2018b) was extended to cover a female's entire lifetime. We quantified female survival using the age at which individuals died and reproductive success as the number of female calves surviving to age 1 year over the lifetime of a female, as well as the changes in these vital rates resulting from environmental and anthropogenic disturbance. In the next sections, we first outline the details of model implementation. We then describe the additional processes that we included in the extended model and present the range of scenarios that we simulated.

The minor changes to the original model to accommodate its extension to a female's lifetime are listed in Supplementary material Appendix 1.

As with the original model, the extended model focused on the subset of the eastern North Pacific blue whale population that uses the Gulf of California and the waters off the southern tip of the Baja California Peninsula as the reproductive range during winter and spring, and the waters off the western USA and Canada during the summer and fall feeding season. This is likely only a segment of the entire population, which ranges more widely (Mate et al. 1999, Calambokidis et al. 2009, Bailey et al. 2010). While this segment is used as a case study for the development of a general approach for the study of anthropogenic disturbance on migratory populations, it should be noted that any conclusion specific to blue whales only applies to this subset of the population. Empirical evidence on the structure and long-term range variation of this population is incomplete, and this information is critical for the successful application of similar modelling exercises to specific populations. Therefore, future research on this population should prioritise the definition of the stock's boundaries, the characterization of any sub-stock structure, and spatio–temporal movement dynamics to inform appropriate management.

### Model implementation

Our model was developed in the context of state-dependent behavioural and life-history theory (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000). We modelled a female's behavioural and life-history strategy over her lifetime. We assumed that a female blue whale could live up to 90 years after sexual maturation (Wilson and Ruff 1999), reaching a maximum age $T = 35\ 252$ days (where $T$ also represented the day her last calf was weaned), and that she was reproductively active over the entire 90 years of sexual maturity (i.e. there was no senescence; Marsh and Kasuya 1986). At each time step $t$ (i.e. each day of her life) we determined decisions on movement and reproduction (see details below) on the basis of the dynamics of a set of state variables (female blubber mass, location, patch type and proportion of mass of the suckling calf that is blubber) using SDP (backward iteration, Supplementary material Appendix 2). We then used the matrices of optimal movement and reproduction decisions in MC simulations (forward iteration) to model the state dynamics of 1000 females from age 1 year until death, under different environmental and anthropogenic disturbance scenarios. We ran a trial forward iteration to obtain the distributions for the initial blubber mass and location of the simulated females. Specifically, we simulated 1000 females starting at a random initial mass and location and identified the moment in time when the state variables had moved away from initial conditions (i.e. the first day of the second year of the trial simulation). In all subsequent simulations, we then drew initial blubber mass and location of simulated females from the distributions of these state variables at that time. Since females of age 1 year are smaller,

we rescaled the distribution of blubber masses for the initial draw: we divided blubber mass by the maximum mass achievable on the first day of the second year, and multiplied the resulting proportion by the maximum mass at age 1 year. The backward and forward iterations of the model were coded in C++ using package Rcpp (Eddelbuettel and Francois 2011) for R (<www.r-project.org>). The code and associated files to run the model are provided in Supplementary material Appendix 5.

## Movement decisions

As in the original model by Pirotta et al. (2018b), a female's location was simplified as the position along a south-to-north axis representing the range over which this segment of the population migrates (from the winter breeding grounds in the south, to the waters south of Vancouver Island in the north). Each location corresponded to a patch size of 100 km by 100 km (Bailey et al. 2010). On each day, a female faced the decision to either stay in the current location and feed, travel forward, travel backward or move within the breeding locations.

## Reproductive states

During the course of her lifetime, a female could be in one of four reproductive states: juvenile, i.e. before reaching sexual maturity; mature and pregnant; mature and lactating, i.e. with a dependent calf; and mature, not pregnant and not lactating (i.e. resting). The evidence is inconclusive as to whether and how frequently blue whales are simultaneously pregnant and lactating (Lockyer 1981, 1984). For simplicity and because the realised inter-birth interval for this blue whale population is greater than 2 years on average (Sears et al. 2013) we excluded this possibility (McHuron et al. (2018) for an example of when it cannot be excluded). Rather than setting hard thresholds of energetic status (i.e. female blubber mass) to determine implantation, foetus abortion and calf abandonment or weaning, transitions among reproductive states were optimised using SDP. In other words, a female could decide to implant and get pregnant, abort the foetus, or wean the dependent calf on the basis of the value of her state variables at a given time.

We imposed biologically meaningful constraints: 1) birth could only occur south of 28°N, where the female and dependent calf were also constrained to remain for the first 40 days after parturition (Pirotta et al. 2018b), to account for potential thermoregulatory benefits for the newborn calf (although these are debated, Corkeron and Connor 1999, Clapham 2001) and restrictions on its swimming abilities (Cartwright and Sullivan 2009); 2) implantation could only occur in the breeding grounds (Gulf of California and off the southern tip of the Baja California Peninsula), because we assumed, for simplicity, that females have to be in this region in order to encounter potential mates; 3) for simplicity, birth and implantation dates were fixed on 1 December and 1 January, respectively (Supplementary material Appendix 1 Fig. A1).

There is no information on weaning times for this population, but lactation is estimated to last seven months on average in Antarctic blue whales *B. musculus intermedia* (Lockyer 1981). In our model, whales could potentially extend lactation up to one year, after which the calf was automatically weaned. In nature, the transition to autonomous feeding is probably gradual for a suckling calf, but, in the absence of fine-scale information on this process, we retained seven months as the threshold after which a calf could feed autonomously. If a calf was weaned before this date, it had to rely on stored lipid reserves until that age. A calf's condition at weaning (if weaned at seven months or later) or after accounting for the energy required to survive until seven months (if weaned before it could feed autonomously) determined its survival probability, which we modelled using the same sigmoidal relationship used in Pirotta et al. (2018b) (Supplementary material Appendix 2). We assumed a 50:50 sex ratio to determine whether the calf was a female. Because reproductive success was defined as the number of female calves reaching age 1 year (the maximum weaning age), the behavioural decisions and state dynamics of female calves weaned before this date were simulated using MC simulations. In other words, if a female calf was weaned before age 1 year and survived, she entered the simulation on the day of weaning, at the location and body condition at the end of lactation, and was followed until 1 year.

## Growth and maturation

Calf and juvenile growth is likely to occur in irregular spurts, because an individual's ability to deposit new lean tissue depends on available food resources. However, individuals may be able to compensate over time for periods when growth slows down or stops (Metcalfe and Monaghan 2001). In light of this, and in order to make the model computationally feasible, we assumed growth was continuous. As a result, we modelled growth as a daily energy requirement (in kJ) given a whale's age in days, $t$: $e_g(t) = \Delta g(t) \times w_{cal}$, where $\Delta g(t)$ was the growth in lean mass on that day (in kg) and $w_{cal}$ was the calorific content of whale tissue (i.e. 6276 kJ kg$^{-1}$; Lockyer 1981). We used the von Bertalanffy growth curve for length (which was then translated to lean mass as described in Pirotta et al. (2018b)) from Lockyer (1981) to calculate $\Delta g(t)$. A juvenile female is thought to become sexually mature when she reaches approximately 20 m in length (Lockyer 1981, Gilpatrick and Perryman 2008). Given the assumed growth curve, this length is reached around 6 years of age. Therefore, we assumed that on 1 January after her 6th birthday, a female could implant for the first time. The size of a female on a given day determined the maximum amount of blubber mass she could carry (that is, 35% of her total mass; Supplementary material Appendix 1).

## Additional mortality rates

As in Pirotta et al. (2018b), a female could die of starvation when her blubber mass fell below the minimum percentage of

body mass required for survival (5%). However, individuals can also die as a result of other causes (e.g. disease, predation, ship collision, etc.). To account for these processes, we modelled a yearly survival rate of 0.975 for juveniles and adults (Ramp et al. 2006). Suckling calves are expected to have a lower survival rate and, in the absence of data on blue whales, we used the first-year survival rate for humpback whale *Megaptera novaeangliae* calves of 0.875 (Barlow and Clapham 1997). We used humpback whales as the closest baleen whale species for which such an estimate was available. For simplicity, we assumed that an individual would die of old age when reaching age = 35 252 days. In addition, a foetus could be aborted irrespective of the energetic status of the pregnant female. We used the proportion of potential perinatal losses (13.5%) reported for North Atlantic right whales *Eubalaena glacialis* (Browning et al. 2010) as a conservative estimate of abortion rate. Although this is likely an underestimation of the true rate, it is well above the minimum estimate of 0.14% for baleen whales reported by Ichihara (1962). Adult, calf and foetal background mortality rates were included in both the backward and the forward iteration, and operated in addition to the mortality due to nutritional status resulting from the state dynamics. The empirical estimates we used to represent these background mortality processes likely include deaths due to poor nutritional status; in the absence of cause-specific estimates, they were used here to illustrate how these additional processes could be included in the model.

