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**ASSESSING NATURAL AND ANTHROPOGENIC STRESSOR IMPACTS ON
MARINE MAMMALS: LINKING SHORT-TERM RESPONSES TO LONG-
TERM POPULATION EFFECTS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY
with an emphasis in COASTAL SCIENCE AND POLICY

by

Kelly Ann Keen

September 2024

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2024

Table of Contents

Table of Contents	iii
List of Tables.....	vii
List of Figures.....	x
Abstract.....	xiii
Dedication	xv
Acknowledgements	xvi
Introduction.....	1
Chapter 1: Emerging themes in Population Consequences of Disturbance models.....	8
1.1 Abstract	8
1.2 Introduction.....	9
1.3 Life-history traits	12
1.3.1 Movement ecology.....	13
1.3.2 Reproductive strategy	16
1.3.3 Body size.....	19
1.3.4 Pace of life	22
1.4 Disturbance source characteristics.....	25
1.4.1 Overlap with biologically important habitats	25
1.4.2 Duration and frequency.....	27
1.4.3 Nature and context	28
1.5 Environmental conditions	30
1.5.1 Natural variability in prey availability	30
1.5.2 Climate change.....	33
1.6 Data gaps and future priorities.....	35
1.7 References.....	39
1.8 Figures	52

1.9	Supplementary material	55
1.9.1	Appendix A: Applicability to other species	55
1.9.2	Appendix B: PCoD model assumptions and limitations.....	58
1.8.3	Appendix C: Supplementary tables and figures.....	61
1.9.4	Supplementary references.....	69
Chapter 2: Effects of reduced krill availability on humpback whales along the western Antarctic Peninsula.....		86
2.1	Abstract	86
2.2	Introduction.....	87
2.3	Methods	91
2.3.1	Model overview	91
2.3.2	A whale's physiological state	94
2.3.3	Prey environment	96
2.3.4	Additional mortality	98
2.3.5	Backward iteration: SDP equations	98
2.3.6	Forward simulation: simulated stressor scenarios	103
2.3.7	Sensitivity analysis.....	105
2.4	Results.....	105
2.4.1	Baseline conditions	105
2.4.2	Stressor scenarios.....	107
2.5	Discussion.....	108
2.6	Conclusions.....	117
2.7	References.....	119
2.8	Figures	133
2.9	Supplementary material	138
2.9.1	Appendix A: SDP conceptual diagram.....	138
2.9.2	Appendix B: Physiological equations and parameters.....	140
2.9.3	Appendix C: Krill densities and regimes in the backward iteration	151

2.9.4	Appendix D: SDP equations	153
2.9.5	Appendix E: Creating a stable-age distribution and identifying starting conditions for the forward simulation.....	158
2.9.6	Appendix F: Sensitivity analysis.....	160
2.9.7	Appendix G: Tables of life-history parameters and Cohen's <i>d</i> values	167
2.9.8	Appendix H: Additional figures	170
2.9.9	Supplementary references.....	171
Chapter 3: Spatial and temporal sensitivities of an endangered humpback whale population to anthropogenic stressors in the California Current Ecosystem ...		176
3.1	Abstract	176
3.2	Introduction.....	177
3.3	Methods	182
3.3.1	Model overview	182
3.3.2	Behavioral and reproductive decisions	183
3.3.3	Prey environment	185
3.3.4	Simulated scenarios and responses to stressors	188
3.3.5	Sensitivity analysis.....	191
3.4	Results.....	191
3.4.1	Baseline conditions	191
3.4.2	General stressor scenarios.....	194
3.4.3	Construction stressor scenarios.....	194
3.5	Discussion.....	195
3.6	Conclusions.....	204
3.7	References.....	206
3.8	Tables and figures	219
3.9	Supplementary material	226
3.9.1	Appendix A: Energy gained from feeding	226
3.9.2	Appendix B: Sensitivity analysis	228

3.9.3	Appendix C: Tables of life-history parameters and Cohen's d values	233
3.9.4	Supplementary references	240
Synthesis		241

List of Tables

Chapter 1

Table C1. Summary of Population Consequences of Disturbance (PCoD) model publications that met our synthesis criteria (i.e., models that quantify the non-lethal effects of anthropogenic disturbance on marine mammal vital rates via the behavioural-bioenergetic pathway). Information is provided on species and citation, and if included in the models, life-history traits (M = movement ecology, R = reproductive strategy, S = body size, P = pace of life), disturbance source characteristics (B = overlap with biologically important habitats, D = duration and frequency, N = nature and context), and environmental conditions (V = natural variability in prey availability, C = climate change) are noted.61

Table C2. Movement patterns and reproductive strategies exhibited by 20 families of marine mammals. An X indicates that the family generally exhibits that movement or reproductive pattern, recognizing that these categories are not mutually exclusive and there may be variation between individuals in a population (e.g., based on sex or age class) and different populations of the same species.63

Table C3. Selected pace-of-life traits exhibited by females across 20 families of marine mammals, including growth (age at sexual maturity), reproduction (length of gestation, lactation, and the interbirth interval), and survival (maximum estimated or recorded lifespan, unless otherwise noted).66

Chapter 2

Table A1. Respiration rates in breaths/minute (presented as mean (SD)) and sources used to calculate respiration rate in breaths/day (mean) for a humpback whale throughout its lifetime depending on location and age class.143

Table A2. Physiological parameters used in the SDP model.150

Table F1. List of model parameters tested in the sensitivity analysis.160

Table F2. List of key vital rates and their values from the original model.161

Table F3. Summary table for the sensitivity analysis for the maximum threshold for female body condition.162

Table F4. Summary table for the sensitivity analysis for the age threshold (for the calf, in days) for a mother/calf to leave the breeding grounds.163

Table F5. Summary table for the sensitivity analysis for the multiplier for the medium krill regime.164

Table F6. Summary table for the sensitivity analysis for the shape parameter of the fitness function.165

Table F7. Summary table for the sensitivity analysis for the scale parameter of the fitness function.166

Table G1. Calculated life-history parameters under baseline conditions (no stressors).167

Table G2. Selected life-history parameters under the climate change stressor scenarios. Pregnancy rate was calculated on day 185 (February 1) of each simulated year.167

Table G3. Selected life-history parameters under the combined climate change and krill fishing stressor scenarios. In the climate change (50%) and krill fishing (50%) stressor scenario, the population crashed before the 25-year simulation completed, as indicated by the dashes in the columns. Pregnancy rate was calculated on day 185 (February 1) of each simulated year.168

Chapter 3

Table 3.1. Simulated stressor scenarios implemented in the forward simulation. General stressor scenarios were simulated for 21 years, and construction stressor scenarios were simulated for 35 years.219

Table B1. List of model parameters tested in the sensitivity analysis.228

Table B2. List of key vital rates and their values from the original model.229

Table B3. Summary table for the sensitivity analysis for the maximum threshold for female body condition.229

Table B4. Summary table for the sensitivity analysis for the age threshold (for the calf, in days) for a mother/calf to leave the breeding grounds.230

Table B5. Summary table for the sensitivity analysis for the multiplier for the prey environment.231

Table B6. Summary table for the sensitivity analysis for the shape parameter of the fitness function.231

Table B7. Summary table for the sensitivity analysis for the scale parameter of the fitness function.	232
Table C1. Calculated life-history parameters under baseline conditions (no stressors).	233
Table C2. Selected life-history parameters under the general stressor scenarios in spring (March to May).	233
Table C3. Selected life-history parameters under the general stressor scenarios in summer (June to August).	235
Table C4. Selected life-history parameters under the general stressor scenarios in fall (September to November).	237
Table C5. Selected life-history parameters under the construction stressor scenarios in location 4.	238

List of Figures

Chapter 1

Figure 1.1. Emerging themes in Population Consequences of Disturbance models that should be considered when assessing the likelihood and duration of exposure and the sensitivity of a population to disturbance.52

Figure 1.2. (A) A population's movement patterns can help determine the degree of exposure to a disturbance-inducing activity. When comparing resident and nomadic movement patterns, the same disturbed area could frequently expose a few resident individuals while infrequently exposing many nomadic individuals. In contrast, many individuals of a migratory population could be exposed, but exposure would be seasonal. Figure adapted from Costa et al. (25). (B) Migratory populations may share common foraging grounds or reproductive areas, which influences whether a single population, a fraction of a population, or multiple distinct populations will be exposed to a disturbance-inducing activity. If individuals share a common reproductive area but return to unique foraging grounds, individuals constitute one population representing one demographic breeding unit. Alternatively, if they share a common foraging ground but return to unique reproductive areas, they represent two or more demographically distinct populations.53

Figure 1.3. A reproductive cycle plot for a North Atlantic minke whale (*Balaenoptera acutorostrata*) showing the variability in the timing and duration of life stages for a 1-year reproductive cycle. The wedge represents a proposed disturbance-inducing activity occurring for approximately 2 months. Reproductive cycle plots can help identify the temporal overlap between sensitive life-history events and a proposed activity. Figure adapted from Wilson et al. (22) and informed based on Christiansen et al. (56).54

