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From individual responses to population effects: Integrating a decade of multidisciplinary research on blue whales and sonar

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Abstract

As ecosystems transform under climate change and expanding human activities, multidisciplinary integration of empirical research, conceptual frameworks and modelling methods is required to predict, monitor and manage the cascading effects on wildlife populations. For example, exposure to anthropogenic noise can lead to changes in the behaviour and physiology of individual marine mammals, but management is complicated by uncertainties on the long-term effects at a population level. We build on a decade of diverse efforts to demonstrate the strengths of integrating research on multiple stressors for assessing population-level effects. Using the case study of blue whales exposed to military sonar in the eastern north Pacific, we model how behavioural responses and environmental effects induced by climate change affect female survival and reproductive success. Environmental changes were predicted to severely affect vital rates, while the current regime of sonar activities was not. Simulated disturbance had a stronger effect on reproductive success than adult survival, as predicted by life-history theory. We show that information on prey resources is critical for robust predictions, as are data on baseline behavioural patterns, energy budgets, body condition and contextual responses to noise. These results will support effective management of the interactions between sonar operations and blue whales in the study area, while providing pragmatic guidance for future data collection to reduce key uncertainties. Our study provides important lessons for the successful integration of multidisciplinary research to inform the assessment of the effects of noise and other anthropogenic stressors on marine predator populations in the context of a changing environment.

Introduction

Wildlife populations face several threats from expanding and changing human activities, on land and in the ocean, in a world that is also rapidly transforming in response to anthropogenic climate change (Halpern *et al.,* 2008; Venter *et al.,* 2016). Effective management of these activities and successful conservation strategies require an understanding of their cumulative effects across individuals, populations, communities and ecosystems (Orr *et al.,* 2020). This effort is complicated by the broad network of mechanistic pathways through which adverse outcomes of multiple stressors occur (National Academies, 2017; Pirotta *et al.,* 2022). At the population level, risk assessments are difficult for long-lived, wide-ranging species that are exposed to overlapping stressors on variable timescales. This is particularly challenging if stressors do not cause death of exposed animals but a sublethal physiological or behavioural response, which may have chronic effects on their health (National Academies, 2017; Wilson *et al.,* 2020a).

Technological and analytical advances have provided tools to tackle these challenges. Biologging devices and other sampling techniques are used to monitor baseline behaviour, physiology and resources available in the environment (Hussey *et al.,* 2015; Borja *et al.,* 2016). Our understanding of wildlife disturbance responses is also progressing, both theoretically (via mechanistic response frameworks; Romero *et al.,* 2009) and empirically (e.g. via controlled-exposure experiments, or CEEs; Southall *et al.,* 2016). While severity assessments of individual responses to acute exposures can inform species-specific response functions, their application to predict population-level effects is limited (Southall *et al.,* 2021). Conceptual frameworks that follow the cascade of effects from physiological and behavioural responses via individual fitness consequences to changes in population dynamics instead provide an underlying structure to map out these processes (National Academies, 2017; Pirotta *et al.,* 2018a; Wilson *et al.,* 2020a). The formalization of conceptual cascades for specific applications, for example using individual-based models, ultimately generates predictions that can support management decisions (Christiansen & Lusseau, 2015; Nabe-Nielsen *et al.,* 2018), and whose sensitivity to various sources of uncertainty can be explored (Travers *et al.,* 2019). However, a multidisciplinary approach is necessary to synthesize this vast body of work coherently and transparently (e.g. Becker *et al.,* 2021), and ensure that key knowledge gaps for future data collection are identified, especially when research needs must be prioritized because of limited resources.

Anthropogenic noise pollution in the ocean provides an example of a pervasive and expanding stressor (Duarte *et al.,* 2021). Individual animals may change their behaviour in response to noise exposure (e.g. marine mammals; Nowacek *et al.,* 2007; Southall *et al.,* 2021), but the management of human activities that generate noise is complicated by the difficulty of assessing the long-term effects on populations (National Research Council, 2005). Here, we demonstrate the strengths of a multidisciplinary approach to address this challenge and inform management, using the case study of a long-lived marine mammal exposed to an anthropogenic noise source. Specifically, we build on a decade of diverse research efforts to predict the effects of military sonar activities on the survival and reproduction of blue whales (*Balaenoptera musculus*) in the eastern north Pacific (ENP). This includes the coalescence of measurements of behavioural patterns and prey availability, information on the spatio-temporal distribution of sonar activities, responses to experimental sonar exposures and models for simulating the effects of disturbance on energy budgets and vital rates. Crucially, we determine the most influential drivers of predicted outcomes. Our aim is to provide both practical advice for managing interactions between sonar operations and blue whales in the study area, and pragmatic guidance for subsequent data collection required to assess the effects of this and other stressors on marine mammal populations.

Materials and methods

Summary

We focus on the subset of the ENP blue whale population that uses the Gulf of California and the waters off Baja California Peninsula for reproduction during winter and spring, and migrates to the waters off the western USA and Canada to feed during summer and autumn. Several data sources collected in recent years were incorporated into existing modelling tools (Fig. 1) to assess the effects of exposure to sonar activities and environmental change on female vital rates (survival and reproductive success) over lifetime. Specifically, behavioural data from multi-day tags, prey measurements at fine and coast-wide scales, the results of CEEs and information on the annual regime of military activities in the population's range were integrated in simulations of the daily energetic costs of individual exposure and response to sonar activities. The results of these exposure-response simulations were then used to develop a scenario of sonar disturbance to use in a model for female vital rates, which was updated in light of new available behavioural and prey data. Additional scenarios of potential environmental change were also investigated.

Multi-day tag data

Data on blue whale movements, activity budget and feeding rates was derived from 27 deployments of multi-day tags between 2014 and 2019 (Calambokidis *et al.,* 2019) and processed as described in Pirotta *et al*. (2021), so that they could be integrated into the exposure-response simulations described below. Empirical rates of feeding lunges were also used to update the lunge rates in the original version of the vital rate model. Blue whales adjust their lunge rate depending on the prey density they encounter (Goldbogen *et al.,* 2015). Using a Gaussian mixture model (Benaglia *et al.,* 2009), the distribution of lunge rates while feeding at two different depths was decomposed into separate Gaussian components, which were assumed to correspond to different ranges of prey density (Supplementary material; Fig. S1). Moreover, multi-day tag data were used to estimate the average number of days spent feeding in a patch, which was calculated from the sequence of days with and without feeding activity. The transition probabilities between feeding and non-feeding days, estimated via a discrete Markov chain algorithm (Spedicato, 2017), were used to simulate 1,000 sequences of 1,000 days. The median duration of the