## Environmental variability

We assumed that blue whales are evolutionarily adapted to the average spatio–temporal variation in food resources in their environment. As detailed in Pirotta et al. (2018b), a female that travelled for the day could encounter one of three patch types (low-quality food patches, high-quality food patches or patches with no food), with probability inferred from telemetry data (Bailey et al. 2010). Patch quality depended on the differences in size of available krill species, corresponding to different amount of biomass (and thus energy) a female could acquire per unit of water engulfed. A whale feeding within a given patch type had a probability of encountering a specific krill density (that is, a given biomass per unit of water), which varied spatially and seasonally to reflect yearly environmental fluctuations in the population's range. This distribution of potential krill densities was assumed to be proportional to the amount of new nutrients entering the system, as measured by the upwelling index provided by the Environmental Research Division, Southwest Fisheries Science Center, NOAA Fisheries (Pirotta et al. 2018b).

The oceanography in the eastern North Pacific Ocean is also strongly influenced by a series of climatic processes with different periodicities (such as the El Niño Southern Oscillation (ENSO), and the Pacific Decadal Oscillation (PDO); Chavez et al. 2011, Fiedler et al. 2013, Fisher et al. 2015). Given their lifespan, we assumed that whales developed behavioural and life history strategies to cope with such environmental oscillations. Therefore, we modified the model

of Pirotta et al. (2018b) to allow for transitions between environmental regimes over a female's lifespan (Supplementary material Appendix 3). Due to computer memory and run time limitations, we could only implement two alternative sets of representative environmental conditions. Specifically, the standard environment corresponded to the average prey distribution and dynamics described in Pirotta et al. (2018b), while the unfavourable environment was taken to represent ENSO conditions (Chavez et al. 2002, Marinovic et al. 2002), corresponding to a northward shift in the distribution of the less-energy-rich krill species *Nyctiphanes simplex* and an overall 70% reduction in upwelling intensity in the southern and central California Current, with productivity reduced, i.e. the ENSO conditions simulated in Pirotta et al. (2018b). The shift between environmental regimes could occur at the start of each year, and unfavourable conditions were simulated to occur with a probability of 0.2, to reflect the mean periodicity of ENSO events (every 4–5 years on average). For simplicity, we assumed that conditions in a given year were independent of conditions in the previous year. In the forward iteration, we modelled 1 in 5 years to be unfavourable under baseline conditions and generated a time series of standard and unfavourable years. Each female entered the simulation at a random year along this time series, so that simulated whales experienced unfavourable conditions at different moments of their life. In addition to these broad-scale environmental fluctuations (e.g. decadal regime shifts observed in marine ecosystems), the forward iteration allowed for small-scale variability in the overall productivity of the environment in a given year. This was informed by the median confidence interval around the time series of the upwelling index used to characterise krill density (Schwing et al. 1996, Pirotta et al. 2018b), corresponding to a median 5% variability in productivity across locations.

## Responses to anthropogenic disturbance

We simulated anthropogenic disturbance in the forward iteration at specific locations in the whales' range, under the assumption that their behaviour was not adapted to disturbance because this is not part of their evolutionary history (McHuron et al. 2017, Pirotta et al. 2018b). In line with the objectives of this study, we did not aim to replicate the wide range of blue whale responses to the variety of anthropogenic stressors they could encounter in their habitat (Goldbogen et al. 2013). Instead, theoretical disturbance scenarios and associated individual responses were kept general, to investigate broad emerging patterns. A given proportion $p_e(l, t)$ of each location, $l$, was exposed to disturbance on any given day, $t$, of the simulation. This proportion was used as a probability in a Bernoulli draw to determine whether an individual that was feeding in that location was exposed on day $t$. Each whale was characterised by a given probability of responding to disturbance when exposed (i.e. a level of responsiveness $r_w$), which was drawn at the start of the simulation (or when the female entered the population at weaning) from a beta distribution, $r_w \sim \beta(5, 5)$ (McHuron et al. 2017).

If she responded, she changed her behaviour and moved away, selecting the second-best alternative location given her set of state variables. If she did not respond, she stayed in the current location and continued to feed, although she incurred a reduction $r_p$ in the productivity of that location. This decrease in the accessible prey was taken to represent the range of mechanisms by which disturbance could affect energy acquisition or expenditure (e.g. spatial avoidance, cessation of feeding, increase in stress levels, indirect effect on the prey, etc.).

## Simulated scenarios

In addition to baseline conditions (i.e. 1 unfavourable year every 5, and no anthropogenic disturbance), we explored a series of scenarios of environmental change and anthropogenic disturbance (Table 1). For the environmental scenarios, we first simulated a progressive increase in the frequency of unfavourable years (scenario 2–4). In scenario 5–6, we simulated the occurrence of years where productivity across the range was reduced to 80% of baseline conditions, at two different frequencies, to which the animals were assumed to respond by adopting the optimal strategy under unfavourable conditions. Finally, we simulated a degradation of environmental conditions across the entire range of the population (scenario 7–10), and assumed the animals would use the same behavioural and reproductive strategy evolved for baseline conditions.

For the anthropogenic scenarios, we first simulated disturbances occurring only once, with increasing duration (two weeks, two months, six months or one year), either during a random year (which we implemented using the same time series we used for the occurrence of unfavourable years; scenario 11–17) or at a specific moment in the life of a female (scenario 18–24). We then simulated repeated disturbance, occurring every year and lasting 2, 6 or 12 months. In the latter case, disturbance was essentially occurring all the time, affecting a female's entire lifespan. Various degrees of disturbance intensity and extent (in terms of proportion of a location that was disturbed $p_e$, corresponding reduction in the productivity $r_p$, and number of disturbed locations) were tested and are detailed in Table 1 (scenario 25–39). Finally, we simulated the effects of disturbance occurring every second or third year (scenario 40–41). To combine environmental and anthropogenic effects, we simulated a set of scenarios where anthropogenic disturbance occurred in the context of a changing environment (Table 1; scenario 42–47).

To assess the effect of environmental and anthropogenic disturbance on female survival and reproductive success, we used Cohen's $d$, which is the difference between means in the undisturbed and disturbed scenarios scaled by their pooled standard deviation (Cohen 1977, McHuron et al. 2017). We computed mean age at death and mean number of female calves surviving to age 1 year across females for each simulated scenario and compared to the baseline scenario. Values of Cohen's $d$ of 0.2, 0.5 and 0.8 were taken to indicate small, moderate and large effect sizes, respectively (Cohen 1977).

## Results

### Baseline conditions

Our model was able to replicate several aspects of the life history and ecology of the population of blue whales. Migratory behaviour emerged from the forward MC simulations: with variability in the exact timing, all females periodically travelled between feeding and breeding grounds to track the seasonal variation in prey resources across the range (Fig. 1A, 2A–B). The occurrence of unfavourable years strongly affected movements, with individuals reaching northern patches to access the remaining pockets of high productivity (Fig. 1A, 2A–B). Similarly, female blubber mass underwent dramatic seasonal oscillations (Fig. 1B, 2C), particularly during unfavourable years. When a female was not lactating, the mean difference between the maximum blubber mass (at the end of the feeding season) and the minimum blubber mass (at the start of spring) corresponded to 18% (16–33%) of the average total weight in the given year, equalling a 48% (41–77%) mean decrease in blubber mass over the winter. However, except in unfavourable years, females were generally able to replenish their energy stores during the following feeding season. A female's reproductive state also had a large influence on both movement and blubber mass. For example, pregnant females were the first to leave the feeding grounds, while juveniles tended to leave the feeding grounds later in the year and had more flexibility in their movements, as indicated by the larger variability shown in Fig. 3A. Females that were not pregnant nor lactating showed intermediate features (Fig. 3A). In contrast, these females tended to reach the feeding grounds later in the spring, compared to the other reproductive classes (Fig. 3C). In terms of blubber mass, juveniles accumulated an increasing amount of reserves as they grew in size with age (Fig. 2C). The relative seasonal mass decrease was stronger for this category, averaging 33% of the mean total weight in the first simulated year, and progressively declining towards the overall mean of 18% over the following 7–8 years. In years when a female had a dependent calf, the energy stored in her blubber mass was severely depleted (Fig. 2C): on average, lactating females lost 22% (20–24%) of their average total weight in these years, corresponding to a 57% (51–68%) decrease in blubber mass, i.e. a 9% additional net loss in blubber mass compared to non-lactating females. Initial blubber conditions only affected survival probability in the first year of the simulation, after which environmental variability drove individual performance.