Figure C1. The Population Consequences of Disturbance (PCoD) framework. The boxes within the dashed gray boundary line represent the effects of exposure to a stressor and a range of ecological drivers on the vital rates of an individual animal. The effects are then integrated across all individuals in the population to project their effects on the population's dynamics. Figure adapted from Pirotta et al. (26).69

Chapter 2

Figure 2.1. Map of the study area, including the breeding grounds, feeding grounds, and 59 locations that made up the migratory corridor. Possible behavioral choices for each region are also provided.133

Figure 2.2. An example of the time series of (A) location and (B) body condition for one simulated whale, colored by reproductive state, under baseline conditions. Gray vertical rectangles represent low krill years.134

Figure 2.3. (A) Mean body condition of whales for one simulation across low, medium, and high krill years under baseline conditions. (B) Mean percent change (for the same simulation in (A)) in birth rate following a low krill year, and weaning day (including both unsuccessful and successful weanings) and weaning success rate during a low krill year, compared to medium and high krill years (dashed line); error bars represent the standard deviation.135

Figure 2.4. The influence of simulated stressors on (A) pregnancy rate (on February 1, in the middle of the feeding season), (B) birth rate, and (C) weaning success rate. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor), error bars represent the average standard deviation within a population as a percent change around the mean, and the colors represent the effect size based on Cohen's *d*. The x-axis represents the simulated stressor scenarios, where the value in parentheses represents the percent reduction in krill due to climate change and the shape represents the percent reduction in krill due to krill fishing. A hollow shape means the population crashed before the simulations ended.136

Figure 2.5. Humpback whale population trajectories under three climate change scenarios, with the percent reduction in krill due to climate change noted in parentheses. The colored trajectories represent baseline (no stressors), single stressor (climate change in isolation), and multiple stressors (climate change and krill fishing) scenarios; the error bars represent the standard deviation. For the multiple stressors scenarios, the percent reduction in krill due to krill fishing is noted in the legend in parentheses.137

Figure A1. Conceptual diagram of the backward iteration of the SDP model. The listed equations can be found in the main text.138

Figure A2. Conceptual diagram of the forward simulation of the SDP model.139

Figure H1. Body condition at the end of the feeding season as a function of reproductive state; the error bars represent the standard deviation (max body condition = 45%). For non-reproductive juvenile, non-reproductive adult, and pregnant states, whales arrived on and departed from the feeding grounds in the same reproductive state. Pregnant to non-reproductive adult, pregnant and lactating (preg/lac) to pregnant, and preg/lac to non-reproductive adult represent reproductive state transitions that occurred on the feeding grounds, where the first reproductive state was a whale's state the day it arrived on the feeding grounds and the second reproductive state was the whale's state the day it departed the feeding grounds. Other reproductive states or transitions (e.g., lactating, lactating to non-reproductive adult) did not occur on those

days (arriving on or departing from the feeding grounds) and, therefore, are not included in the figure.143

Chapter 3

Figure 3.1. Map of the feeding grounds and 14 foraging locations.220

Figure 3.2. (A) Mean body condition of whales for one simulation near the end of the feeding season (ordinal day 319 or November 15) across El Niño, neutral, and La Niña years. (B) Proportion of prey in the diet of whales (for the same simulation in (A)) across El Niño, neutral, and La Niña years. The white points represent the proportion of krill in that individual's diet.221

Figure 3.3. Percent time feeding across whales in each of the 14 foraging locations during El Niño, neutral, and La Niña years. A missing bar means that feeding did not occur in that location during the associated environmental regime. The approximate center latitude for each location is included next to the corresponding location.222

Figure 3.4. The influence of simulated general stressors on vital rates in (A) location 4 (B), location 5, and (C) location 6, with their approximate center latitudes included in parentheses. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor); error bars represent the standard deviation as percent change around the mean; shapes represent the measured vital rates (i.e., pregnancy rate, birth rate, and weaning success rate); and colors represent the effect size based on Cohen's *d*.223

Figure 3.5. The influence of simulated general stressors on population growth rate in (A) spring, (B) summer, and (C) fall. The colors of each location represent the effect size based on Cohen's *d*.224

Figure 3.6. (A) The influence of simulated construction stressors on vital rates. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor); error bars represent the standard deviation as percent change around the mean; shapes represent the measured vital rates (i.e., pregnancy rate, birth rate, and weaning success rate); and colors represent the effect size based on Cohen's *d*. The x-axis represents the simulated construction stressor scenarios. (B) Population trajectories for baseline conditions and four construction scenarios; error bars represent the standard deviation.225

Abstract

Assessing Natural and Anthropogenic Stressor Impacts on Marine Mammals: Linking Short-Term Responses to Long-Term Population Effects

by

Kelly Ann Keen

Human activities are having widespread and pervasive impacts on terrestrial and aquatic ecosystems. In addition to intensifying climate change, from rising sea levels to shifting weather and climate patterns, these impacts are causing habitat degradation and even species extinctions. As a result, assessing the effects of these stressors on ecosystems and dependent wildlife populations is necessary for their management and conservation. This requires a framework to identify vulnerability and, subsequently, tools to quantify impacts that can inform strategies to mitigate negative consequences.

For my dissertation, I used qualitative and quantitative approaches to assess the population consequences of disturbance (PCoD) from human and environmental stressors on marine mammal populations. First, I synthesized existing PCoD models developed for marine mammals to provide insights into what contextual factors influence a population's likelihood and duration of exposure and sensitivity to disturbance (Chapter 1). Then, I added to the existing suite of PCoD models by developing the first stochastic dynamic programming model for humpback whales. With this model, I examined the temporal sensitivities of humpback whales to climate-

and fishery-driven changes in krill availability on their western Antarctic Peninsula feeding grounds (Chapter 2). Finally, I extended the model to examine the spatial and temporal sensitivities of an endangered population of humpback whales to stressors on their feeding grounds in the California Current Ecosystem (Chapter 3).

Overall, a population's resilience to disturbance largely depended on its life-history traits, the stressor's characteristics, and the environmental conditions. Stressors had varying effects on a population depending on the type of stressor, the severity of the disturbance, and whether multiple stressors were present. However, impacts to the population could generally be reduced when the overlap between stressors and biologically important areas was minimized, especially during energetically vulnerable and reproductively sensitive times. Finally, stressors had a greater impact on a population when the prey environment was already poor due to natural variability, with effects worsening within the context of a changing climate. Collectively, my dissertation provides a qualitative and quantitative basis for assessing the effects of stressors on population dynamics and comparing different stressor scenarios associated with our expanding offshore footprint.

Dedication

To my husband and family for their endless encouragement and support

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Statement of contribution

The text from this dissertation includes a reprint of the following published material, which was published as open access under a CC-BY license; note that small adjustments to the article reprinted in Chapter 1 were made to accommodate formatting guidelines for this dissertation:

Chapter 1: Keen KA, Beltran RS, Pirotta E, Costa DP. 2021 Emerging themes in Population Consequences of Disturbance models. *Proceedings of the Royal Society B: Biological Sciences*. **288**: 20210325. <https://doi.org/10.1098/rspb.2021.0325>

This work was original research by KAK, with contributions from co-authors. KAK and DPC conceived the manuscript; KAK led the writing of the manuscript; and KAK, RSB, EP, and DPC contributed critically to the drafts and revisions of the manuscript. All authors read and approved the final manuscript.

Introduction

Background

Determining when human activities and changing environmental conditions cause biologically significant effects on a population has been a long-term goal for scientists, managers, and decision-makers. When human activities lead directly to the death of an individual, the consequences on the population are relatively clear and quantifiable; however, non-lethal effects, such as short-term changes in behavior and physiology, are more difficult to characterize and link to negative consequences for the population (1). As a result, management decisions are often made based on studies of individual responses, although such responses may not lead to a population-level effect (2). Thus, a mechanistic understanding of the links between short-term responses and long-term effects at the individual level is necessary to assess the consequences of disturbance on a population, which is a requirement for most risk assessments under European Union (e.g., Habitats Directive 92/43/EEC) and United States (e.g., Marine Mammal Protection Act, 16 U.S.C. §§ 1361 *et seq.*) legislation (3).

To address this need, the Population Consequences of Disturbance (PCoD) framework was developed to conceptualize how disturbance can lead to changes in population dynamics via changes in behavior and physiology that impact an individual's health and vital rates (4-6). While this framework was originally developed for marine mammals, it is generally applicable across vertebrates (7). The PCoD framework separates the behavioral and physiological effects of disturbance into acute and chronic impacts, where acute impacts directly affect an individual's vital rates (e.g.,

increasing their risk of predation, decreasing their probability of survival following injury), and chronic impacts result from persistent or recurring activities that affect an individual's health (e.g., seismic surveys, wildlife tourism). An individual's health is related to many aspects of its physiology, including stress levels, immune status, and energy stores. While our understanding of marine mammal stress physiology and immunology is incomplete (8), bioenergetics has proven useful for implementing the PCoD framework (5, 9). Consequently, most implementations to date have focused on the behavioral-bioenergetic pathway, where a stressor leads to changes in behavior that affect energy acquisition and expenditure (10-12).