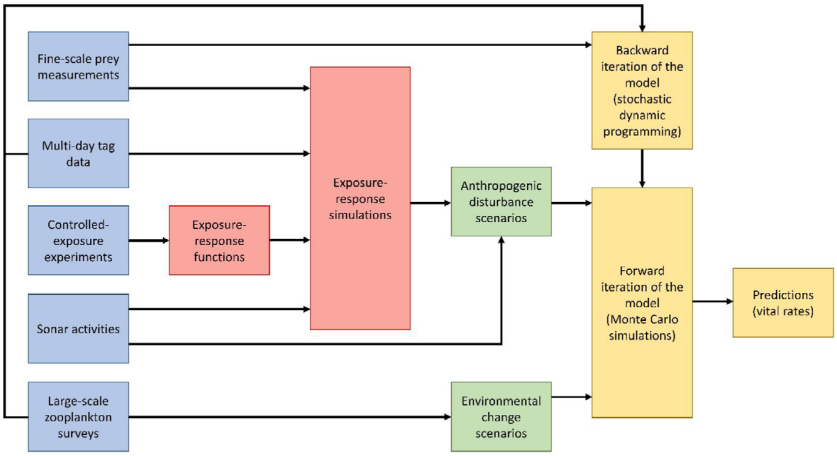

Figure 1 Data integration and modelling flow. New data sources are reported on the left (in blue), informing exposure-response functions and simulations (in red; Pirotta *et al.,* 2021) and the development of scenarios of anthropogenic disturbance and environmental change (in green) in a model for female vital rates (in yellow; Pirotta *et al.,* 2019).

resulting feeding bouts (10 days) was incorporated in the forward iteration of the vital rate model (see below).

Prey data

Blue whales target reliable krill hotspots in the California Current. The fine-scale distribution of krill densities in feeding patches was obtained from acoustic backscatter data from the Southern California Bight and Monterey Bay, collected between 2011 and 2018 and processed following Cade *et al*. (2021). Specifically, we used two krill density distributions that pooled acoustic backscatter data from two sites (the Southern California Bight and Monterey Bay), characterized by geometric means 0.513 kg/m^3 and 0.757 kg/m^3, and geometric SDs 1.917 kg/m^3 and 1.468 kg/m^3, respectively (Fig. S3) (Pirotta *et al.,* 2021). The first of these distributions corresponded to the mean density, assuming a whale foraging randomly within a patch, while the second was derived from the top 50% of densities, assuming that a whale chooses where to forage in a patch to maximize efficiency (Cade *et al.,* 2021; Pirotta *et al.,* 2021).

The variation of krill availability across the year and population's range was approximated from the Bakun upwelling index, which provides a measure of upwelling rate along the west coast of North America and can act as a proxy of the nutrients entering the system (Schwing *et al.,* 1996). A scaled and lagged krill index was derived from the Bakun index as described in Pirotta *et al*. (2018b) and summarized in the Supplementary material. Here, we used data collected during yearly zooplankton surveys in the California Current (Santora *et al.,* 2017) to validate this Bakun-derived index. Specifically, acoustic backscatter data from May to June 2000–2010 were summarized as nautical area scattering coefficient (NASC, m^2 nmi^{-2}) over a 25-km^2 spatial scale. We fitted a negative binomial Generalized Additive Model (Wood, 2006) to estimate the relationship between latitude and NASC. While the Bakun-derived index provided a satisfactory representation of relative krill abundance at most corresponding locations in the California Current, there was a mismatch between the two indices at 36°N (Fig. S4). Therefore, the index was rescaled using the ratio between the maximum predicted NASC (at 36°N) and the predicted NASC at the location where the Bakun-derived index was maximum (33°N) (Fig. S5).

Sonar activity data

The annual regime of military sonar activities in the Southern California testing and training range was derived from data provided by the U.S. Navy, based on the Environmental Impact Statement for the Hawaii-Southern California range complex (https://www.hstteis.com/Documents/2018-Hawaii-Southern-California-Training-and-Testing-Final-EIS-OEIS/Final-EIS-OEIS). Activities were categorized into unique combinations of type (amphibious warfare, anti-submarine warfare, major training events, mine warfare and vessel evaluation, other training activities or unmanned systems), platforms (one ship, one aircraft, two or more ships or other) and mean duration of sonar per day. Additional combinations emerged when an activity extended beyond one model location (see Supplementary material), for a total of 55 unique combinations (TABLE S1). Each activity was associated with representative coordinates, the average duration in days, and the average number of events per year. Activities that occurred outside the typical blue whale habitat (i.e. more than 250 km from the coast) were excluded. The acoustic footprint of each activity type was calculated via the Comprehensive Acoustic Simulation System using the Gaussian Ray Bundle (CASS-GRAB) acoustic model (Keenan, 2000) (Supplementary material). Finally, we generated a time series of annual sonar regimes. On each year, we randomly distributed all activities based on the corresponding number of events and duration in days. Repetitions of the same activity were assumed not to overlap on a day.

Behavioural responses to sonar: CEE Data and exposure-response simulations

Individual behavioural responses to sonar were characterized using data from 42 CEEs conducted in the Southern California Bight between 2010 and 2014 (Southall *et al.,* 2019b). Results were synthesized into exposure-response functions (Pirotta *et al.,* 2021), which describe the relationship between a given level of exposure (e.g. received sonar level) and the probability of an individual responding by interrupting its feeding activity. Three types of exposure-response functions were developed as described in Pirotta *et al*. (2021) and summarized in the Supplementary material, to assess their influence on the predicted effects of sonar disturbance. Specifically, we generated relatively coarse functions, reporting only discrete response probabilities but specific to a behavioural state and range from source, as well as non-state-specific continuous functions for noise received level and range from source (Pirotta *et al.,* 2021).

For each of the 55 combinations of activity type, platform and sonar duration described above, we ran the daily exposure-response simulations developed in Pirotta *et al*. (2021) for 1,000 iterations. Briefly, these simulations use data on the daily ranging patterns (area covered per day) and activity budget of individual blue whales, paired with the duration and acoustic footprint of a sonar source, to determine the overlap of an individual with sonar on a given day within a simulated 100 km by 100 km location. If an individual is exposed to sonar, the probability of responding is drawn from one the exposure-response relationships mentioned above. When a simulated individual responds, it stops feeding. Recovery times before resuming to feed are sampled from the empirical intervals between foraging bouts (Pirotta *et al.,* 2021). The simulations convert the number of hours lost due to disturbance to a number of lunges lost (using empirical lunge rates) and a total energy loss (based on empirical krill densities and the feeding model in Pirotta *et al*. (2019). Finally, energy loss is divided by the theoretical gross energy acquired on that day in the absence of disturbance, to obtain the proportional loss in energy acquired. Each simulation returned a distribution of potential energy costs (expressed as the percentage of daily energy acquisition lost due to the event) and percentage of feeding time lost.