In addition to background levels of mortality, mortality due to starvation was most concentrated in young juveniles, which had less energy reserves to buffer against seasonal and stochastic environmental variability (Fig. 4). Many of these juvenile individuals died during unfavourable years. Starvation also occurred during the last reproductive cycle before reaching the maximum age. This is an artefact of the SDP backward iteration: because individuals that were not lactating on the last year had no reproductive potential left, alternative behavioural strategies showed no difference in

Table 1. Details of the simulated scenarios of environmental change and anthropogenic disturbance. The effects on survival and reproductive success were quantified using Cohen's $d$ (Cohen 1977, McHuron et al. 2017). Cohen's $d$ is the difference between means in the undisturbed and disturbed scenarios scaled by their pooled standard deviation, and values of 0.2, 0.5 and 0.8 were taken to indicate small, moderate and large effect sizes, respectively (Cohen 1977, McHuron et al. 2017).

| Scenario number | Environment | Anthropogenic disturbance | Duration | Frequency | Locations | Proportion disturbed $p_e(l, t)$ | Productivity reduction $r_p$ | Cohen's $d$ survival | Cohen's $d$ reproductive success |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Baseline | no | – | – | – | – | – | – | – |
| 2 | 1 unfavourable year every 4 | no | – | – | – | – | – | 0 | 0.2 |
| 3 | 1 unfavourable year every 3 | no | – | – | – | – | – | 0.04 | 0.18 |
| 4 | 1 unfavourable year every 2 | no | – | – | – | – | – | 0.14 | 1.04 |
| 5 | 1 in 10 years is unfavourable (80%) across the range | no | – | – | – | – | – | 1.07 | 0.99 |
| 6 | 1 in 20 years is unfavourable (80%) across the range | no | – | – | – | – | – | 0.52 | 0.55 |
| 7 | Conditions worsen overall (75% of baseline productivity) | no | – | – | – | – | – | 1.37 | 1.08 |
| 8 | Conditions worsen overall (85% of baseline productivity) | no | – | – | – | – | – | 1.25 | 1.08 |
| 9 | Conditions worsen overall (95% of baseline productivity) | no | – | – | – | – | – | 0.19 | 0.38 |
| 10 | Conditions worsen overall (97.5% of baseline productivity) | no | – | – | – | – | – | 0.06 | 0.14 |
| 11 | Baseline | yes | 2 weeks | once – random year | all | 0.95 | 95% | -0.04 | -0.04 |
| 12 | Baseline | yes | 2 months | once – random year | all | 0.95 | 95% | -0.04 | -0.04 |
| 13 | Baseline | yes | 6 months | once – random year | all | 0.95 | 95% | -0.04 | -0.03 |
| 14 | Baseline | yes | 1 year | once – random year | all | 0.95 | 95% | 0.34 | 0.33 |
| 15 | Baseline | yes | 1 year | once – random year | half (random) | 0.95 | 95% | -0.02 | -0.02 |
| 16 | Baseline | yes | 1 year | once – random year | four locations (southern California) | 0.95 | 95% | 0.17 | 0.13 |
| 17 | Baseline | yes | 1 year | once – random year | half (random) | 0.5 | 50% | -0.06 | -0.06 |
| 18 | Baseline | yes | 2 weeks | once – same year (3) | all | 0.95 | 95% | -0.04 | -0.03 |
| 19 | Baseline | yes | 2 months | once – same year (3) | all | 0.95 | 95% | 0.02 | 0.03 |
| 20 | Baseline | yes | 2 months | once – same year (9) | all | 0.95 | 95% | -0.08 | -0.06 |
| 21 | Baseline | yes | 6 months | once – same year (9) | all | 0.95 | 95% | -0.02 | -0.01 |
| 22 | Baseline | yes | 1 year | once – same year (3) | half (random) | 0.95 | 95% | 1.33 | 1.08 |
| 23 | Baseline | yes | 1 year | once – same year (9) | half (random) | 0.95 | 95% | 1.1 | 1.06 |
| 24 | Baseline | yes | 1 year | once – same year (16) | half (random) | 0.95 | 95% | 0.87 | 0.88 |
| 25 | Baseline | yes | 2 months | every year | fourteen locations (Baja California Peninsula and southern California) | 0.95 | 95% | -0.05 | -0.02 |
| 26 | Baseline | yes | 2 months (Apr–May) | every year | fourteen locations (Baja California Peninsula and southern California) | 0.95 | 95% | 0.02 | 0.08 |
| 27 | Baseline | yes | 2 months | every year | all | 0.95 | 95% | 0.11 | 0.09 |
| 28 | Baseline | yes | 6 months | every year | all | 0.95 | 95% | 0.15 | 0.19 |
| 29 | Baseline | yes | 6 months | every year | half (random) | 0.95 | 95% | 0.04 | 0.09 |
| 30 | Baseline | yes | 6 months (second semester) | every year | half (random) | 0.95 | 95% | -0.03 | -0.02 |

(Continued)

Table 1. Continued

| Scenario number | Environment | Anthropogenic disturbance | Duration | Frequency | Locations | Proportion disturbed $p_e(l,t)$ | Productivity reduction $r_p$ | Cohen's $d$ survival | Cohen's $d$ reproductive success |
|---|---|---|---|---|---|---|---|---|---|
| 31 | Baseline | yes | 1 year | every year | half (random) | 0.25 | 25% | −0.04 | −0.02 |
| 32 | Baseline | yes | 1 year | every year | half (random) | 0.5 | 50% | 0.65 | 0.79 |
| 33 | Baseline | yes | 1 year | every year | a third (random) | 0.5 | 50% | −0.01 | 0.03 |
| 34 | Baseline | yes | 1 year | every year | a fourth (random) | 0.5 | 50% | 0.02 | 0.01 |
| 35 | Baseline | yes | 1 year | every year | four locations (southern California) | 0.5 | 50% | 0.66 | 0.8 |
| 36 | Baseline | yes | 1 year | every year | two locations (southern California) | 0.5 | 50% | 0.64 | 0.81 |
| 37 | Baseline | yes | 1 year | every year | half (random) | 0.5 | 25% | 0.66 | 0.75 |
| 38 | Baseline | yes | 1 year | every year | half (random) | 0.25 | 50% | 0.34 | 0.3 |
| 39 | Baseline | yes | 1 year | every year | half (random) | 0.95 | 95% | 1.31 | 1.08 |
| 40 | Baseline | yes | 1 year | every two years | half (random) | 0.5 | 50% | 0.61 | 0.66 |
| 41 | Baseline | yes | 1 year | every three years | half (random) | 0.5 | 50% | 0.39 | 0.49 |
| 42 | 1 unfavourable year every 4 | yes | 2 months | once – same year (3) | all | 0.95 | 95% | 0.13 | 0.32 |
| 43 | 1 unfavourable year every 4 | yes | 6 months | once – same year (9) | half (random) | 0.95 | 95% | −0.04 | 0.23 |
| 44 | 1 unfavourable year every 4 | yes | 6 months | once – same year (9) | all | 0.95 | 95% | 0.07 | 0.3 |
| 45 | 1 unfavourable year every 4 | yes | 2 months | every year | all | 0.95 | 95% | 0.19 | 0.38 |
| 46 | 1 unfavourable year every 4 | yes | 1 year | once – random year | half (random) | 0.95 | 95% | 0.18 | 0.39 |
| 47 | 1 unfavourable year every 4 | yes | 1 year | every year | half (random) | 0.25 | 25% | 0.03 | 0.25 |

fitness value; as a result, these animals were behaving randomly. Some individuals did reach 35 252 days and died of old age (Fig. 4).