Since the PCoD framework was first proposed, a suite of quantitative models has been developed for several marine mammal species to estimate the short- and long-term consequences of disturbance. Several modeling approaches have been used to implement the PCoD framework, including matrix models (13), physiologically structured population models (14), bioenergetic models (9), and stochastic dynamic programming (SDP) (15), with model selection driven by data availability and the questions being addressed. However, PCoD models require considerable time, funding, and data for model construction and implementation; thus, developing species-specific PCoD models for a given risk assessment is not always possible nor feasible. Nevertheless, determinations regarding risk and potential effects on populations must be made. Without species-specific PCoD models, a holistic view of existing model findings across species and stressor scenarios can provide valuable insights into what contextual factors influence a population's likelihood and duration of exposure and

sensitivity to disturbance (7). As such, synthesizing these disparate, quantitative models can help guide qualitative risk analyses for data- and model-deficient populations. This information may be particularly valuable for managers and practitioners looking to identify and prioritize populations most vulnerable to disturbance and industry in planning activities that avoid or mitigate population-level effects.

When species-specific PCoD models are feasible to develop, they can provide valuable information for conserving and managing populations. In recent years, SDP has received increased attention due to the flexibility it offers for exploring how an individual's current physiological state (e.g., blubber/energy stores, reproductive status) and changes in the environment (e.g., prey availability, the addition of a stressor) affect the individual's decision-making. Within this context, SDP models are generally comprised of two steps: a backward iteration and a forward simulation. In the backward iteration, optimal reproductive and/or behavioral decisions that maximize an individual's fitness (e.g., lifetime reproductive success) are identified, which are functions of time, the individual's internal physiological state, and the state of the external environment. These optimal strategies are summarized in a matrix of decisions used in Monte Carlo forward simulations to predict an individual's fitness in the absence and presence of one or multiple stressors (15-17). Therefore, within the SDP modeling framework, one can quantify how an individual's optimal decisions, given a set of benefits, costs, and constraints, affect its health and vital rates, and what the cumulative effect of those decisions have on a population. As such, the outputs from

SDP models can be helpful in planning disturbance-inducing activities and assessing the effectiveness of proposed mitigation strategies (e.g., time/area closures) while also meeting conservation and management goals. They can also highlight critical knowledge gaps that can inform future research directions and ultimately increase the model's utility in mitigating adverse effects.

Dissertation summary

In Chapter 1, I provide a comprehensive synthesis of existing quantitative PCoD models developed for several marine mammal species that have been used to forecast the possible consequences of disturbance. By taking a holistic view of model results, I identify common themes and highlight general principles to consider when assessing risk. This information can help managers identify which species are most vulnerable to disturbance, thus allowing them to prioritize efforts and focus subsequent analyses.

In Chapter 2, I create the first SDP model for a humpback whale, which will add to the existing suite of PCoD models available for marine mammals. Developing an SDP model for humpback whales is important because of their global and cosmopolitan distribution, which makes them vulnerable to human activities worldwide. This model examines the temporal sensitivities of humpback whales to climate- and fishery-driven changes in krill availability on their western Antarctic Peninsula feeding grounds. This region is experiencing both rapid climate change and a growing krill fishing industry, and this model can provide a general framework to predict the impact of multiple stressors on humpback whale population dynamics.

In Chapter 3, I extend the SDP model from Chapter 2 to examine the spatial and temporal sensitivities of an endangered population of humpback whales to stressors on their feeding grounds in the California Current Ecosystem. This model explores the influence of environmental variability on prey choice and whale distribution, when and where individuals are most sensitive to disturbance on the feeding grounds, and how a stressor's temporal features influence a population's fitness. This model can provide a general framework for managers to quantitatively compare different stressor scenarios when assessing risk for this vulnerable population, which is particularly valuable given our expanding offshore footprint.

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Chapter 1: Emerging themes in Population Consequences of Disturbance models

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1.1 Abstract

Assessing the non-lethal effects of disturbance from human activities is necessary for wildlife conservation and management. However, linking short-term responses to long-term impacts on individuals and populations is a significant hurdle for evaluating the risks of a proposed activity. The Population Consequences of Disturbance (PCoD) framework conceptually describes how disturbance can lead to changes in population dynamics, and its real-world application has led to a suite of quantitative models that can inform risk assessments. Here, we review PCoD models that forecast the possible consequences of a range of disturbance scenarios for marine mammals. In so doing, we identify common themes and highlight general principles to consider when assessing risk. We find that, when considered holistically, these models provide valuable insight into which contextual factors influence a population's degree of exposure and sensitivity to disturbance. We also discuss model assumptions and limitations, identify data gaps, and suggest future research directions to enable PCoD models to better inform risk assessments and conservation and management decisions. The general principles explored can help wildlife managers and practitioners identify and prioritize the populations most vulnerable to disturbance and guide industry in planning activities that avoid or mitigate population-level effects.

1.2 Introduction

A significant hurdle for wildlife conservation and management is knowing when and how short-term responses to human activities result in biologically meaningful changes that affect population dynamics (1). For many vertebrates, human activities may elicit behavioural (e.g., avoidance, reduced foraging, changes in vocalizations) and physiological (e.g., increased stress levels, temporary reductions in hearing) responses that can, in the aggregate, affect individual fitness and cause population- and ecosystem-level effects (2-4). Assessing the consequences of anthropogenic disturbance is therefore necessary for the long-term persistence of populations in increasingly human-altered ecosystems (5). For marine mammals, this is a requirement for most risk (or impact) assessments under European Union (Habitats Directive 92/43/EEC) and United States (Marine Mammal Protection Act (MMPA), 16 U.S.C. §§ 1361 *et seq.*) legislation (6). However, the links between behavioural and physiological responses and their long-term individual- and population-level effects are poorly understood, making comprehensive risk assessments difficult (2, 7).

To address this issue, the Population Consequences of Disturbance (PCoD) framework was developed to conceptualize how disturbance-induced changes in individual behaviour and physiology affect population dynamics via changes in individual health and vital rates (supplementary material, Figure C1) (7, 8). While this framework was developed for use with marine mammals, it is generally applicable across most vertebrates. The PCoD framework separates the behavioural and physiological effects of disturbance into acute and chronic impacts. Acute impacts

directly affect an individual's vital rates by, for example, increasing their risk of predation or decreasing their probability of survival following injury (e.g., collision with a vessel, entanglement in fishing gear). In contrast, chronic impacts result from persistent or recurring activities that affect an individual's health over a prolonged period (e.g., seismic surveys, whale watching), potentially reducing lifetime reproductive output. An individual's health is related to many aspects of its physiology, including stress levels, immune status, and energy stores. While our understanding of marine mammal stress physiology and immunology is incomplete (9), bioenergetics has proven to be a useful approach for implementing the PCoD framework (7, 10). Consequently, most implementations to date have focused on changes in a female's time-energy budget concerning lost foraging time, the subsequent effects on energy delivery from mother to offspring, and the cascading long-term impacts on the population (11-13).

Since the PCoD framework was first proposed, a suite of models has been created to evaluate the short- and long-term consequences of disturbance (2). These models take a quantitative approach to the PCoD framework using a combination of matrix modelling (14), physiologically structured population modelling (15), bioenergetic modelling (10), and stochastic dynamic programming (16). PCoD models have been developed for several marine mammal species and parameterized via species-specific empirical data and alternative methods, including extrapolating from other species (17), proxy relations (18), expert elicitation (19), and informed assumptions (20), when empirical data are lacking (see Pirotta et al. (2) for how

empirical data and alternative methods have been used to parameterize PCoD models). PCoD models have been used to forecast the possible consequences of a range of disturbance scenarios and identify the disturbance level likely to result in a population impact (21). As such, PCoD model outputs can provide valuable insights into what contextual factors influence a population's likelihood and duration of exposure and sensitivity to disturbance. However, the findings from these disparate models have yet to be synthesized in a single review to guide risk assessments for marine mammals. This information can help wildlife managers and practitioners identify and prioritize the populations most vulnerable to disturbance (see decision framework in Wilson et al. (22)) and guide industry in planning activities that avoid or mitigate population-level effects.

In this synthesis, we review common themes that have emerged from these disparate PCoD models. In so doing, we highlight essential intrinsic and extrinsic factors to consider when assessing risk and describe how they can be evaluated when determining a population's degree of exposure and sensitivity to disturbance. We also identify data gaps and suggest future research directions that will enable PCoD models to better inform risk assessments and conservation and management decisions. Finally, in the supplementary material, we discuss how the PCoD framework and the emerging themes in this synthesis can be broadly applied to guide risk assessments for other species (see *Appendix A: Applicability to other species*), as well as underlying model assumptions and limitations that can influence model predictions but may not be self-

evident to non-specialists or non-statisticians (see *Appendix B: PCoD model assumptions and limitations*).