Vital rate model

The new available data and exposure-response simulation results were incorporated into the existing model for ENP blue whales (Pirotta *et al.,* 2018b; Pirotta *et al.,* 2019) to predict female vital rates under different environmental change and anthropogenic disturbance scenarios. This dynamic state variable model (Mangel & Clark, 1988; Houston & McNamara, 1999) uses stochastic dynamic programming (backward iteration) to derive the matrix of optimal movement and reproductive decisions for a female blue whale on each day of her life as a function of a set of state variables (female blubber mass, location, patch type and proportion of mass of the suckling calf that is blubber), her current reproductive state (juvenile, pregnant, lactating and resting) and the state of the external environment. On any given day, movement decisions determine whether a female stays in the current model location to feed, travels to adjacent locations or moves within the breeding locations. Model locations are simplified as 36 ‘100 km by 100 km’ areas, which are taken to represent broad latitudinal sections of the range of this subset of the population. Reproductive decisions concern the transitions between reproductive states, that is, whether to implant and get pregnant, abort a foetus or wean a dependent calf.

The dynamics of a female’s energy reserves are modelled via bioenergetic equations that regulate energy acquisition from feeding and allocation to maintenance, movement and activity, growth, gestation and lactation. Energy acquisition results from a mechanistic feeding model that determines the number of hours spent feeding per day given lunge rates, body size, digestive capacities and krill availability and abundance (as approximated by the corrected, Bakun-derived index and fine-scale density distribution described above). The probability of encountering a food patch was originally derived from telemetry data (Bailey *et al.,* 2010; Pirotta *et al.,* 2018b). In order to capture some of the complex climatic processes affecting regional oceanography currently, the baseline model includes two possible environmental regimes; unfavourable years, which occur once every 5 y, are modelled to represent El Niño Southern Oscillation (ENSO) conditions, corresponding to a northward shift in the distribution of subtropical krill and an overall 70% reduction in upwelling intensity in the southern and central California Current (latitude $\geq$31.5°N and $\leq$ 41.5°N), with productivity reduced (see Pirotta *et al.,* 2018b; Pirotta *et al.,* 2019).

The matrix of optimal movement and reproductive decisions can then be used in Monte Carlo simulations (forward iteration) to generate the life trajectories of 1,000 individuals, from age 1 year until their death or the end of their reproductive lifespan. Female survival can be summarized as the age at which individuals died, while reproductive success is defined as the number of female calves surviving to age 1 year over the lifetime of a female. In addition to baseline conditions, different environmental and anthropogenic disturbance scenarios can be simulated. The differences between baseline and disturbed scenarios can be assessed using Cohen’s d, which is the difference between the mean vital rates in the undisturbed (baseline) and each disturbed scenario scaled by their pooled standard deviation (Cohen, 1977). Values of Cohen’s d of 0.2, 0.5 and 0.8 are taken to indicate small, moderate and large effect sizes, respectively, while negative values imply an improvement in vital rates (Cohen, 1977). Full details of the model, including the equations for state dynamics, parameter values and assumptions, are available from Pirotta *et al*. (2018b) and Pirotta *et al*. (2019).

Simulated scenarios

In addition to a scenario without sonar or environmental disturbance (baseline), we simulated a scenario of anthropogenic disturbance representing the current sonar regime

(Fig. 2a). For each individual, we sampled a random starting year in the simulated time series. If a simulated female was in a location where a sonar event took place on a given day of a given year, a value of percentage energy acquisition lost due to disturbance was randomly drawn from the corresponding distribution of simulated costs, as suggested by Pirotta *et al*. (2021). Energy acquisition on that day was then scaled accordingly. The corresponding percentage of feeding time lost was also used to correct daily energy expenditure. If an individual was exposed to multiple sonar events in the same location on the same day, we conservatively assumed that the total percentage of energy acquisition lost was equal to the sum of the sampled percentage losses associated with each event (capped at 100%).

Moreover, we developed a set of scenarios of environmental change, representing alternative ways in which the environment in ENP blue whale range might vary over the coming decades in response to changing climate conditions. First, we progressively increased the frequency of unfavourable years: from 1 in 5 years in the baseline, to 1 in 3 years (Fig. 2b). Next, we simulated a decline in resource density across the entire range of the population (Fig. 2c). Specifically, we assumed that 1 in 10 years, on average, showed a 20% reduction in resources. We repeated the simulation with a permanent 20% decline in resources, as well as assuming that there was some autocorrelation in poor conditions (i.e. a 50% chance that a poor year would be followed by a second poor year). The latter scenario was taken to represent a marine heatwave event, whose effects can extend over a subsequent year (Santora *et al.,* 2020). We then simulated three scenarios where a permanent 20% decline in resources was restricted either to locations in the California Current (latitude ≥31.5°N; Fig. 2d), or to locations in the southern and central California Current (latitude ≥31.5°N and ≤41.5°N; Fig. 2e), to represent changes that may be localized to portions of the whales' range. When only the southern and central California Current was affected, we first assumed that whales responded to these changed conditions by mimicking their movement and reproductive decisions in unfavourable (ENSO-like) years; next, we assumed that whales did not adjust their decisions to changed conditions. Finally, we simulated a 1-in-10 years average frequency of a 20% decline in resource density paired with a change in phenology of krill hotspot formation (Fig. 2f), at five hotspot locations in the California Current (Fiechter *et al.,* 2020). First, we used the yearly standard deviation of the timing of the hotspot peak to randomly sample a shift (in days) of the krill index at the corresponding model locations (i.e. locations 20, 22, 23, 26, 28). The yearly standard deviation varied between 19 and 32 days. Second, we used the observed annual trend in