In terms of reproduction, most individuals attempted the first pregnancy as soon as they matured (mean age = 6.4 years (6–8)), but average age at which the first pregnancy was carried to term was 7.6 years (7–12). Pregnancy rate, defined as the proportion of females that got pregnant at a given age divided by the number of females that could get pregnant (i.e. excluding lactating females) increased with age but remained high (mean = 0.95 (0.87–1) after age 15 years; Fig. 5A). Mean pregnancy rate including lactating females was 0.60 (0.49–0.69). Individuals that did not get pregnant in a given year appeared to be in poorer condition (Fig. 5B). In addition, females that were pregnant in unfavourable years prioritised their own survival and travelled north to access remaining prey resources, even though this resulted in loss of the foetus (Fig. 2B). This led to a dramatic reduction in pregnancy success in unfavourable years (Fig. 6E). With the exception of the first year post-maturation (when all foetuses were aborted), the proportion of pregnancies that were carried to term was independent of female age and had a mean of 0.675 (0.554–0.894). In addition to background foetal mortality (13.5%), on average 19% of foetuses were aborted as a result of female condition and the external environment. Across females, the mean interval between consecutive births was 2.42 years (1–6). The probability of successfully raising a calf to age 1 year increased with age and blubber mass of the female at the start of lactation (Fig. 6C–D). Ignoring background mortality levels, 32% (19–81%) of calves (across age of the mother) did not survive due to their condition at weaning. On average, females did not produce a calf that survived to age 1 year until their 12th year, but there was large variability among females (8–25 years). The mean interval between the production of calves of any sex that successfully reached age 1 year was 6.34 years. The histogram of recorded durations of lactation shown in Fig. 6A identifies three main strategies that females may follow for deciding when to abandon or wean a calf. Some females abandoned their calf early on (approximately 40 days post-partum), before investing much energy into lactation; other females continued lactation to bring the calf closer to the time where it could feed autonomously (7 months post-partum); and finally, when possible given their condition, females extended lactation to ensure the calf was weaned in the best condition. During unfavourable years, most calves were abandoned early, which caused them to die before reaching 1 year (Fig. 6E). No calf weaned before 4.8 months survived to age 1 year, while longer durations of lactation resulted in an increased chance of survival (Fig. 6B). Mean female lifetime reproductive success was 2.9, with a median of 1 and a range between 0 and 18 (Fig. 6F).

## Disturbance scenarios

Environmental change had severe consequences for simulated individuals: increasing the frequency of unfavourable years led to a progressive reduction in reproductive success
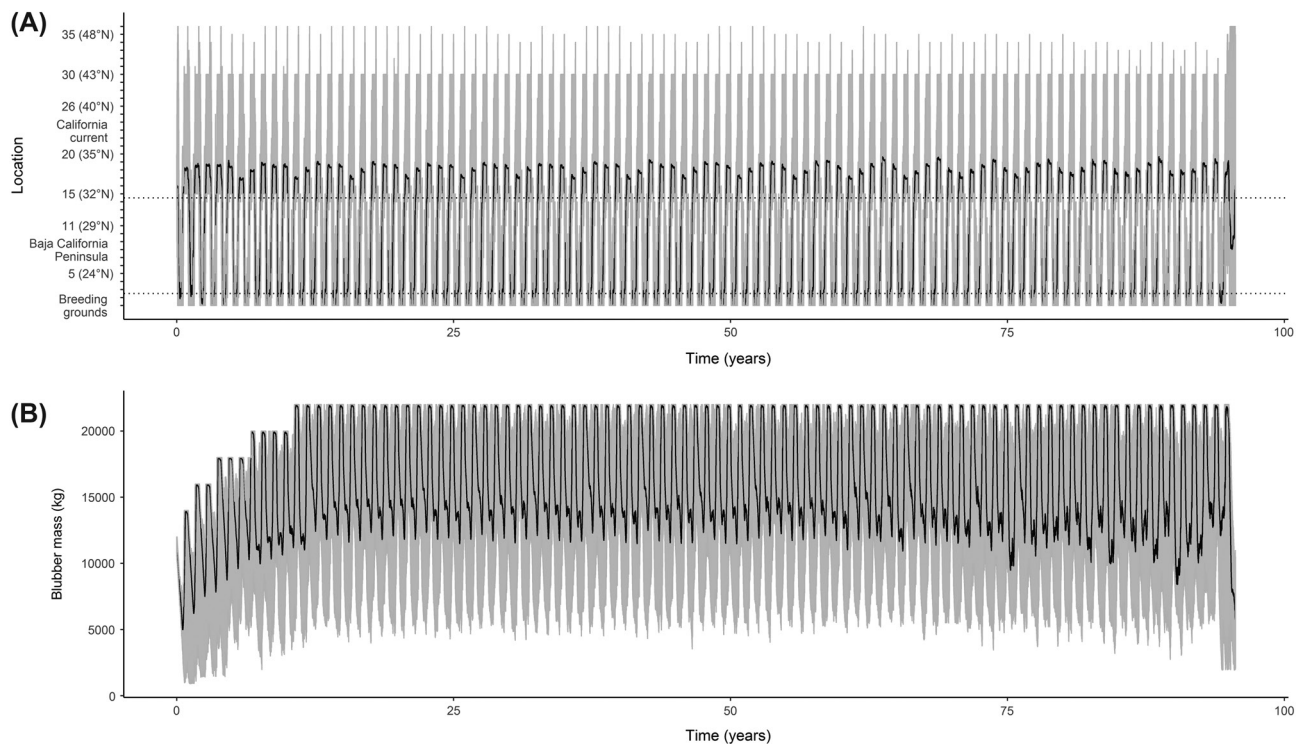
Figure 1. Results of the forward Monte Carlo simulations under baseline conditions. Mean (black line) and range (grey shaded area) of location (A) and blubber mass (B) over time across all simulated females. Locations are numbered progressively from south to north from 1 to 36, where location 1 corresponds to the Gulf of California and location 36 to the waters south of Vancouver Island, which is the northernmost extent of the summer migration. The corresponding latitude is reported in brackets.

(Table 1, scenario 2–4; Fig. 7). These changes were mediated by a female's reduced ability to sustain her calf through lactation, resulting in calves being weaned early (Supplementary material Appendix 3 Fig. A2). In scenario 2, the mean interval between calves successfully reaching age 1 year increased to 8.34 years, and the mean age at which a female's first calf survived to age 1 year increased to 12.1 years (8–29). Females were, on average, attempting to reproduce more frequently (inter-birth interval = 2.26 years (1–9)), because abandoning a calf early gave them the opportunity to become pregnant again. Similarly, rare events of extreme depletion of prey resources had dramatic effects on both survival and reproduction (scenario 5–6). In general, whales appeared to tolerate only small reductions in overall productivity (scenario 7–10). However, they were able to survive at the expense of reproduction (Supplementary material Appendix 3 Fig. A2), provided the changes in productivity were not extreme (e.g. scenario 2, 3 or 10).

In contrast, whales appeared to be able to compensate for substantial levels of anthropogenic disturbance in their range (Table 1, Fig. 7). Singular disturbance events, even at very high intensity (95% probability of exposure for an individual in a disturbed location, with 95% reduction in feeding efficiency when staying in disturbed conditions), were only predicted to affect the whales' vital rates when they occurred for an entire year and affected all locations in the home range. The only exception was disturbance localised in