We searched for PCoD model publications from 2005 (when the PCoD framework was first proposed (8)) through March 2021 on Google Scholar using the search terms “marine mammal”, “bioenergetics”, “model”, “population consequences”, and “disturbance”. We located additional publications by searching the references cited in a review paper by Pirotta et al. (2) and the citing literature of each publication that met our synthesis criteria. To meet our criteria, the publication had to quantify the non-lethal effects of anthropogenic disturbance on marine mammal vital rates via the behavioural-bioenergetic pathway. The publications included in the synthesis are in Table C1 of the supplementary material.

1.3 Life-history traits

When assessing the risk associated with a proposed activity, it is essential to determine (1) if the population will be exposed, (2) the proportion of the population exposed, (3) the duration of individual exposure, and (4) the sensitivity of the exposed individuals (22, 23). The answers to these questions are influenced by the life-history traits of an individual or population, including their movement ecology, reproductive strategy, body size, and pace of life. In the following sections, we examine the importance of each life-history trait for mediating risk (Figure 1.1). A summary of the life-history traits exhibited by marine mammals (at the family level) is provided in Tables C2 and C3 of the supplementary material.

1.3.1 Movement ecology

A population's movement ecology influences its degree of exposure to a disturbance-inducing activity (18, 24-26). Marine mammal movement patterns broadly fall into three categories: resident, nomadic, and migratory (Figure 1.2A; supplementary material, Table C2). Individuals that exhibit resident movement patterns (e.g., sea otters (*Enhydra lutris*) (27)) occupy small home ranges relative to the population's overall range (28), whereas nomadic individuals (e.g., spinner dolphins (*Stenella longirostris*) (29)) move over much of the population's range without spatial or temporal consistency (30). Consequently, the same disturbed area could frequently expose a few individuals of a resident population while infrequently exposing many individuals of a nomadic population (Figure 1.2A) (25, 31). However, the proportion of the population exposed will depend on the spatial extent of the disturbance relative to the population's range. Because foraging grounds and reproductive areas spatially overlap for both resident and nomadic populations, PCoD modelling shows that the behaviours potentially disrupted will depend on the timing of the disturbance event (32).

In contrast, individuals that exhibit migratory movement patterns transit annually or seasonally between sites within their range (30, 33), which reduces the potential for year-round, prolonged exposure, as simulated in several PCoD models (Figure 1.2A) (13, 18, 25). Some migratory populations (e.g., southern elephant seals (*Mirounga leonina*) (34)) have spatially (e.g., by thousands of kilometres) and temporally (e.g., by several months) separate foraging grounds and reproductive areas.

Consequently, if a disturbance-inducing activity occurs in reproductive areas when the population is at the foraging grounds, the likelihood of exposure is zero unless it has lasting environmental effects (e.g., Deepwater Horizon oil spill in the Gulf of Mexico (35)). The reverse scenario is also generally true, but some individuals may remain at the foraging grounds during the reproductive season (36). Other migratory populations do not have separate foraging grounds and reproductive areas and instead migrate in response to seasonal ecological conditions, such as advancing sea ice and migration of prey (e.g., beluga whales (*Delphinapterus leucas*) (37)). For these populations, PCoD modelling shows that foraging and/or reproductive behaviours may be disrupted if there is spatial and temporal overlap (13).

Migratory populations may also be exposed to anthropogenic disturbance within migratory corridors. While the proportion of the population exposed will be high during synchronous migrations, individual exposure levels will be relatively low because individuals generally transit quickly (26). Recent studies on the behavioural responses of migrating humpback whales (*Megaptera novaeangliae*) to seismic airgun noise found that individuals deviated from their predicted path and slowed their progression until the source had passed or ceased (38, 39). Because humpback whales rely on finite energy stores during migration, these behavioural changes could alter a female's energy budget, thereby reducing calf growth rates, and delay arrival at the foraging grounds (40). When incorporated into a PCoD model, Dunlop et al. (41) found that similar behavioural responses to a simulated 10-day seismic survey during peak migration had negligible effects on female body condition and population growth.

However, the costs of repeated exposures may accumulate over the long migration, particularly for populations migrating along coastlines with high levels of human activity.

Although not explicitly included in PCoD models to date, it is also necessary to consider whether migratory populations share common foraging grounds or reproductive areas when assessing population-level effects. This will influence whether a single population, a fraction of a population, or multiple distinct populations are exposed (Figure 1.2B). If individuals share a common foraging ground but return to unique reproductive areas, they represent two or more demographically distinct populations. Alternatively, if they share a common reproductive area but return to unique foraging grounds, individuals still represent one demographic breeding unit (42). Consequently, a disturbance-inducing activity within a foraging ground utilized by more than one breeding unit will affect more than one population. Distinct breeding units may also overlap spatially but not temporally (43). Thus, disturbance-inducing activities that spatially overlap with these reproductive areas may impact one or more populations depending on the activity's temporal extent.

Individual movement patterns are also influenced by demographic factors, including the age, sex, and reproductive status of individuals within a population. For example, demographic differences may impact where individuals forage (44), when individuals migrate (45), and how individuals aggregate (46). Identifying which population segments will be affected can benefit mitigation and activity planning by

reducing or avoiding interactions with sensitive individuals (see *Reproductive strategy* and *Body size*).

Understanding a population's movement ecology can help determine the likelihood and duration of exposure and the proportion of the population exposed. Biologging devices and visual and acoustic survey methods provide valuable information on marine mammal movements (47) that can be incorporated into risk assessments to help identify which populations may be present in a disturbed area and thus require further assessment (22). This information can also be used to plan activities that avoid areas with high concentrations of marine mammals. For example, Hückstädt et al. (48) utilized tracking data for several humpback whale and blue whale (*Balaenoptera musculus*) populations to identify which were particularly susceptible to exposure from seismic surveys and where surveys could have the largest impacts. PCoD models have been developed to be spatially explicit, using both coarse- (13) and fine-scale (49) movement data, or spatially implicit, with movement data reflected in activity budgets (12) or not included at all (15). Ultimately, the scale of movement necessary to assess risk depends on the target population and the management or policy issue being addressed.

1.3.2 Reproductive strategy

Reproduction is the most energetically expensive period of a female's life cycle because she must balance her own needs with those of her dependent offspring. Strategies for financing reproductive costs are often described on a continuum from income breeding, where energy is acquired throughout lactation, to capital breeding,

where energy for lactation is stored as endogenous reserves prior to parturition (50, 51). A population's position on this continuum can influence its sensitivity to disturbance (supplementary material, Table C2). For example, the need for income breeders to feed during lactation strongly ties reproductive success to local prey abundance (52), leaving females particularly vulnerable to prolonged foraging loss due to disturbance during lactation (53). As such, these sensitivities to disturbance in income breeders can lead to declines in offspring recruitment and overall population size (12). In contrast, capital breeders are less sensitive to short-term foraging losses, particularly during the lactation period, because they rely on energy that has already been stored (13, 52). This buffer may also provide capital breeders with the ability to adjust their foraging behaviour and seek out productive prey patches or alternative prey sources (52). However, energy stores are finite, and if disturbance is prolonged, particularly within important foraging areas (see *Disturbance source characteristics*) (13), or if the available foraging habitat is spatially limited (25), capital breeders may not be able to accumulate sufficient energy for successful reproduction.

PCoD models provide a framework for quantifying the baseline energetic requirements for reproduction and survival and simulating the downstream impacts of compromised foraging success on population growth. These models show that reduced foraging opportunities can delay sexual maturity or age at first reproduction (15, 54, 55) and increase the interval between reproductive events (15, 54), which could impact a female's lifetime reproductive output and, ultimately, population abundance. Reduced foraging may also decrease the energy transferred to offspring, resulting in

reduced foetus growth (56) and/or lower weaning mass, which could affect offspring survival (11-13). If foraging or energy reserves are reduced such that females struggle to meet their own metabolic demands, termination of gestation or lactation may also occur (12, 13, 15, 57). Ultimately, a series of physiological thresholds are reached when a female lacks sufficient resources to reproduce or transfer energy to offspring, which may lead to the termination of an existing reproductive attempt (58, 59). However, how and when these thresholds are reached is poorly understood.