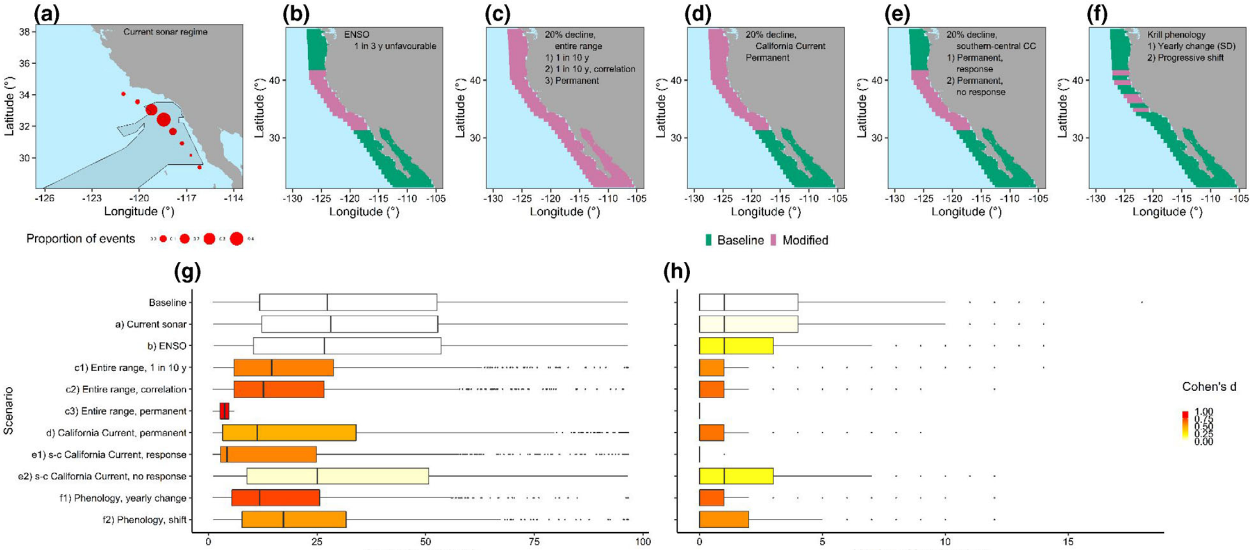

Figure 2 Simulated scenarios of anthropogenic disturbance and environmental change, and their predicted effects on female vital rates. (a) Spatial distribution of sonar activities under the current sonar regime; the dots represent the centre of model locations, scaled in size by the proportion of events simulated to occur in each. (b–f) Sets of environmental scenarios, simulating an increase in the frequency of unfavourable years (ENSO, which applies to the southern and central California Current), a decline in resources across the entire range, a decline in the California Current, a decline restricted to the southern and central California Current, and a change in krill phenology at five model locations, respectively. The pink areas on the maps indicate the portion of the population's range that is affected in each scenario. In the bottom plots, results of the simulated scenarios on (g) female survival, expressed as the age at death, and (h), female reproductive success, expressed as the number of female calves that reached age 1 year per simulated female. The alphanumeric code of each scenario from the top half of the figure is included on the y-axis of panels (g) and (h). Boxplots are coloured based on mean effect size, as represented by the value of Cohen's *d*. In these plots, the box reports the median vital rates across simulated females and the interquartile range, while the whiskers extend to 1.5 times this range; outliers are represented using dots.

the timing of the peak at those five hotspots to simulate a progressive shift over the simulated years (Fiechter *et al.,* 2020). The annual trend varied between −0.57 and 0.75 days/year.

Additional simulated anthropogenic and environmental scenarios are described in the Supplementary material, where we also report the investigation of the combined effects of anthropogenic and environmental disturbance (TABLE S2).

Sensitivity analysis

We conducted a sensitivity analysis to assess the influence of model parameters and assumptions. Due to computation times, we focused on a set of parameters relating to the environmental layer, activity patterns, bioenergetic equations, whale morphology and disturbance simulations. These were selected because they were either associated with new data incorporated here, or a potential target for future data collection. We perturbed original values either using alternative values available in the literature or arbitrarily higher and lower values (e.g. ± 20%), resulting in a total of 50 sensitivity perturbations (full details in TABLE S4).

Results

In the baseline scenario (without sonar or environmental change), females died at a mean age of 35.3 years (median: 27.3; range: 1.0–96.6; Fig. S6). Mean reproductive success was 2.5 calves (median: 1; range: 0–18; Fig. S6). Baseline vital rates and their comparison with values from this and other baleen whale populations are discussed in Pirotta *et al*. (2019). The predicted daily energetic costs of sonar disturbance emerging from the exposure-response simulations varied substantially among combinations of activity type, platform and sonar duration, including many simulations resulting in no cost, because of a lack of either spatio-temporal overlap or behavioural response (Fig. S7).

When the results of these exposure-response simulations were used in the vital rate model, the spatial overlap with sonar was largely driven by where events occurred, and concentrated at latitudes 29.0°N-34.4°N (highest incidence around 32.4°N and 33.0°N) (Fig. 3). Temporal patterns were attributable to whale movements: potential exposure was limited between mid-May and late-September, with additional overlap during the southward migration (Fig. 3). Over lifetime, females were potentially exposed to a median of 227 sonar events (range: 0–1023), corresponding to a mean of 7.6 events per year (range: 0–19). As a result of their modelled behavioural responses, females lost a median of 37 days of feeding over lifetime (range: 0–162), corresponding to 1.2 days per year, on average (range: 0–3.4). However, there was no effect of the current sonar regime on either survival or reproductive success (TABLE 1; Fig. 2).

Modelled environmental changes affected reproductive success more than survival (Fig. 2). An increased frequency of unfavourable years (Fig. 2(b)) resulted in a small decline in reproductive success (TABLE 1). A decline in resources across their entire range on random years caused moderate effects on both vital rates, partly worsened by a continuation of poor conditions (as in multi-year marine heatwaves; TABLE 1). In contrast, a permanent decline had dramatic effects on both survival and reproductive success (TABLE 1). Simulated whales performed better if the decline did not affect the southern portion of their range (TABLE 1). In scenarios with changes restricted to the southern and central California Current, whale survival was not affected if they did not respond using the strategy evolved to cope with ENSO conditions, while there was only a small effect on reproductive success (TABLE 1). Changes in krill phenology caused a moderate to large effect on both vital rates (TABLE 1). When environmental change was combined with the sonar regimes, there was no clear indication that cumulative effects were stronger than in isolation (Fig. S10).

Sensitivity analysis

For simplicity, we only report the influence of the sensitivity perturbations on the vital rates emerging from the baseline scenario (without stressors), expressed in terms of the absolute change in mean survival and reproductive success compared to the original model. All other sensitivity results (including the effects on the simulated scenarios of anthropogenic and environmental disturbance) are described in detail in the Supplementary material, but results were broadly comparable.

Some environmental (krill index, density distribution, energy density and species' size ratio) and whale-specific parameters (lunge rates and metabolic rates) had the largest influence (Fig. 4). Sensitivity perturbations mostly affected reproductive success (Supplementary material); in particular, morphology (length and maximum reserves) affected reproductive success but not survival (Fig. 4). Perturbations that implied a detriment to the energy budget had a stronger influence than beneficial perturbations (Supplementary material).

Discussion

We integrated results from a decade of multidisciplinary research to quantify the effects of military sonar activities and potential future environmental changes on the vital rates of a long-lived, wide-ranging marine mammal. Synthesizing the lessons from these diverse research efforts at different spatio-temporal scales ensured a coherent interpretation of the various data streams and the identification of key knowledge gaps.