the central part of their summer feeding ground (scenario 16), when whales were severely impacted. When the year of disturbance was not random (i.e. ensuring that all whales got exposed to the stressor), most animals died of starvation, even if only half of the locations were disturbed (scenario 22–24). Repeated disturbance caused stronger effects on reproductive success and, to a lesser extent, survival. Depending on the locations and times of disturbance, an effect was visible starting at two months of disturbance repeated every year (scenario 26–29). However, it was only when disturbance was present year-round and every year that larger effects could be detected. For example, under a scenario where half of the locations were characterised by 50% probability of exposure and 50% reduction in feeding efficiency (scenario 32), the mean female age at which the first pregnancy was successfully carried to term increased to 10 years (7–15), calves were weaned earlier (Supplementary material Appendix 3 Fig. A3), the mean interval between calves successfully reaching age 1 year increased to 12.68 years, and the mean age at which the first calf survived to age 1 year increased to 16.1 years (8–36), resulting in an overall reduction of female reproductive success (Supplementary material Appendix 3 Fig. A3). More severe disturbance (95% probability of exposure, with 95% reduction in feeding efficiency) exacerbated these effects even further (scenario 39). However, even under these extreme conditions, a weaker disturbance (25% probability of exposure for an individual in a disturbed location, with
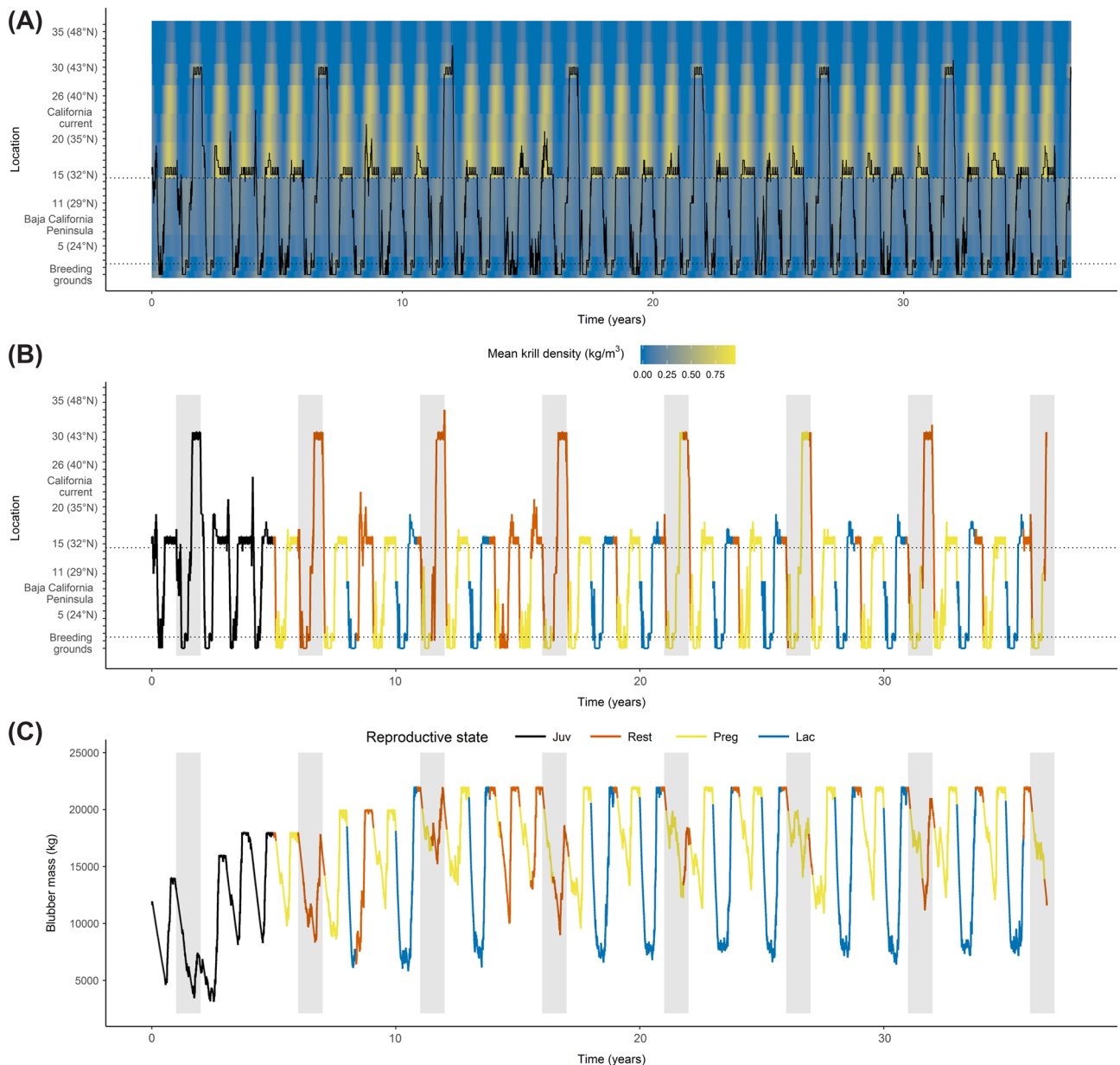
Figure 2. An example of the time series of location (A–B) and blubber mass (C) for one female. In (A), the time series of location is overlaid on a heat map of the spatiotemporal variation in mean krill density (as derived in Pirotta et al. 2018b from the upwelling index). In (B) and (C), the time series is coloured by reproductive state. Possible reproductive states are juvenile (Juv), not pregnant and not lactating (Rest), pregnant (Preg) and lactating (Lac). The grey shaded areas represent unfavourable years. Locations are numbered progressively from south to north from 1 to 36. The corresponding latitude is reported in brackets.

25% reduction in feeding efficiency when staying in the disturbed location) was predicted to have no effect on whales' vital rates (scenario 31). The extent and location of the disturbance appeared to be quite critical in determining the size of the effect (scenario 32–36), although these consequences dissipated when the frequency of the disturbance was reduced from every year to once every 2–3 years (scenario 40–41). The probability of being exposed to disturbance had more influence on the size of the effect when compared to the percentage reduction in feeding efficiency following disturbance (scenario 38 versus 37).

When anthropogenic disturbance occurred in the context of a changing environment (scenario 42–47, represented by a higher frequency of unfavourable years), the ability of whales to tolerate disturbance was reduced. As a result, disturbance scenarios that had no effect under baseline environmental conditions (e.g. scenario 19) had small to moderate effects when the environment was also changing (e.g. scenario 42).
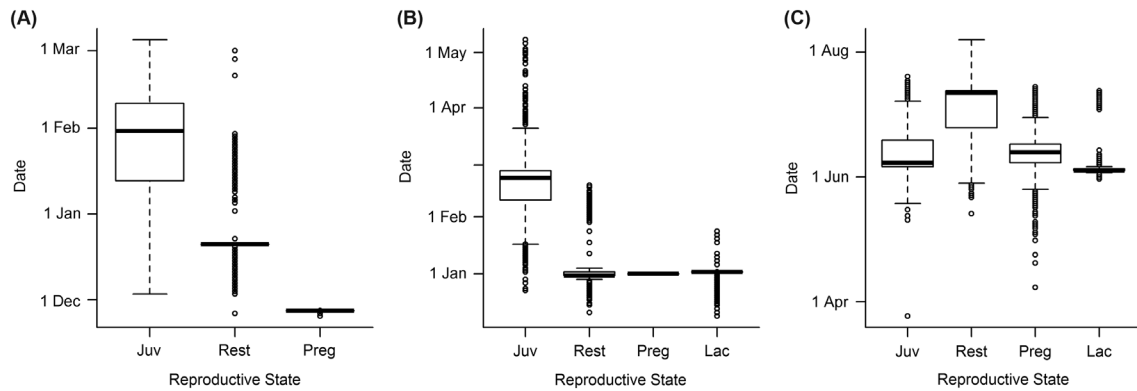
Figure 3. Movement dynamics of simulated females, represented as boxplots of the dates at which females in different reproductive states left the feeding grounds (A), reached the breeding grounds (B) and reached the feeding grounds (C). Possible reproductive states are juvenile (Juv), not pregnant and not lactating (Rest), pregnant (Preg) and lactating (Lac).

Moreover, predicted consequences on vital rates appeared to be stronger than the sum of the effects of environmental and anthropogenic disturbances alone. For example, a random one-year disturbance had no effect on vital rates (scenario 15) and an increase in frequency of unfavourable years to one every four (scenario 2) only had a small effect on reproductive success (Table 1); however, the combination of the two scenarios (scenario 46) led to a small change in female survival and a small to moderate change in reproductive success, suggesting that these stressors may act in synergy.

## Discussion

We developed a model to investigate the processes influencing the lifetime survival and reproductive success of females in a migratory population, quantify the effects of environmental and anthropogenic disturbance on these vital rates, and assess the relative contribution of multiple stressors acting concurrently. Our model illustrates the behavioural and reproductive strategies individuals can use to maximize expected reproductive success and how they respond to disturbance. Because it is formulated in terms of fundamental

state variables that characterise the internal physiology of individuals and external features of the environment, it can be adapted to any migratory species where comparable information is available.