PCoD models identify lactation as the most sensitive reproductive state for income breeders because energy is acquired during lactation to support dependent offspring (12, 17). In contrast, PCoD models identify pregnancy as the most sensitive reproductive state for capital breeders because energy reserves are accumulated during pregnancy to support lactation (11, 17). Model simulations have also demonstrated that the timing of a disturbance-inducing activity during these sensitive states influences whether a female can compensate for reduced or lost foraging. For income-breeding California sea lions (*Zalophus californianus*), simulations carried out by McHuron et al. (60) found that the costs associated with nursing a pup were much greater during late lactation than early lactation because the total energy delivered to the pup increased as the pup grew. In contrast, for capital-breeding northern elephant seals (*Mirounga angustirostris*), Pirotta et al. (61) found that simulated females could better compensate for disturbance during the first phase of their 8-month foraging trip if the disturbance was not severe. However, irrespective of reproductive strategy, extrinsic factors related to the disturbance source (see *Disturbance source characteristics*) and environment

(see *Environmental conditions*) will also influence the outcome of an existing reproductive attempt.

The reproductive strategies exhibited by marine mammals can help assess a population's sensitivity to disturbance and should be considered in risk assessments. Reproductive cycle plots can help identify the temporal overlap between sensitive life-history events and a proposed activity (Figure 1.3) (22). Management plans that limit or avoid interactions with sensitive reproductive states are ideal. However, as this is not always possible, limiting interactions by avoiding biologically important habitats or reducing the duration and frequency of disturbance-inducing activities may provide individuals with an opportunity to avoid or compensate for the disturbance (see *Disturbance source characteristics*). Additionally, when preparing a risk assessment for a long-term activity, environmental conditions that affect prey availability and marine mammal distribution should be considered when known (see *Environmental conditions*).

1.3.3 Body size

Body size profoundly influences marine mammal life-history strategies because it affects the rate at which energy is acquired from the environment and how it is allocated to growth, reproduction, and survival (62). While an individual's absolute metabolic rate increases with increasing body size, its mass-specific metabolic rate decreases (63). This negative allometry between body size and metabolic rate offers a suite of benefits for large marine mammals (64), including a lower cost of transport (65) and enhanced fasting (66) and diving abilities (67). Smaller individuals or species

expend more energy per unit mass than larger ones and thus require a relatively higher resource acquisition rate to meet their metabolic demands. These species, such as sea otters and harbour porpoises (*Phocoena phocoena*), are generally non-migratory or exhibit an income breeding strategy, relying on concentrated, predictable prey year-round. In contrast, larger species, such as most mysticetes (i.e., baleen whales; suborder *Mysticeti*), have lower mass-specific metabolic rates that result in a more economical lifestyle. These species are generally migratory and exhibit a capital breeding strategy, as large body sizes enable them to undergo long migrations while fasting due to their increased energy storage capacity.

Within the context of disturbance, larger body size may be valuable in buffering against periods of reduced food availability (66, 68). For example, PCoD modelling showed that blue whales may be able to compensate for periods of decreased food availability due to their greater capacity to store energy, which allows them to fast for extended periods (13, 69). In contrast, the small size of harbour porpoises may require them to forage nearly continuously to meet their energy needs (70) (but see Booth (71)). As a result, even a moderate disturbance that disrupts foraging or increases energy expenditure could have severe fitness consequences (72). However, when prey is reduced or limited, smaller-bodied species may be better able to meet their energetic needs than larger ones because they require less food in total (64). Interactions between body size, reproductive strategy, and movement ecology ultimately add complexity to these general patterns. For example, sperm whales (*Physeter macrocephalus*) may be less resilient than whales of similar size due to their income breeding strategy coupled

with the physiological properties of their blubber (e.g., the vast majority of their blubber lipids are stored as wax esters, a less accessible source of metabolizable energy, rather than as triacylglycerols (73)). As a result, PCoD model outputs suggest that sperm whales may be poorly adapted to handle foraging disruptions (55).

The physiological constraints of body size may also affect how individuals in early life stages respond to disturbance. Among all life stages, PCoD models often identify juveniles and younger (i.e., smaller) mature females as the most sensitive groups within a population (13, 15, 55, 74). Their small body size limits the amount of energy that can be stored and, subsequently, their ability to compensate for reduced or lost foraging opportunities (75, 76). This may be particularly relevant during years of unfavourable environmental conditions or intense disturbance as younger individuals are less experienced and thus less able to respond to environmental stressors. In addition, young marine mammals have physiological limitations such as limited oxygen-carrying capacities that constrain their diving abilities (i.e., dive depth and duration) and limit their behavioural flexibility (77). Due to their small body size, PCoD models predict that juveniles will be more prone to starvation and younger mature females will be less likely to bring a pregnancy to term or successfully wean offspring (13, 15, 55, 74). Reduced energy acquisition during this important developmental period can also affect the amount of energy allocated to growth. While individuals may be able to compensate for slowed growth over time, their lifetime reproductive output could be impacted (78).

Understanding which species and life stages may be exposed can help assess which populations may be most sensitive to a disturbance-inducing activity. Among long-lived mammals, juvenile survival and fertility are the vital rates most sensitive to changes in prey availability (79, 80). Thus, a disturbance source that affects foraging may increase juvenile and offspring mortality and impact population dynamics. If the disturbance is severe, adult mortality, which has the strongest influence on population dynamics in long-lived species (79, 80), may also be impacted. Therefore, a disturbance event causing changes in adult survival, although more unlikely, has the potential to cause larger population-level effects.

1.3.4 Pace of life

PCoD models are parameterized with a population's (or related species') life-history traits, such as age at sexual maturity, interbirth interval, and lifespan, which determine the intrinsic rate of population growth, a fundamental component of population dynamics. These traits covary on a fast-slow continuum of strategies that describe how individuals allocate resources to growth, reproduction, and survival, which sets the pace of life. Thus, populations that exhibit early maturity, high reproductive rates, and short lifespans are said to lead a fast pace of life, whereas those characterized by late maturity, low reproductive rates, and long lifespans lead a slow pace of life (59, 81). A population with a fast pace of life will thus have a higher growth rate than a population with a slow pace of life, which has implications for how quickly a population can recover after disturbance disrupts vital rates.

There is considerable variation in life-history strategies across marine mammal species and populations (supplementary material, Table C3) (82). Within cetaceans, for example, harbour porpoises reach sexual maturity around 3.5 years, can reproduce annually, and generally live for 10 to 15 years (83, 84), whereas bowhead whales (*Balaena mysticetus*) become sexually mature around 25 years, reproduce every 3 to 5 years, and can live for over 100 years (85). The pace-of-life traits of otariids (i.e., sea lions and fur seals; family *Otariidae*) and phocids (i.e., true seals; family *Phocidae*) are comparatively less varied, with the average age at sexual maturity ranging from 3 to 7 years, a reproductive cycle of 1 year, and lifespans typically ranging from 20 to 40 years (86). For mysticetes and some odontocetes (i.e., toothed whales; suborder *Odontoceti*), multi-year reproductive cycles mean that a subset of the population is pregnant in any given year. In contrast, most otariids and phocids have an annual reproductive cycle (although there are some exceptions, including Australian sea lions (*Neophoca cinerea*) (87)) but have been shown to breed intermittently, so the possibility of producing one offspring per year is not always realized (88).

On the fast-slow continuum of odontocete life-history strategies, harbour porpoises are an iconic example of “life in the fast lane” (84). Due to their high metabolic requirements, reproductive success is directly tied to prey availability, meaning that harbour porpoises will reproduce annually when prey is abundant (or energy-rich) and less often when prey is scarce or absent (or energy-poor) (84, 89). Therefore, any given reproductive event is likely to be more sensitive to reduced or lost foraging. If the disturbance is severe, adult survival may also be impacted (70).

However, due to their high reproductive rate and short generation time, PCoD model simulations predicted that populations should be quick to recover following a disturbance event (49). In contrast, long-finned pilot whales (*Globicephala melas*) are an example of “life in the slow lane”, with females reaching sexual maturity around 8 to 9 years, after which they reproduce every 5 years, and live for approximately 60 years (90). Like harbour porpoises, long-finned pilot whales feed year-round and their energy reserves respond rapidly to prey availability (15), but their larger body size provides a buffer between prey patches. Therefore, under a similar disturbance scenario, any given reproductive event will likely be more resilient to reduced or lost foraging for long-finned pilot whales. However, PCoD model simulations predicted that a female’s lifetime reproductive output will decrease if the disturbance is severe (15, 91). For these populations, recovery will take longer due to their lower reproductive rate and longer generation time.

Understanding how disturbance may affect vital rates such as fecundity and survival can provide valuable insight into a population’s response to a disturbance event (74, 92) and guide mitigation or management strategies that target important life-history stages (e.g., mating, reproduction) or specific age classes (e.g., juveniles, adults) (93). Knowing a population’s life-history strategy can also be helpful when comparing the sensitivities of multiple species within a disturbed area (22). When sufficient data are not available to determine a species’ life-history strategy, species with similar paces of life may be appropriate substitutes.

1.4 Disturbance source characteristics

An individual's sensitivity to a disturbance-inducing activity is also affected by the characteristics of the disturbance source. For example, the spatial and temporal features and nature of the disturbance source (e.g., type (sonar), operational characteristics (intensity, frequency), behaviour (moving, stationary)) can interact with life-history traits and other contextual factors to influence the probability and severity of individual responses (94). In the following sections, we examine the importance of these disturbance source characteristics when assessing risk and mitigating effects (Figure 1.1).