Simulated disturbance scenarios had a stronger effect on reproductive success than adult survival, as predicted by life-history theory (Stearns, 1992). Thus, monitoring for changes in demographic characteristics associated with reproduction (e.g. the ratio of calves to mature females) may provide early warnings of impending population change, which could support prompt conservation interventions (Booth *et al.,* 2020). However, extending the model to include population dynamics would be needed to understand the consequences of these effects on population growth rate (Fig. S26). Environmental

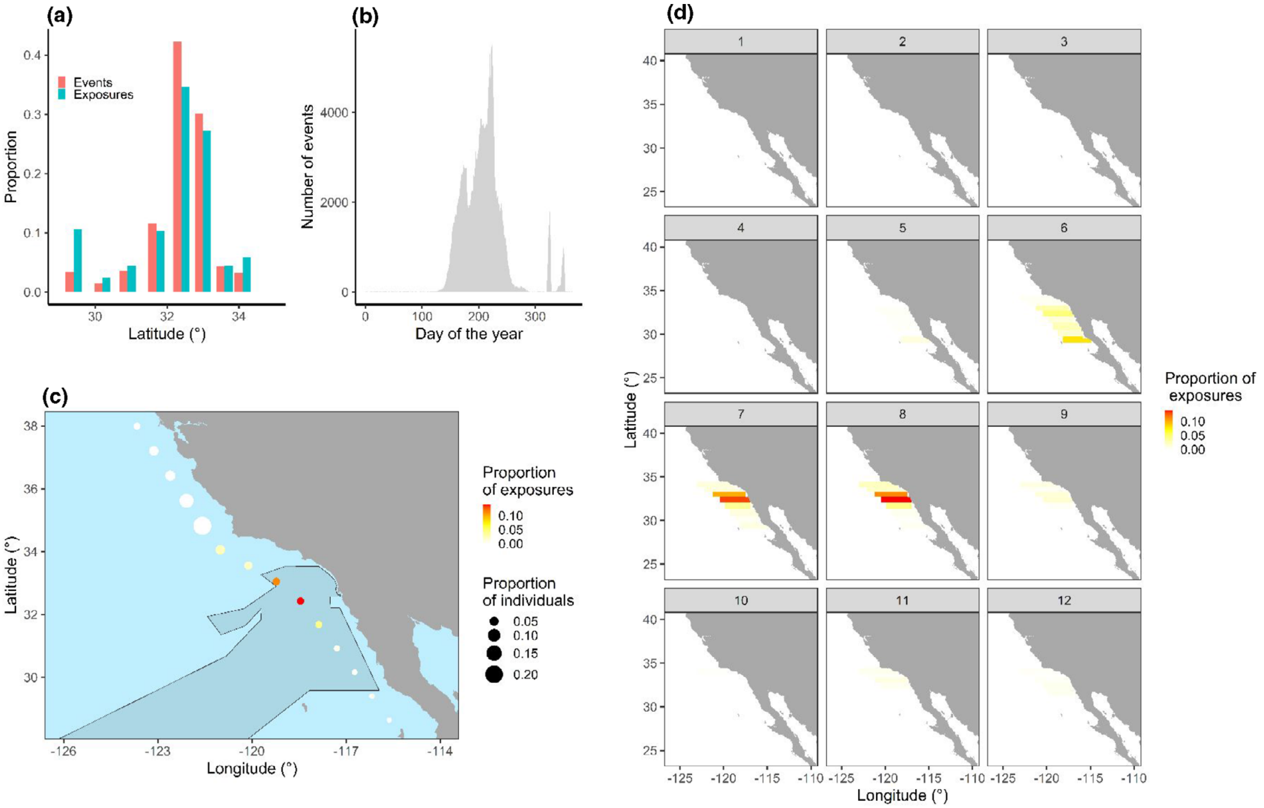

Figure 3 Spatio-temporal distribution of exposure to sonar activities (defined as the occurrence in the same model location on the same day). (a) Spatial distribution of sonar events and exposures across all simulated individuals. (b) Distribution of exposure events over the course of the year. (c) Overlap with sonar activity in the Southern California testing and training range. The dots represent the centre of model locations, scaled in size by the proportion of simulated individuals occurring in each location in the month of August (peak exposure period – see (d) across all simulated years). Dots are coloured by the proportion of exposures occurring at each location in August compared to other months of the year. The black line indicates the boundary of the Southern California testing and training range. (d) Distribution of exposure events by month and model location, plotted as the proportion of exposures across all simulated individuals and years. Model locations were arbitrarily extended in the longitudinal direction to facilitate visualization.

changes resulted in particularly strong impacts: whales accommodated for some habitat degradation restricted to specific times or areas, but intense or permanent changes could lead to severe effects on reproductive success and, in extreme cases, reductions in survival. Moreover, if movement and reproductive decisions developed over evolutionary time to cope with periodic climatic oscillations (such as ENSO) were adopted in response to changes in productivity or prey phenology, they could worsen the consequences of environmental change. There is large uncertainty on the magnitude and direction of changes in the North Pacific ecosystem, but climate change could result in increased frequency and intensity of extreme events and climatic oscillations, as well as region-specific alterations of the abiotic habitat and resource base (Sydeman *et al.,* 2013; Howard *et al.,* 2020; Santora *et al.,* 2020). The time required to adjust to these new environmental patterns is unknown, but some marine mammal populations have shown limited resilience (e.g. Kershaw *et al.,* 2021). Blue whales are thought to rely on long-term memory to inform habitat use and movements, suggesting that their adaptation to changing conditions may also be slow (Abrahms *et al.,* 2019). Globally, the species is classified as 'Endangered' (Cooke, 2018), with most populations still recovering from past exploitation; our results indicate that their recovery may be challenged by increased environmental variation.