Model results supported the importance of the seasonal nature of the environment in shaping the ecology of migratory populations, with migration emerging as the optimal strategy to maximise energy input throughout the year (Alerstam et al. 2003). Despite their latitudinal movements to track waves of productivity along the west coast of North America, simulated blue whales underwent dramatic variations in blubber mass between summer and winter. This variation was amplified in years when females were lactating, because this left them in a severely depleted condition at weaning. Seasonal and reproductive changes in energy reserves are an emergent property of the model, and can be compared with empirical data on blue whales and other marine mammal species. Historical estimates of seasonal weight variation in Antarctic blue whales indicate a 50% increase in body mass on the feeding grounds (Lockyer 1981). This estimate was calculated as the percentage increase on lean body weight, and contrasts with our estimate of a net 18% weight loss calculated over the average total weight for a given year. However,
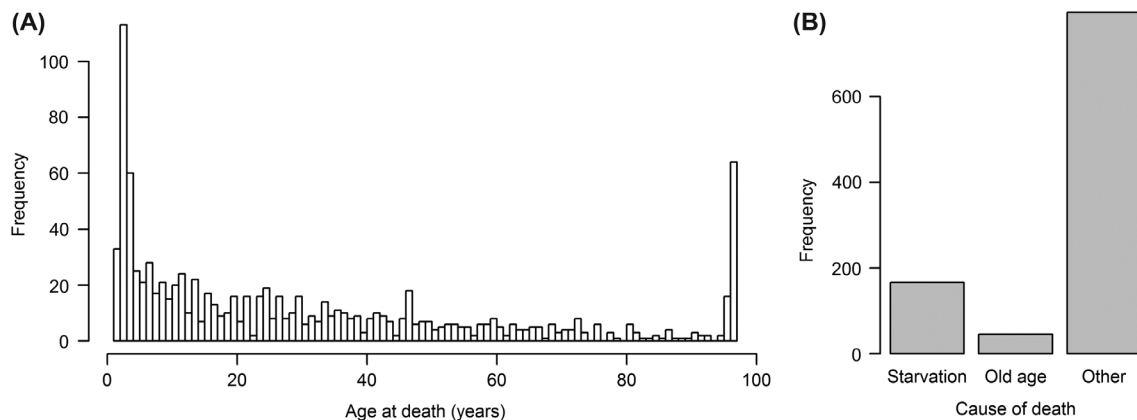


Figure 4. Survival patterns of simulated females. In (A), distribution of age at death; in (B), bar plot of the causes of death.
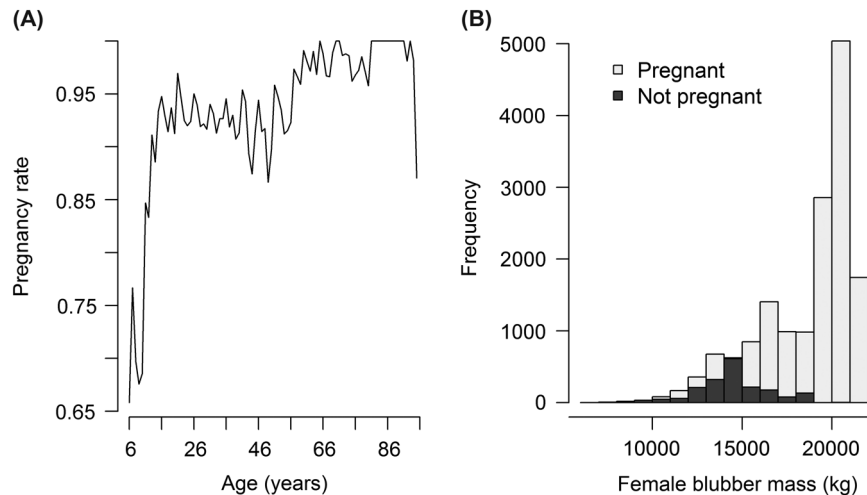
Figure 5. Pregnancy dynamics of simulated females. In (A), relationship between age and pregnancy rate (defined as the proportion of females of a given age that got pregnant on implantation day over the number of females of that age that could get pregnant, excluding lactating females). In (B), distributions of blubber mass on implantation days, based upon females' decision of whether to get pregnant.

eastern North Pacific blue whales are smaller (Gilpatrick and Perryman 2008), and are presumed to continue feeding during winter months (Etnoyer et al. 2006), allowing them to counterbalance the loss in energy reserves. Our results are comparable to the 11–29% seasonal weight loss observed in grey whales, *Eschrichtius robustus* (Rice and Wolman 1971), but grey whales do not feed during migration. The predicted

percentage decrease in total mass in lactating years (22%) is also comparable with the 25% change in body volume observed in southern right whales (*Eubalaena australis*) during the first three months of lactation (Christiansen et al. 2018) and the loss of 13–43% of body mass in phocid seals during 80% of the lactation period (Table 4 in Bowen et al. 1992). Overall, patterns emerging from our model broadly
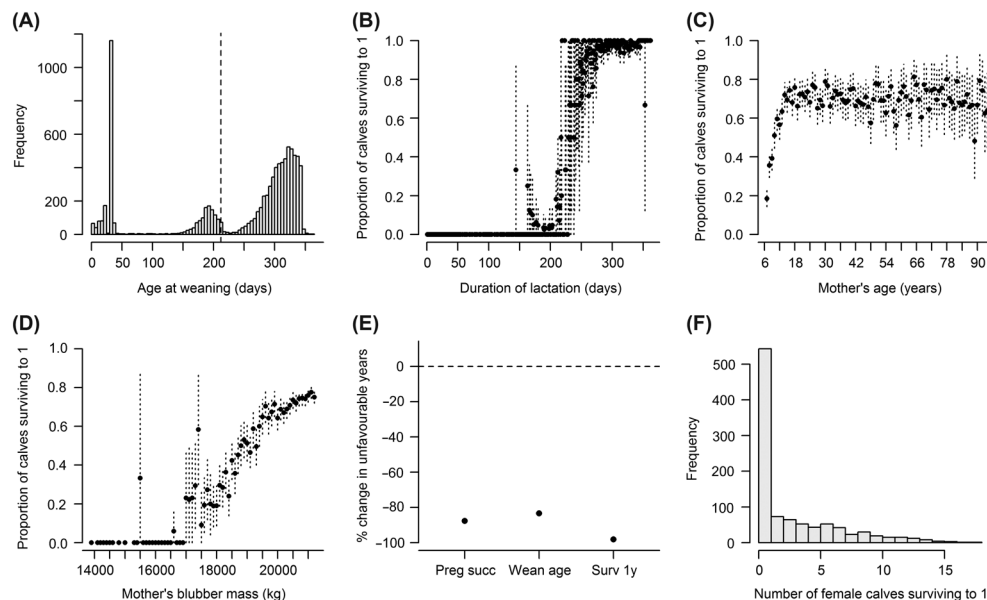


Figure 6. Patterns of lactation and calf survival for the simulated females in baseline conditions. In (A), the distribution of the age at weaning for all calves; the vertical dashed line indicates the threshold for autonomous feeding (seven months). In (B–D), the proportion of calves that survived to age 1 year as a function of the duration of lactation, the age of the mother and the blubber mass of the mother at the start of lactation, respectively; dashed segments represent the 95% confidence intervals around the proportions. Calves that died due to background levels of mortality were excluded from these plots. In (E), the mean percentage change in the proportion of successful pregnancies (Preg succ), age at weaning (Wean age) and proportion of calves surviving to 1 year (Surv 1y) in years when environmental conditions were unfavourable, compared to favourable years (dashed line). In (F), female reproductive success, expressed as the distribution of the number of female calves that reached age 1 year per simulated female.
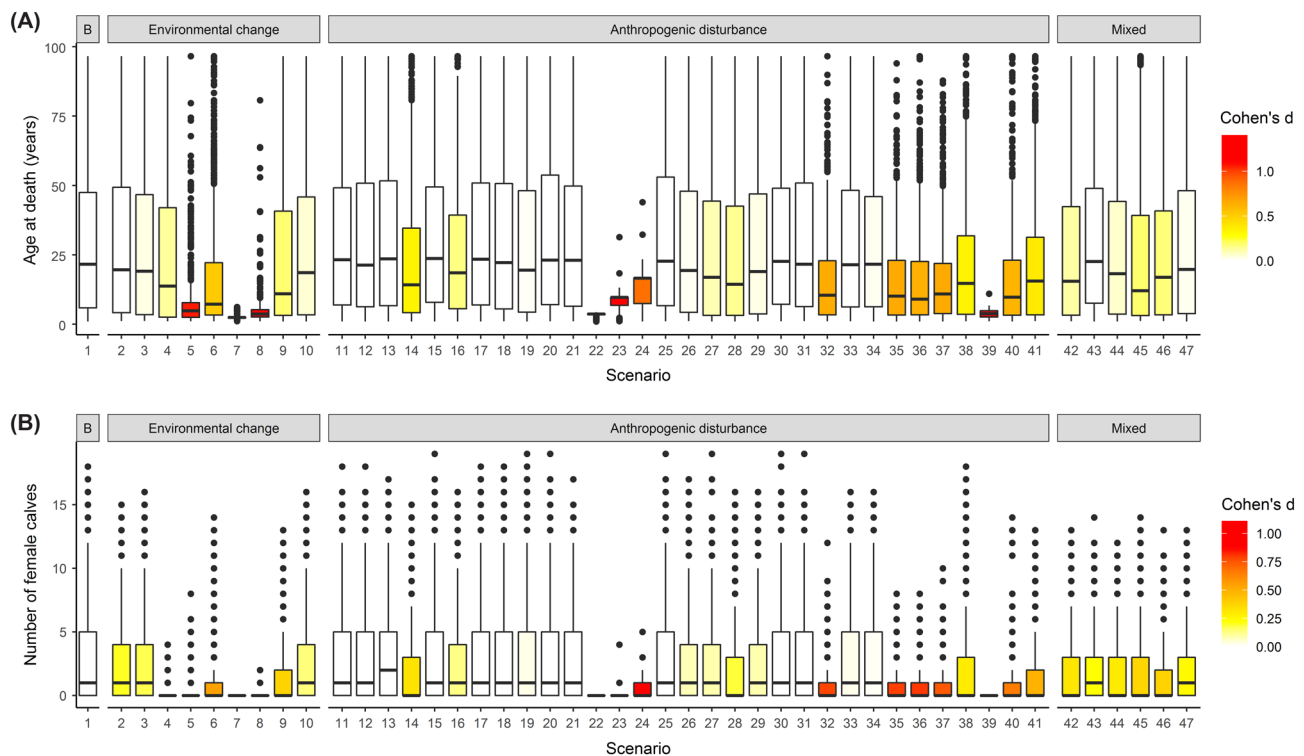
Figure 7. Results of the simulated scenarios of environmental change (scenario 2–10), anthropogenic disturbance (scenario 11–41) and anthropogenic disturbance occurring in a changed environment (scenario 42–46). Anthropogenic scenarios include disturbance occurring once in a random year of a female's life (scenario 11–17), once in the same year for all females (scenario 18–24), every year (scenario 25–39), every two years (scenario 40) and every three years (scenario 41). Within each of these sets, the duration, location and intensity of the disturbance vary as detailed in Table 1. In (A), female survival, expressed as the age at death; in (B), female reproductive success, expressed as the number of female calves that reached age 1 year per simulated female. Boxplots are coloured based on mean effect size, as represented by the value of Cohen's d. Scenario 1 corresponds to the baseline.