1.4.1 Overlap with biologically important habitats

A population's sensitivity to disturbance will be strongly influenced by the importance of the disturbed area for foraging, reproduction, and migration, as shown in several PCoD models (13, 49, 57, 61, 95, 96). For example, simulations carried out by Pirotta et al. (61) found that disturbance within important foraging areas had a more dramatic effect on adult female northern elephant seal energy budgets than a similar disturbance located in less important habitat within the population's range. Thus, by leaving optimal foraging habitat undisturbed, individuals may be able to meet their energy needs even if other portions of their range are disturbed. In simulations with sperm whales, Farmer et al. (57) found that even partial closures of important habitat to seismic surveys could nearly eliminate the risk of individuals reaching terminal starvation. Ultimately, the magnitude of any effect will depend on whether similar habitat of sufficient area is available within the population's range, as well as the

temporal characteristics (see *Duration and frequency*) and nature of the disturbance source and the exposure context (see *Nature and context*).

The International Union for Conservation of Nature's (IUCN) Marine Mammal Protected Areas Task Force began identifying Important Marine Mammal Areas (IMMAs) to inform wildlife managers of the spatial and temporal extent of habitat necessary for the viability of marine mammal populations (97). Since IMMAs have yet to be identified for all populations, similar tools (e.g., the Convention on Biological Diversity's Ecologically or Biologically Significant Areas, the United States' and Australia's Biologically Important Areas, the IUCN's Key Biodiversity Areas) can be used in the interim to assess whether important marine mammal habitats overlap with proposed disturbance-inducing activities. For activities that span decades (e.g., offshore wind farms), these static spatial management tools may be less effective unless they consider ecological shifts in response to environmental variability and climate change (e.g., IMMA designations include 10-year review periods to account for climate change-related shifts (97)).

Dynamic spatial management tools, which consider the shifting nature of the ocean and its users, can also be used to identify biologically important habitats (98). An example of this flexible management approach is WhaleWatch, which uses location data (via Argos satellite transmitters) and remotely sensed environmental data (e.g., sea surface temperature, chlorophyll concentrations, wind speed) to predict where and when blue whales are likely to occur within the California Current (99). Dynamic spatial management tools such as WhaleWatch are comparatively more robust to

environmental variability and climate change because they utilize near real-time data to forecast marine mammal distributions. However, challenges include the amount of data, advanced analytical processing and modelling, and equipment maintenance required, and the need for improved data sharing and open access (98, 100). Additionally, the processes underpinning the distribution models may change, thus impacting their predictive ability (101). Nevertheless, these tools can be used to inform activity planning and the extent of closures to disturbance-inducing activities or to enact real-time management actions (57, 102).

1.4.2 Duration and frequency

The temporal features of disturbance also greatly influence the extent to which vital rates are impacted, as highlighted in several PCoD models (7, 12, 13, 15, 49, 55). For example, simulations conducted by New et al. (7) predicted that an increase in the number of disturbance days would lead to a decline in southern elephant seals' lipid mass and, subsequently, a decrease in pup weaning mass and survival. They also found that the predicted decrease in pup survival resulting from a prolonged disturbance (i.e., reducing the duration of a female's foraging trip by half) in any one year had seemingly minor impacts on the population. However, the effects of repeated exposures over a 30-year period led to a substantial decline in population size. Simulated disturbances for California sea lions yielded similar adverse effects on reproductive success, and, due to their income breeding strategy, McHuron et al. (12) found that even relatively short, infrequent disturbances adversely affected population dynamics.

PCoD models demonstrate that reducing the duration and frequency of disturbances can help mitigate any energetic consequences by allowing individuals to regain energy reserves (13, 15, 49, 55, 57). For example, Nabe-Nielsen et al. (49) found that varying the time and spatial distribution of wind farm construction in the North Sea, from ordered (where wind farms were built east to west) to random (where wind farms were built randomly), could reduce the duration of noise exposure experienced by harbour porpoises in important foraging areas. Additionally, they demonstrated that the length of breaks between piling events influenced the predicted effects of noise, where longer breaks gave individuals more time to recover. Farmer et al. (55) also found that less frequent disturbance provided opportunities for sperm whales to compensate for missed foraging, with the time to terminal starvation being roughly inversely proportional to the frequency of the disturbance event. Such information can support activity planning and area-specific caps on disturbance-inducing activities, especially within biologically important habitats (11, 57).

1.4.3 Nature and context

Marine mammals are exposed to a wide variety of human activities, including offshore energy development, military training exercises, shipping, fishing, and wildlife tourism (5). In recent years, research on behavioural responses has largely focused on the potential vulnerability of marine mammals to acoustic disturbance sources (e.g., naval sonars, seismic airguns, vessels) (39, 103), with individual responses often depending on the behaviour of the source (e.g., moving, stationary), the distance between the source and receiver, and the nature of the sound itself (e.g.,

source frequency and intensity) (94, 104), which all affect the consequences of disturbance in PCoD models (57, 96). This research has led to the development of analytical tools such as dose-response functions, which provide a framework for relating an individual's probability of responding to some metric of exposure (e.g., received sound level) (104). Several environmental factors (e.g., depth, bottom sediments, sea ice, sound speed profile of the water column) can also influence the propagation distance of the acoustic signal and thus the received sound level experienced by an individual (105).

An individual's propensity to respond and the severity of the response likely depend on additional, intrinsic factors. For example, PCoD models show that species (17), sex (55), age class (13), and body condition (61), as well as context (e.g., current behavioural state (96) or energetic state (32)), can influence the effect of disturbance on individual health and vital rates. An individual's experience can also influence the severity of response, although changes in responsiveness have yet to be incorporated into PCoD models. For example, a novel disturbance may cause an overt reaction, while prior experience may lead to habituation or sensitization (94, 104).

Disturbance sources may have radically different effects depending on both intrinsic and extrinsic factors, making it difficult to compare across scenarios. Nevertheless, generalizations can be made (as demonstrated in this synthesis) regarding which factors have the greatest effects, and an improved understanding of the underlying processes for how and why individuals respond to disturbance may allow for more accurate predictions. As outputs of behavioural response studies become

available, they should be incorporated into PCoD models and risk assessments (e.g., via improved dose-response functions) and used to develop mitigation and monitoring protocols that validate predictions (96, 104).

1.5 Environmental conditions

Environmental conditions can influence female body condition and impact reproductive success via changes in prey, from distribution and abundance to composition and caloric value (106, 107). Changes in prey availability can occur across a range of spatial and temporal scales, from hour-long tidally driven hotspots and mesoscale features that can persist for months (e.g., eddies, fronts) to ocean basin-wide shifts resulting from within- (e.g., seasonal variability) and between-year (e.g., climatic oscillations) variability (108, 109). Climate change affects these natural oceanographic and atmospheric processes (110, 111) and, subsequently, the distribution and viability of marine mammal populations (112, 113). In the following sections, we examine the importance of environmental conditions when assessing a population's sensitivity to disturbance and mediating risk (Figure 1.1).

1.5.1 Natural variability in prey availability

PCoD models show that prey availability strongly influences a population's sensitivity to disturbance (13, 15, 91). As a result, strategic planning for the timing of disturbance-inducing activities relies upon understanding the links between abiotic and biotic factors that drive marine mammal sensitivity to disturbance.

Within-year variability or seasonal changes in temperature and light level coupled with nutrient availability influence the distribution and abundance of primary producers, their consumers, and higher trophic levels (114). This results in annual cycles of high and low productivity, with higher latitudes experiencing more pronounced seasonal variation and higher ocean productivity than equatorial regions (115). In response to seasonal variability, marine mammals have evolved various behavioural and life-history strategies to maximize fitness. For example, prey availability has been shown to affect reproductive strategies, with higher food availability and seasonality favouring a capital breeding strategy (51), which is reflected in the current distribution of many marine mammal populations (116).

Capital breeders, including many mysticetes and phocids, cycle between periods of intensive foraging and fasting that are synchronized with seasonal changes in productivity (117). Because there is a limited period to acquire energy, PCoD models show that disturbance-inducing activities that reduce foraging time can affect an individual's energy balance and thus reproduction and survival (11, 13). However, the magnitude of the effect will likely depend on the proximity of the disturbance source to important foraging areas, as shown in some PCoD models (13, 61), and whether the disturbance coincides with periods of increased energy intake (118). In contrast, income breeders, including many odontocetes and otariids, rely on more predictable environments to finance their expensive lifestyle. In response to seasonal variability, many will shift their diet, change their foraging behaviour, and/or travel to more productive areas (119). However, PCoD models show that some populations may be

more spatially and/or temporally restricted in their ability to adapt to disturbance-induced changes in foraging during periods of low prey availability (15) and increased energy intake (32). As such, this has important implications for the timing of disturbance-inducing activities, particularly where prey or the environment fluctuates seasonally.