In contrast, the current sonar regime did not affect the vital rates of female blue whales, despite individuals changing their behaviour in response to sonar exposure (Southall *et al.,* 2019b), which reinforces the idea that response severity criteria based on acute effects are not necessarily good indicators of population-level consequences (Gill *et al.,* 2001; Southall *et al.,* 2021). The relatively limited overlap between whales and military activities in space and time resulted in a small exposure of individuals to sonar disturbance (similarly to Christiansen & Lusseau, 2015). Our results thus emphasize that a robust quantification of the spatio-temporal exposure to potential stressors, aggregated for individuals over biologically relevant timeframes, is paramount (Pirotta *et al.,* 2018a). The timing of sonar events in

Table 1 Mean, median and standard deviation (SD) of female vital rates (survival and reproductive success) under the simulated scenarios

Simulated scenario	Mean survival (years)	Median survival (years)	SD survival (years)	Cohen's *d* survival	Mean reproductive success (no. of calves)	Median reproductive success (no. of calves)	SD reproductive success (no. of calves)	Cohen's *d* reproductive success
Baseline	35.3	27.3	28.3	–	2.5	1	3.1	–
Current sonar regime	36.0	28.2	29.2	−0.02	2.4	1	3	0.02
Increased ENSO frequency	35.6	26.6	29.9	−0.01	1.9	1	2.5	0.19
Entire range decline, 1 in 10 years	20.6	14.6	19.3	0.61	1.0	0	1.8	0.58
Entire range decline, with correlation	18.9	12.7	17.5	0.7	0.8	0	1.6	0.66
Entire range decline, permanent	3.6	3.7	1.5	1.58	0	0	0	1.12
Decline in California Current, permanent	22.9	11.2	26.1	0.46	0.9	0	1.7	0.64
Decline in southern-central California Current, respond as to ENSO	19.0	4.3	26.8	0.59	0	0	0.1	1.12
Decline in southern-central California Current, no response	33.8	25.1	29.3	0.05	1.9	1	2.6	0.19
Krill phenology, yearly change	18.0	11.8	17.1	0.74	0.8	0	1.6	0.68
Krill phenology, shift	22.6	17.3	19.2	0.52	1.1	0	1.7	0.56

Effects are assessed using Cohen's *d*, with values of 0.2, 0.5 and 0.8 taken to indicate small, moderate and large effect sizes; negative values imply an improvement in vital rates.

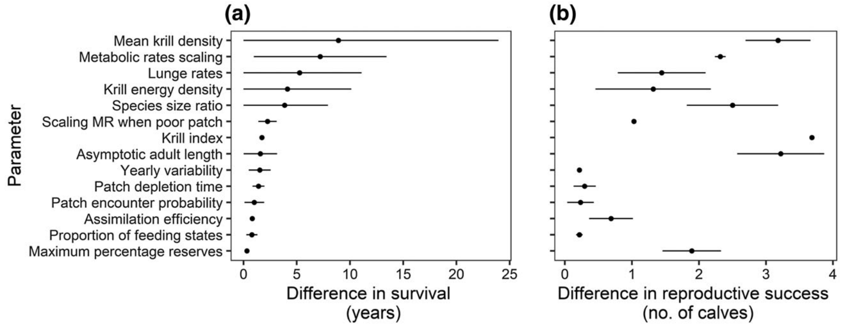

Figure 4 Results of the sensitivity analysis for the baseline scenario (without stressors). The influence of perturbations of parameter values is reported as the absolute difference in mean adult survival (a) and reproductive success (b). The dots and bars represent the mean difference and the standard deviation across perturbations of each parameter, respectively.

the feeding season is also relevant, since feeding effort may vary with body condition and prey availability. Biologgers with dosimeters (e.g. measuring received noise; Johnson & Tyack, 2003) should be deployed to estimate aggregate exposure rates to stressors over multiple weeks, while a detailed sampling of movements patterns or the resource base could support fine-scale simulations where direct measurements are unfeasible (Donovan *et al.,* 2017). We only considered sonar in isolation, but other stressors in the population's range (e.g. shipping, hydrocarbon exploration, tourism, pollution) may interact to worsen the combined impact (National Academies, 2017). Although we explored the combined effects of sonar and environmental change (Supplementary material), their relationships with vital rates are likely to be non-linear and it is challenging to judge the occurrence of interactions based on limited combinations of stressor levels (National Academies, 2017; Pirotta *et al.,* 2022).

From a management perspective, the U.S. Navy could minimize any future impact by monitoring for environmental changes in relation to the spatio-temporal distribution of sonar activities. For example, robust indicators of habitat quality (e.g. based on indices of primary or secondary productivity) could be developed. The characteristics of the environment drive the movements of the animals in our model; therefore, relatively small shifts in habitat quality in space and time may rapidly alter individual exposure rates and affect response severity, changing the predicted consequences of disturbance. Similarly, variations in whale movements might provide clues that the underlying environment is changing, which could initiate management interventions before any population-level effects (Becker *et al.,* 2021). In particular, monitoring environmental conditions and whale occurrence in transition areas and seasons could provide useful early warnings, since this is where exposure may vary first and most evidently if the environment changes. In general, the impact of human activities could be minimized by avoiding areas intensely used for feeding, such as the southern California Current, during periods of the year when individuals are present (e.g. summer and autumn) (Foley *et al.,* 2010). Quantifying the dynamic overlap between sonar and whale densities would thus support adaptive management approaches (Southall *et al.,* 2019a): for example, spatial planning could be informed by dynamic models of critical habitat that adaptively respond to shifting conditions (Maxwell *et al.,* 2015). Going forward, management strategies should increasingly be ecosystem-based (Levin *et al.,* 2009), treating specific stressors and marine mammal populations as part of the complex network of interactions underpinning ecosystem functioning.

The sensitivity analysis highlighted the critical influence of environmental parameters on model predictions (TABLE 2). Patterns of prey availability, abundance and energy density affect resilience to disturbance, compensatory abilities, movements (i.e. exposure rates) and sensitive periods (Harwood, 2001). Our results thus emphasize that no conclusive assessment of the consequences of anthropogenic stressors can be achieved without robust environmental data. A multiscale, multidisciplinary data collection is required, where year-round (e.g. monthly), large scale (e.g. tens of kilometres) surveys of prey dynamics (Santora *et al.,* 2017) are paired with targeted measurements of localized high densities that can support efficient feeding (Cade *et al.,* 2021) at whale-relevant scales (e.g. hourly and daily; hundreds of meters). Analysis of the energy content and assimilation efficiency of different prey items is also essential to understand how measured densities translate into energy intake (Sibly *et al.,* 2013).

Sensitivity results indicated other key uncertainties. Future CEEs should explicitly test the effect of contextual variables on response probability, particularly source distance, individual state, body condition and environmental quality (Southall *et al.,* 2019b) (TABLE 2). These studies also provide the platforms and opportunity to collect extensive baseline data on movements, activity budgets and feeding rates (all strongly affecting model predictions), before any experimental exposure (Hussey *et al.,* 2015). Longer-term tag deployments that characterize spatial, temporal and individual heterogeneity in behaviour, and how this relates to body condition, will be particularly important (Pirotta *et al.,* 2021). Similarly, longer post-exposure sampling could shed light on recovery times, since the duration and magnitude of most disturbance responses is unclear. The energetic costs of different life functions are hard to measure directly for some species, but high-resolution accelerometry loggers and respiration rate sampling have provided robust estimation of metabolic rates (Fahlman *et al.,* 2016; Wilson *et al.,* 2020b). Given the importance of body size and size of energy reserves on the ability to withstand interrupted feeding and changing environmental conditions, uncertainty around morphological traits could be reduced through photogrammetry, for example, measuring length and variation in volume across seasons and life stages (Christiansen *et al.,* 2019). Despite these useful insights, the sensitivity analysis was limited to a subset of parameters and a small range of alternative parameter values. A thorough exploration of sensitivity is often an important limitation of such complex models. Uncertainty in parameter values could also be built directly into the model and propagated through to the results, to facilitate the communication of the degree of confidence in the predictions (Pirotta *et al.,* 2018a), albeit with comparable limitations resulting from model complexity. In general, validating the results of these models remains challenging, because empirical observation of their many components is often unfeasible. However, pattern-oriented modelling can be used to ensure that multiple emergent properties of the model reproduce the observable patterns in the real system (Grimm & Railsback, 2012).