match the observed variation in blubber mass in other marine mammals. Reproductive constraints and costs also influenced movement patterns. Newly pregnant females were among the first to arrive in the feeding grounds in the California Current in the spring; this behaviour emerged from the SDP optimisation as a way for individuals to maximise the time spent feeding before giving birth. However, despite the constraint to spend some time in the breeding grounds after the birth of the calf, lactating females arrived earlier on average, to compensate for the additional loss of energy reserves during the winter. Unconstrained by reproductive needs, juveniles tended to extend their time in the feeding grounds. Pregnant females were constrained to give birth in southern waters and thus left the California Current feeding grounds earlier in late autumn. These predictions are in contrast with results from baleen whales in the Antarctic (Lockyer 1981), but in line with observations of grey whales (Rice and Wolman 1971). The ability of eastern North Pacific blue whales to feed outside the main feeding grounds (Reilly and Thayer 1990, Stafford et al. 2005, Etnoyer et al. 2006), together with their shorter migration distances, may explain some of these differences.

Across all scenarios, juveniles were the most sensitive portion of the population. This was due to their small size,

which constrained the amount of energy reserves they could carry and thus limited their ability to compensate for lost foraging opportunities. As a result, juvenile individuals were more prone to starvation in unfavourable years or during years of intense disturbance, as has been observed in populations exposed to intense climatic oscillations (Trillmich and Limberger 1985). The higher sensitivity of juvenile survival compared to other vital rates is a recurrent feature in populations of long-lived mammals (Gaillard et al. 1998, Eberhardt 2002). Younger (and thus smaller) mature females were also less likely to complete a pregnancy or successfully raise a calf to age 1 year, suggesting a mechanism through which body size could constrain maturation (Roff 1993, Sand 1996). These results highlight the importance of body size (i.e. the volume of reserves that can be accumulated; Irvine et al. 2017) as a way to buffer stochastic and periodic variability in the environment (Lindstedt and Boyce 1985, Millar and Hickling 1990, Costa 1993) while sustaining high costs of reproduction (Christiansen et al. 2018). In concert with many other recognized benefits of large size, such as a low mass-specific metabolic rate (White et al. 2009) and an efficient cost of transport (Williams 1999), this could have acted as an evolutionary force driving the development of the large sizes of baleen whales (Brodie 1975, Slater et al. 2017).

In terms of reproductive strategy, because the first phase of pregnancy is relatively less costly from an energetic perspective, individuals were predicted to get pregnant whenever they could. This resulted in high pregnancy rates: the mean predicted pregnancy rate (60%) tended to be at the high end of the range of existing estimates for baleen whales (Lockyer 1984), but was comparable to the mean of 63.5% estimated for Antarctic humpback whales (Pallin et al. 2018). However, there were limitations on whether pregnancy was carried to term, with younger females often failing. Abortion rate (combining background levels of foetal mortality and pregnancies interrupted by the female) was comparable to that of other marine mammals, e.g. 32% for New Zealand fur seals *Arctocephalus forsteri* (McKenzie et al. 2005). Skipped or failed pregnancies were associated with poor energetic state of the female, as observed in many pinniped species (Guinet et al. 1998, Pitcher et al. 1998, Desprez et al. 2018). Similarly, many newborn calves were abandoned at an early stage of lactation, before any substantial energy was invested in them, if the females did not have sufficient energy reserves to support milk delivery without compromising their own survival or the environment was unfavourable. These early abandonments could justify the lower mean inter-birth interval (2.42 years) and younger age at first parturition (7.6 years) predicted in this study compared to the empirical estimates for this population (2.57 years and >10 years, respectively) (Sears et al. 2013), if these calves are abandoned before they can be photographed by localised monitoring studies. Our results also suggest that calves need to be brought to a certain condition at weaning if they are to survive autonomously, and that early abandonment rarely results in the calf successfully reaching age 1 years. A relationship between condition at weaning and survival has been observed in many pinniped species (McMahon et al. 2000). Given their condition, we predicted that whenever possible females maximised the milk deliveries to the calf (Christiansen et al. 2016, 2018), and extended lactation beyond the age at which calves could begin to feed autonomously (Lee et al. 1991, Hamilton and Cooper 2010). These results may be affected by the hard threshold of autonomous feeding built into the model. In nature, weaning is likely to occur as a gradual transition from lactation to autonomous feeding, and the bond between the mother and the calf may follow more complex dynamics.

Overall, seasonality and stochasticity in the environment resulted in large variability in reproductive success across females (Hirshfield and Tinkle 1975, Boyce 1979). The age at which females could successfully raise a calf to 1 year, the success of any given reproductive attempt and, as a result, their lifetime reproductive output were highly variable, despite the relatively homogeneous features of simulated females and the limited role that initial blubber mass appeared to have on an individual's performance. In nature, individuals are also expected to be born at different sizes, which, given the importance of body size that our results highlighted, may exacerbate this heterogeneity in reproductive performance even further (Reiter et al. 1981). In light of the influence of baseline environmental stochasticity, it is therefore not surprising that we predicted environmental change to have severe consequences on whales' vital rates. Small reductions in productivity, the rare occurrence of particularly unfavourable years, or an increase in the frequency of unfavourable years resulted in rapid changes in reproductive success, even if the whales employed the strategies developed through their evolutionary history to cope with poorer habitats. Empirical evidence indicates that climatic oscillations such as ENSO can have large effects on marine mammal reproductive success (Trillmich and Limberger 1985, McMahon and Burton 2005, Leaper et al. 2006, Seyboth et al. 2016). Our results suggest that migratory marine mammals may be impacted by climate changes if they do not rapidly develop new strategies to adjust to altered conditions or if the overall availability or quality of prey ultimately decreases (Hazen et al. 2013).