Between-year variability, including climatic oscillations, also affects prey availability by exerting large control over physical (e.g., intensity and direction of ocean currents) and biological processes (e.g., intensity and duration of bottom-up productivity) (109). Some climatic oscillations follow predictable cycles or quasi-predictable patterns, while others have no periodicity (109). One of the strongest modes of climate variability is the El Niño Southern Oscillation (ENSO), which causes increased sea surface temperature and decreased upwelling and biological productivity for up to a year on a 3- to 7-year cycle (120). Although ENSO originates in the eastern tropical Pacific Ocean, its impacts can be felt at higher latitudes (106), and its effects can be amplified significantly by coinciding with other modes of climate variability (e.g., Pacific Decadal Oscillation (PDO) (121)). Dramatic impacts on the vital rates and distribution of marine mammals due to changes in productivity have been described for previous ENSO events (75) and other climatic oscillations, such as the North Atlantic Oscillation (122), PDO (123), and Southern Annular Mode (124). A disturbance-inducing activity that overlaps with ENSO or a similar large-scale anomaly (including marine heatwaves (125)) will likely interact with the effects of these naturally occurring events. For example, Pirotta et al. (13) found that, during an ENSO event, the location,

duration, and frequency of a simulated disturbance mediated the cumulative effect on blue whale vital rates.

PCoD models show that changes in prey availability interact with disturbance sources to affect reproductive success and survival (13, 15, 91), which emphasizes the importance of timing to minimize risk when planning a disturbance-inducing activity. The outputs of PCoD models can be used to determine whether an activity can be carried out in a way that does not exacerbate the energetic impacts of local or regional environmental conditions. Model parameterization, however, will depend on the wealth of knowledge about environmental conditions. For example, the patterns that drive biophysical change on seasonal timescales are well studied and can be used to forecast prey and marine mammal hotspots (99, 126). However, the underlying forces driving climatic oscillations are less understood and more unpredictable (see Table 1 in Crespo et al. (109) for the periodicity, distribution, and characteristics of the primary climatic oscillations in the ocean). Nevertheless, identifying the climatic oscillations in the disturbed area, including the periodicity and most recent occurrence, can help wildlife managers, practitioners, and industry understand the probability of a proposed activity overlapping with these periods of reduced prey availability.

1.5.2 Climate change

Aquatic and terrestrial ecosystems are undergoing complex changes in response to climate change. Observed and predicted changes include warmer temperatures, higher sea levels, increased acidity, and reduced sea ice, as well as changes in precipitation patterns and the frequency of storms and extreme events (127). For marine

mammals, these changes may cause geographic range shifts, loss of habitat, and changes in the food web, as well as increased exposure to toxins and susceptibility to disease (112, 113). Climate change may also result in new and more frequent interactions between marine mammals and humans (128). Therefore, climate change coupled with anthropogenic disturbance may have interactive and cumulative effects on reproductive success and survival (129, 130).

While several PCoD models have examined how changes in prey availability (via natural variation or anthropogenic disturbance) affect individual vital rates and population dynamics, they have only recently started to assess the effects of disturbance occurring within a changing environment. Pirotta et al. (13) found that, in the absence of disturbance, simulated scenarios of environmental change (using changes in the frequency of ENSO and declines in productivity as proxies) could have severe consequences on the vital rates of eastern North Pacific blue whales, with females tolerating only small reductions in overall productivity and prioritizing their survival at the expense of reproduction. In scenarios with both environmental change and anthropogenic disturbance, they found that the combined effects on vital rates might be larger than in isolation.

The evolutionary history of marine mammals demonstrates their ability to adapt to ecosystem change, but long generation times restrict the rate at which evolution can occur (113). While highly mobile populations may be able to respond more rapidly to climate change through phenotypic plasticity, others may be less able to adapt and thus more sensitive to changing conditions, including populations that have specialized

diets, occupy reduced or fragmented geographic ranges, or depend on specific substrates or sites for important life-history stages (e.g., sea ice for pupping) (112, 113).

A population's vulnerability to climate change will likely be determined by the magnitude of change expected to occur within its current distribution, as well as its sensitivity to environmental change and adaptive capacity to respond (131). Climate vulnerability assessments can help identify which populations may be most vulnerable to climate change and thus more at risk to a proposed activity under changing environmental conditions, especially for activities that span several years to decades, but these assessments will remain challenging for most populations.

1.6 Data gaps and future priorities

The real-world applications of the PCoD framework have provided valuable insights into implementation challenges and data gaps, thereby guiding model development and focusing data collection (also see Pirotta et al. (2)).

The amount of data and processing time required for PCoD models can limit their direct application in decisions about proposed activities. Additionally, due to species and contextual differences, there is not a simple, "one-size-fits-all" approach for applying the PCoD framework in risk assessments. As such, its application will need to be adapted based on the data available and issue being addressed. Collaborations between modellers and wildlife managers can help identify ways to increase model accessibility and adaptability and the outputs necessary to make decisions. Furthermore, model assumptions and their influence on outputs should be made transparent to and considered by end users, such as wildlife managers and

policymakers, in subsequent decisions (see supplementary material, *Appendix B: PCoD model assumptions and limitations*). Critical data gaps for the parameterization of PCoD models include prey availability across a population's range, including abundance, variability, type, and energetic content; disturbance-related changes in physiology that compromise individual health; baseline health dynamics and how they relate to variation in vital rates; and the effect of intrinsic and extrinsic contextual factors on an individual's response to disturbance. Efforts are currently underway to systematically evaluate these gaps and inform future research to better parameterize PCoD models. In the absence of sufficient empirical data, an interim PCoD approach has been used in risk assessments and parameterized via expert elicitation to quantify the relationship between changes in behaviour and physiology to fitness (19, 132, 133).

Extensive baseline knowledge on demography is also required, including life-history parameters (e.g., population growth rate, age at first reproduction or sexual maturity) and abundance estimates (2). However, this information is not known for many marine mammal populations (but see Booth et al. (134) for how monitoring programs can be designed to collect such data), which makes quantitative population-level analyses difficult to undertake. In the absence of demographic information for the target population or a related species, first principles can be used to predict how the population may respond to disturbance (135). For example, Natrass and Lusseau (135) demonstrate how a basic understanding of a species' physiology and the productivity dynamics of the environment can be used to estimate a population's resilience to

disturbance. Many of the general principles explored in this synthesis can help inform such an assessment.

To determine whether the effects of disturbance, as predicted by PCoD models, are compatible with the conservation objective for a given population or stock, allowable harm limits also need to be established (136). This has important implications for determining whether a disturbance-inducing activity can move forward as proposed or whether mitigation strategies are needed to reduce potential effects. For example, the United States' MMPA's Potential Biological Removal (PBR) equation represents the number of individuals that can be removed annually (not including natural mortalities) while allowing the population to reach or maintain its optimum sustainable population size (137). While PBR only accounts for the cumulative effects of severe and lethal injuries by commercial fisheries, it has the potential to include non-fishery mortalities and the cumulative impact of sublethal effects. For example, the National Research Council (8) provided recommendations for how PBR can be improved to reflect total mortality losses and other cumulative impacts, including assigning severity scores to various physical injury and behavioural harassment levels. Expanding PBR to include sublethal effects is just one example of how allowable harm limits can be established.

Gauging allowable harm limits for a proposed activity requires wildlife managers to consider the cumulative effects of multiple disturbance sources (136). As such, the PCoD framework has recently been extended to include the effects of multiple disturbance sources, or stressors, that may cumulate (138). Research into the

Population Consequences of Multiple Stressors (PCoMS) framework is just beginning, and several key research needs include identifying the stressors and dosages to which individuals are exposed, determining dose-response functions to predict the effects of single stressors, and understanding the mechanistic pathways underpinning the effects of varying stressor combinations (138).

PCoD models can provide valuable insight into which contextual factors influence a population's degree of exposure and sensitivity to disturbance, including species for which data are limited and models are unavailable. By identifying emerging themes in existing PCoD models, we have highlighted general principles to consider when assessing risk. Future models could be developed for representative populations or species exposed to common disturbance scenarios to investigate broad patterns in population responses to disturbance (e.g., see New et al. (31), Reed et al. (92)). By identifying population characteristics and other contextual factors that could lead to population-level effects, model findings could be used to further guide decision making and develop mitigations that target populations most at risk or sensitive to a proposed activity. Ultimately, advancing the PCoD and PCoMS frameworks will provide wildlife managers, practitioners, and industry with the information necessary to better assess and effectively mitigate disturbance risks so that environmental and social considerations can be balanced.