The multidisciplinary modelling effort presented in this study was essential to evaluate the biological significance of observed short-term changes in behaviour by individual blue whales exposed to sonar. Due to the life-history characteristics of this species, modelling the underlying mechanistic pathways is required to predict long-term, population-level effects that cannot be measured directly. Most disturbance research to date has focused on the bioenergetic pathway (Pirotta *et al.,* 2018a), using energy as the common currency to integrate experimental results in individual-based models (Pirotta *et al.,* 2021). However, other adverse outcomes may be mediated by physiological responses (e.g. increased stress), or affect other components of health (e.g. immune status); these could be assessed via remote sampling (e.g. of blows or faeces). An increased mechanistic understanding of such pathways will allow a holistic assessment of the consequences of heterogeneous stressors on individuals and populations (National Academies, 2017; Pirotta *et al.,* 2018a; Pirotta *et al.,* 2022).

Climate change is projected to severely alter the dynamics of terrestrial and marine ecosystems and interact with other stressors in complex ways (Malhi *et al.,* 2020). We showed that the consequences of environmental change alone could be much more severe than those of localized sources of disturbance, such as military sonar, but the patterns of individual exposure in space and time are critical to determine the magnitude of any effect. Overall, these results contribute to the accumulating evidence that the population consequences of anthropogenic disturbance are influenced by a species' life history and ecology, and how these interact with the features of the disturbance source (Keen *et al.,* 2021). We presented an example of how predictive mechanistic tools, developed using lessons and data from many diverse fields, can inform management decisions so that they minimize risks for wildlife populations, direct the monitoring of ongoing effects and highlight key data required to reduce uncertainties. Our proposed integrative approach can guide similar efforts in other species of marine mammals and long-lived predators that are exposed to noise and other sources of sublethal anthropogenic disturbance.

Table 2 Key information required to predict the effects of anthropogenic stressors on marine mammal populations, and suggested methodologies, scale and resolution for the associated data collection (also summarized in Fig. S26)

Key information	Methodology	Scale and resolution	Can data collection be incorporated in BRS?
Exposure rates to sonar and other stressors	Biologgers with dosimeters; telemetry and prey data to inform movement simulations (robust data on the distribution and intensity of human activities are often hard to obtain and compile)	Year-round and range-wide; monthly and diel variation is also required, to pair with patterns of animal distribution and activity budget	The data collected during BRS are useful, but longer deployments within ancillary studies may be required
Prey availability and abundance (energy intake)	Surveys of broad prey dynamics paired with targeted measurements around feeding individuals, using active acoustics and net samples; autonomous underwater vehicles (e.g. gliders) to sample oceanographic features associated with prey aggregations	Year-round and range-wide; both coarse (e.g. monthly, tens of km) and fine resolutions (e.g. hourly and daily; hundreds of meters) are required to characterize the broad variation in average densities as well as the occurrence of extreme, localized high-density patches	No
Prey energy content (energy intake)	Requires collected prey samples (see above) to be analysed with bomb calorimetry	In different seasons (to capture prey life cycle) and range-wide; for all prey species	No
Assimilation (or digestive) efficiency (energy intake)	Use of inert markers (e.g. dietary manganese); extrapolation from comparable species	For all prey species or groups	No
Baseline feeding rates (energy intake)	High-resolution accelerometry loggers and acoustic tags (for echolocating species), ideally lasting for multiple days to weeks	Year-round and range-wide; high-resolution is ideally required to characterize feeding attempts; deployments should capture spatial, temporal and individual heterogeneity; ancillary data (e.g. body condition and reproductive status) could help explain some of the observed variation	The data collected during BRS are useful, but longer deployments within ancillary studies may be required
Metabolic rates (energy expenditure)	High-resolution accelerometry loggers; respiration rate data; hydrodynamic modelling	In different activity states and for individuals in different body condition	The data collected during BRS are useful, but longer deployments within ancillary studies may be required
Baseline movements and activity budgets	Multi-day loggers recording individual location, diving behaviour and 3D acceleration (pre-exposure)	Year-round and range-wide; high-resolution (multiple locations per day; 32 Hz for accelerometry and depth) is ideally required to characterize movement mode and activity; deployments should capture spatial, temporal and individual heterogeneity; ancillary data (e.g. body condition and reproductive status) could help explain some of the observed variation	The data collected during BRS are useful, but longer deployments within ancillary studies may be required
Individual morphology	Photogrammetry (e.g. using images from unmanned aerial vehicle); stroke cycle frequencies during swimming; direct measurements for pinnipeds and small cetaceans	Individual variation in length across the population; seasonal variation and extremes of body condition. Detailed estimation of the body condition of individuals, its variation in response to stressors, and the relationship with vital rates could support a fully empirical characterization of the cascade between exposure and vital rates, bypassing the need to develop a bioenergetic model	Yes

Table 2 Continued.

Key information	Methodology	Scale and resolution	Can data collection be incorporated in BRS?
Effect of context on the probability of responding to a stressor	Controlled-exposure experiments targeting individuals in different behavioural state, body condition, distance from source, and in environments of varying quality; opportunistic (observational) studies of individual exposures to real-world scenarios; mechanistic models of anticipated interaction pathways	Large sample sizes are required to quantify these interactions empirically (tens of individuals across different combinations of contexts); context-dependency likely varies among species, so extrapolation may not be possible	Yes
Duration of disturbance response (recovery time)	Multi-day loggers recording individual location, diving behaviour and 3D acceleration (post-exposure); empirical and theoretical studies of marine mammal sensory ecology (i.e. the cues used to locate prey, affecting the time required to find a new patch); availability and persistence of prey patches; experimental studies of the effects of stressors on the prey	High-resolution (multiple locations per day; 32 Hz for accelerometry and depth) is ideally required to characterize movement mode, activity state and feeding attempts; characterize individual heterogeneity; prey sampling at fine scales (e.g. hourly and daily; hundreds of meters)	Yes (but additional data will be required on the distribution and persistence of prey patches)
Physiological responses	Physiological loggers; biopsy, blow or faecal sampling; health assessment for pinnipeds and small cetaceans; theoretical study of the physiological pathways for adverse effects	Large sample sizes are required to quantify physiological responses empirically (tens of individuals)	Possibly, depending on technological developments
Cumulative effects of multiple stressors	Multi-stressor controlled-exposure experiments; mechanistic models of anticipated interaction pathways	Large sample sizes are required to quantify cumulative effects empirically (tens of individuals across combinations of stressors and contexts)	Possibly, but experimental studies involving multiple stressors are challenging
Future environmental changes	Oceanographic modelling; climate scenarios; use changes and extreme events observed in recent years as proxy of future scenarios	Ocean basin, regional and mesoscale (10-1000’s km) synthesis of ocean climate and ecosystem conditions	No
Marine mammal resilience and adaptability to environmental changes	Analysis of responses to past changes in environment; mechanistic modelling of ecosystem dynamics	–	No