Blue whales were much more resilient to anthropogenic disturbance than to environmental changes. Simulated disturbance only appeared to have an effect when involving the entire range of the population for a whole year at high intensity, or when repeated every year for large portions of the year. It is hard to imagine anthropogenic activities that could result in such extreme scenarios for the blue whale population under analysis. Individuals of this population are exposed to high levels of shipping traffic across their range, but behavioural responses are unlikely to be as intense as the ones that were required to cause an effect in our simulations. However, the predicted effect size was strongly influenced by the importance of disturbed locations to the ecology of the whales (Ellison et al. 2012). Therefore, a relatively localised disturbance (e.g. a naval sonar exercise, a seismic survey for oil and gas exploration, or the construction of an offshore wind farm) could have large effects if it occurred in areas that were critical for supporting females' resource acquisition in the summer, after a winter spent in suboptimal feeding habitats and possibly delivering large amounts of milk to a dependent calf. In general, effects tended to attenuate as long as females had the opportunity to compensate for lost or reduced feeding opportunity at alternative times and locations, similarly to Nabe-Nielsen et al. (2018). For example, reducing the frequency of the disturbance and leaving regions of optimal habitat undisturbed ensured that whales could replenish their blubber stores even when large portions of their range were disturbed. Similarly, the probability of exposure to disturbance within a given location appeared to matter more than the effect exposure had on feeding performance. Exposure rates to stressors have been shown to have a strong influence on the predicted effects of disturbance (Christiansen and Lusseau 2015, Costa et al. 2016, Nabe-Nielsen et al. 2018, Pirotta et al. 2018a). Applications of our model to management requires information on the characteristics of the stressors and the associated dose–response curves (Harris et al. 2018). Blue whales have shown complex and variable behavioural responses to specific disturbance sources (Goldbogen et al. 2013), and future model development should explore ways to include this empirical evidence in

disturbance simulations. However, our analysis highlights the aspects of disturbance that might have the largest long-term population consequences, and therefore helps in prioritising management efforts nonetheless. For example, our findings stress the need for reducing disturbance at key periods of the year and of the reproductive cycle, and in important locations along the population's range. More generally, for a wide-ranging species like blue whales, reducing repeated or continuous exposure to a stressor is critical to ensure individuals can compensate for foraging opportunities that are missed as a result of disturbance. For model development, disturbance was intentionally handled in a generic manner; if required, specific disturbance sources could be parameterised and the model could be used to test alternative management scenarios before their implementation.

The predicted effects of anthropogenic disturbance rapidly worsened when they occurred in the context of an environment that was also changing. Scenarios of disturbance that showed no effect on vital rates under baseline environmental conditions were predicted to have small to moderate effects when combined with environmental change. Importantly, these effects were not merely cumulative, but appeared to be synergistic, resulting in greater alterations in reproductive success and survival than the two stressors acting in isolation (Crain et al. 2008). This predicted synergy likely arises from the reduced ability of the whales to compensate outside the disturbed areas and times. In other words, a poorer environment meant that individuals had less ability to buffer against degraded feeding performance resulting from anthropogenic disturbance.

Different strategies emerged as a way to compensate for stochastic, environmental and disturbance events while maximizing expected lifetime reproductive success. In comparison with the model for one reproductive cycle (Pirotta et al. 2018b), females had the choice to favour their own survival by abandoning or delaying a reproductive attempt until the environment and their own conditions were suitable to ensure success. Animals make tradeoffs between current reproduction and future reproductive potential (Stearns 1992). For long-lived species living in variable environments, it is advantageous for a female to prioritise her own survival at the expense of the current reproductive event, because of the ability to compensate in future attempts (Hirshfield and Tinkle 1975, Stearns 1992). Eberhardt (2002) proposed a paradigm under which a progressive reduction in resource availability causes a sequence of changes in a population's vital rates: first, early (juvenile) survival is affected, followed by an increase in the age of first reproduction, a reduction in the reproduction rate of adults and, finally, an increase in adult mortality. In our simulations, calf and juvenile mortality increased with increasing environmental and anthropogenic disturbance, accompanied by an increase in the mean age at which a calf successfully survived to 1 year and a higher chance of adult females abandoning reproductive attempts; only in extreme scenarios was adult female survival affected. One aspect that remains unexplored in our model is the potential effect of disturbance and reduced energy acquisition on growth, either for an independent individual or via reduced milk received from the mother. While animals can compensate for slowed growth over time, there may be subtle costs on their lifetime reproductive performance (Metcalfe and Monaghan 2001).

From a methodological perspective, this work demonstrates that dynamic state variable modelling is an effective approach for assessing the population consequences of environmental change and anthropogenic disturbance on populations of long-lived species (McHuron et al. 2017, Pirotta et al. 2018b). The state equations that constitute the core of the model characterise the dynamics of the system in terms of an individual's energy levels, which act as the fundamental currency influencing its behavioural and reproductive decisions (McNamara and Houston 1986). Optimisation by SDP then ensures that these decisions maximise lifetime fitness in light of the stochasticity of the environment (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000). As a result, the model captures the tradeoffs among vital rates that individuals make at different moments of their life. In addition, because disturbances are also codified using the same energy currency, the approach allows the forecasting of the cumulative and synergistic effects of different disturbances acting concurrently. We currently assume that individuals have a complete knowledge of the levels of spatial and temporal variation in their environment, which is supported by recent findings on the role of long-term memory for migrating blue whales (Abrahms et al. 2019). An informational state variable could be introduced into the backward iteration to relax this assumption and allow a female to update her knowledge of the environment, for example as she grows older or experiences repeated disturbance (Mangel and Clark 1988, Clark and Mangel 2000, McHuron et al. 2017). The model requires a substantial amount of information to be adapted to a specific case study. Even in the case of eastern North-Pacific blue whales, for which a large body of empirical data exists, many uncertainties remain on the species' physiology, movement and reproduction, and we informed several model parameters using empirical estimates from other populations or species (Pirotta et al. 2018b). In addition, we demonstrated the ability to model background mortality rates for different age groups using empirical estimates that likely include mortality due to nutritional status; however, this is treated separately in our model, and future efforts should aim to obtain cause-specific mortality rates. These assumptions and uncertainties should be considered if our results are used for guiding management measures. In the present application, we assumed that the population was not affected by density-dependent processes, which operate when a population's size approaches carrying capacity (Fowler 1981). Future extensions of the approach could include this aspect in the backward iteration (Mangel and Clark 1988), in order to estimate how optimal behavioural and reproductive decisions are adjusted as individuals compete for increasingly limited prey resources. In Supplementary material Appendix 4, we provide an example of how density

dependence could be included in the forward iteration, as a temporary solution to this issue. The example shows that density dependence processes could have a large effect on the average vital rates (survival and reproductive success) emerging from the simulations. By leading to deprivation of the environment, density dependence could also exacerbate the effects of anthropogenic disturbance.

The complexity of blue whale life history forced a series of additional simplifications to make the model tractable, particularly with regard to growth patterns and state transitions. For example, we could not allow for growth in length to stop or slow down during periods of reduced food availability. Reduced growth could have important long-term consequences on the capacity of an individual to store energy reserves, which would not be captured in our model. Moreover, we had to simplify the intricate nature of Pacific climate and the other processes that affect the productivity of the environment inhabited by blue whales (Chavez et al. 2011, Fiedler et al. 2013, Fisher et al. 2015). Despite these necessary simplifications, the model returns clear broad patterns that can be used to explore important question on the biology and ecology of the focal species and inform management decisions. Our application also provides an example of how to achieve an effective balance between fidelity to nature and feasibility if this model were to be adapted to other contexts and species. Beyond the predictions of the consequences of environmental and anthropogenic disturbance, this modelling approach is a powerful tool to explore the properties of vital rates (e.g. reproductive rates, survival, sensitivity of different life stages) in populations of long-lived marine vertebrates for which empirical estimates are difficult to obtain (Mangel and Clark 1988, Clark and Mangel 2000). Our estimates, together with the predicted movement and behavioural dynamics, could be used as working hypotheses for designing targeted data collection. For example, future studies could use photogrammetry to assess the relative condition of different classes of individuals in the population in different parts of the range (Christiansen et al. 2018). Determination of reproductive state using hormones in the blow also offers a promising direction for validating some of the estimates of vital rates emerging from our model (Hogg et al. 2009). Finally, we showed that the characteristics of the simulated environment had a large influence on the baseline dynamics of the system and the predicted effects of disturbance. We informed this model component using a relative measure of spatiotemporal variation in productivity (Pirotta et al. 2018b), but further effort should be dedicated to prey sampling across the population's range to assess whether our results are partly driven by modelled environmental conditions being excessively favourable.

In conclusion, the environmental context in which human activities operate should not be disregarded when devising strategies to manage increasing anthropogenic pressures. Climate change is predicted to cause large-scale ecological shifts across several habitats; our results suggest that these changes might synergistically enhance the effects of anthropogenic disturbances on the demography of migratory wildlife populations (Crain et al. 2008, Maxwell et al. 2013). Approaches such as the one we developed in this study, which formalises these processes using individual energy levels as the currency to quantify the fitness consequences of behaviour and reproductive decisions (McNamara and Houston 1986), will allow us to make more reliable predictions that can direct increasingly limited conservation resources.

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