These critical components emerged from the sensitivity analysis on the blue whale model in this study, but are relevant across marine mammal taxa. However, they are characterised by different levels of existing uncertainty and empirical tractability across species. The last column discusses whether the suggested data could be collected as part of Behavioural Response Studies (BRS); it should be noted that BRS are logistically difficult efforts, and including the collection of additional data streams may thus be challenging.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Gaussian mixture distributions of lunge rates (lunges/h) in deep-feeding (a) and shallow-feeding (b) state.

Figure S2. Comparison of modelled and observed foraging time (i.e. the number of hours per day spent feeding) for two sample model locations (location number 19 and 24).

Figure S3. Updated distributions of krill density in California.

Figure S4. Data from yearly zooplankton surveys in the California Current (details are available in Santora *et al.,* 2017).

Figure S5. Updated Bakun-derived krill index used in the model, plotted for each model location (characterized by different latitudes).

Figure S6. Distribution of vital rates across 1000 simulated females in the baseline scenario.

Figure S7. Distribution of simulated percentages of daily energy acquisition lost due to sonar disturbance (i.e. potential energetic costs) for each unique combination of activity type, platform, mean duration of sonar per day and area ensonified (Table S1).

Figure S8. Results of the simulated scenarios of anthropogenic disturbance (scenarios 2, 3 and 4) on (a) female survival, expressed as the age at death and (b), female reproductive success, expressed as the number of female calves that reached age 1 year per simulated female.

Figure S9. Results of the simulated scenarios of environmental change (scenarios 5–21) on (a) female survival, expressed as the age at death and (b), female reproductive success, expressed as the number of female calves that reached age 1 year per simulated female.

Figure S10. Results of the simulated scenarios of environmental change and anthropogenic disturbance (current sonar regime, labelled as ‘Mixed 1’: scenarios 22–38; modified sonar regime, labelled as ‘Mixed 2’: scenarios 39–55) on (a) female survival, expressed as the age at death, and (b), female reproductive success, expressed as the number of female calves that reached age 1 year per simulated female.

Figure S11. Scaled sensitivity of baseline adult survival (i.e. age at death) to the perturbation of some parameter values, expressed as the absolute value of the effect of that sensitivity perturbation (i.e. the Cohen’s *d* difference from the original model) divided by the proportional parameter change.

Figure S12. Scaled sensitivity of baseline reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of some parameter values, expressed as the absolute value of the effect of that sensitivity perturbation (i.e. the Cohen’s *d* difference from the original model) divided by the proportional parameter change.

Figure S13. Sensitivity of the effects of anthropogenic disturbance (scenarios 2, 3 and 4) on adult survival (i.e. age at death) to the perturbation of some parameter values, expressed as the difference in Cohen’s *d* values for those scenarios between each sensitivity perturbation and the original model.

Figure S14. Sensitivity of the effects of anthropogenic disturbance (scenarios 2, 3 and 4) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of some parameter values, expressed as the difference in Cohen’s *d* values for those scenarios between each sensitivity perturbation and the original model.

Figure S15. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime (‘Mixed 1’; scenarios 22–38) and environmental change paired with the modified sonar regime (‘Mixed 2’; scenarios 39–55) on adult survival (i.e. age at death) to the perturbation of environmental parameter values (SensID 1–22), expressed as the distribution of the difference in Cohen’s *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S16. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime (‘Mixed 1’; scenarios 22–38) and environmental change paired with the modified sonar regime (‘Mixed 2’; scenarios 39–55) on adult survival (i.e. age at death) to the perturbation of activity parameter values (SensID 23–31), expressed as the distribution of the difference in

Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S17. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38) and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on adult survival (i.e. age at death) to the perturbation of bioenergetic parameter values (SensID 32–37), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S18. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38) and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on adult survival (i.e. age at death) to the perturbation of morphological parameter values (SensID 38–41), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S19. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38), and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on adult survival (i.e. age at death) to the perturbation of disturbance parameter values (SensID 42–50), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S20. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38), and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of environmental parameter values (SensID 1–22), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S21. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38), and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of activity parameter values (SensID 23–31), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S22. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38), and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of bioenergetic parameter values (SensID 32–37), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S23. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38), and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of morphological parameter values (SensID 38–41), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S24. Sensitivity of the effects of environmental change (scenarios 5–21), environmental change paired with the current sonar regime ('Mixed 1'; scenarios 22–38) and environmental change paired with the modified sonar regime ('Mixed 2'; scenarios 39–55) on reproductive success (i.e. the number of female calves surviving to age 1 year) to the perturbation of disturbance parameter values (SensID 42–50), expressed as the distribution of the difference in Cohen's *d* values for those sets of scenarios between each sensitivity perturbation and the original model.

Figure S25. Scaled effect sensitivity of survival (a) and reproductive success (b) under the simulated scenarios of anthropogenic disturbance, environmental change and environmental change paired with the current (mixed 1) or modified (mixed 2) sonar regime, to the perturbation of some parameter values.

Figure S26. Extension of Figure 1 (in the main text) highlighting how the data requirements listed in TABLE 1 would inform the cascade from individual responses to population effects.

Table S1. Summary of sonar activities in a typical year, as derived from the Environmental Impact Statement for testing and training activities in the Hawaii-Southern California range complex.

Table S2. Simulated scenarios of anthropogenic disturbance and environmental change. CC stands for California Current.

Table S3. Combined effects of environmental change and anthropogenic disturbance, reported for those instances where the absolute difference between the effect of a mixed scenario and the sum of the corresponding separate effects was at least 0.1.

Table S4. Details of the sensitivity analysis.

Table S5. Effects of the sensitivity perturbations on survival and reproductive success in the baseline scenario.