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1.8 Figures

life-history traits	movement ecology	• resident: individuals occupy small home ranges compared to population's range, year-round and prolonged exposure potential • nomadic: individuals move over population's range without spatial or temporal consistency, year-round and unpredictable exposure potential • migratory: individuals undertake annual or seasonal movements between sites within population's range, seasonal exposure potential • demographic: age, sex, and reproductive status influence spatial and temporal movements
	reproductive strategy	• income breeder: feeds during lactation, vulnerable to prolonged foraging loss during lactation • capital breeder: stores energy prior to parturition for lactation, vulnerable to prolonged foraging loss during gestation
	body size	• body size: a larger body size may buffer against periods of reduced prey availability • life stage: juveniles and young mothers may be more sensitive to reduced food availability due to physiological constraints related to body size
	pace of life	• fast pace of life: reproduction is more sensitive to reduced or lost foraging, but populations will be quicker to recover due to high reproductive rates and short generation times • slow pace of life: reproduction is more resilient to reduced or lost foraging, but populations will be slower to recover, particularly if adult survival is impacted, due to low reproductive rates and long generation times
disturbance source characteristics	overlap with biologically important habitats	• the effect of disturbance is strongly influenced by whether it overlaps with biologically important habitats when individuals are present • avoiding biologically important habitats will provide opportunities for individuals to compensate for reduced or lost foraging if large portions of their range are disturbed
	duration and frequency	• continuous disruption will have a greater impact than intermittent disruption • reducing the duration and frequency of disturbance or incorporating breaks between disturbance events may allow individuals to recover • energy loss can be translated into days of disturbance to inform area- or population-specific disturbance caps
	nature and context	• the probability and severity of individual responses depends on the interactions between the type and nature of the disturbance source and the context of the exposure • incorporating context into risk assessments can significantly reduce the uncertainty in managing populations and mitigating effects
environmental conditions	natural variability in prey availability	• sensitivity to disturbance strongly depends on the availability of prey in the environment • avoiding periods of low productivity and increased energy intake can reduce the potential for interactive and cumulative effects
	climate change	• climate vulnerability assessments can help identify populations most vulnerable to climate change and the factors contributing to their vulnerability • climate change coupled with disturbance may have interactive and cumulative effects that affect reproductive success and survival

Figure 1.1. Emerging themes in Population Consequences of Disturbance models that should be considered when assessing the likelihood and duration of exposure and the sensitivity of a population to disturbance.

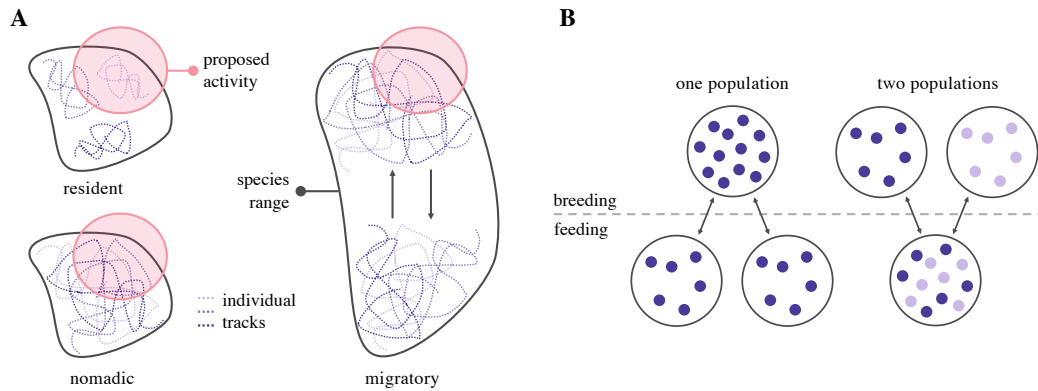


Figure 1.2. (A) A population's movement patterns can help determine the degree of exposure to a disturbance-inducing activity. When comparing resident and nomadic movement patterns, the same disturbed area could frequently expose a few resident individuals while infrequently exposing many nomadic individuals. In contrast, many individuals of a migratory population could be exposed, but exposure would be seasonal. Figure adapted from Costa et al. (25). (B) Migratory populations may share common foraging grounds or reproductive areas, which influences whether a single population, a fraction of a population, or multiple distinct populations will be exposed to a disturbance-inducing activity. If individuals share a common reproductive area but return to unique foraging grounds, individuals constitute one population representing one demographic breeding unit. Alternatively, if they share a common foraging ground but return to unique reproductive areas, they represent two or more demographically distinct populations.

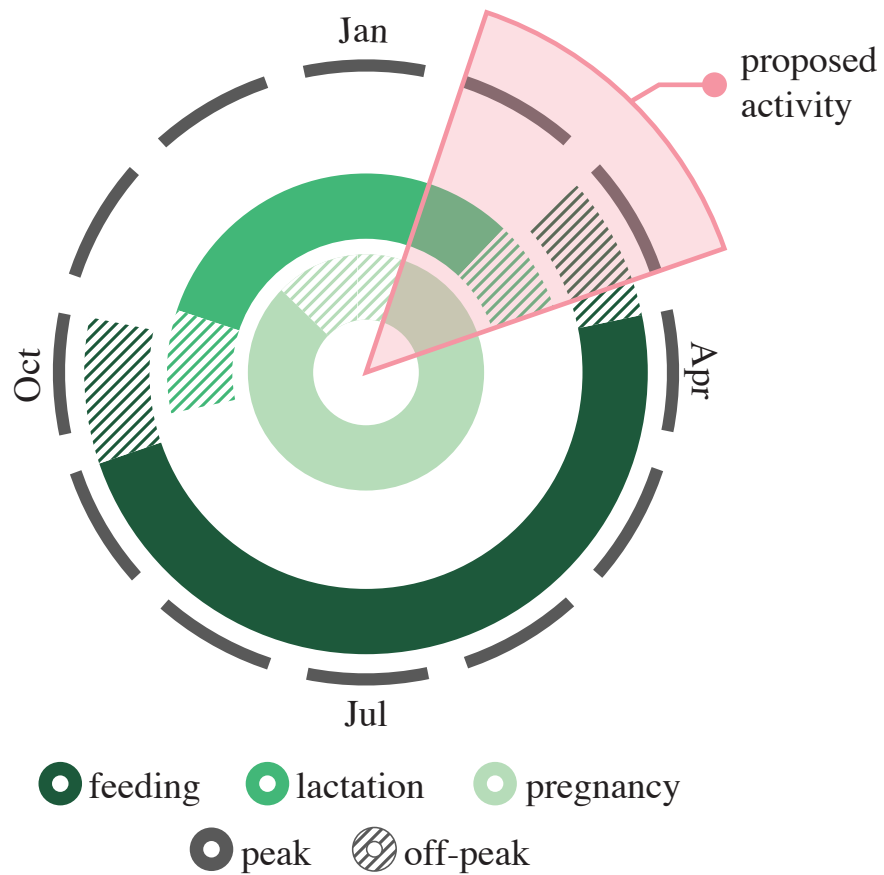


Figure 1.3. A reproductive cycle plot for a North Atlantic minke whale (*Balaenoptera acutorostrata*) showing the variability in the timing and duration of life stages for a 1-year reproductive cycle. The wedge represents a proposed disturbance-inducing activity occurring for approximately 2 months. Reproductive cycle plots can help identify the temporal overlap between sensitive life-history events and a proposed activity. Figure adapted from Wilson et al. (22) and informed based on Christiansen et al. (56).

1.9 Supplementary material

1.9.1 Appendix A: Applicability to other species

The Population Consequences of Disturbance (PCoD) framework is a conceptual model that can be used to assess the population consequences of non-lethal changes in behaviour and physiology. Although originally developed to assess the risks to marine mammal populations from anthropogenic noise (particularly naval sonar), it has since been used to explore the effects of other disturbance sources (e.g., wildlife tourism, renewable energy developments, and vessels) and can, in principle, be applied to other vertebrate species. The literature on the effects of anthropogenic disturbance on the behaviour of non-marine mammal taxa is extensive (1-3). In addition, many studies have linked disturbance-induced changes in behaviour to reproductive success and survival (4-6) and quantified the long-term effects on population dynamics (7-10). As such, these studies could be reformulated following the PCoD framework.

Many of the emerging themes reviewed in this synthesis are not unique to marine mammals and can be used to guide risk assessments for other vertebrate species. For example, we describe movement patterns that are prevalent across widely disparate taxa, regardless of body size, mode of movement, or environment (11), and can be used to determine the degree of exposure to a disturbance-inducing activity. If exposure is likely, sensitivity can be assessed by understanding how parents acquire and allocate resources to offspring. The concepts of capital and income breeding have been used to describe reproduction in other taxa (12-15), and where a population falls on this continuum can be used to determine whether a proposed activity overlaps with sensitive

reproductive stages. Body size can also help assess sensitivity to disturbance, particularly among vertebrates where an individual's mass-specific metabolic rate decreases with increasing body size (16). Thus, a larger body size may provide a temporary buffer during disturbance events that result in reduced or lost foraging opportunities. Pace of life is also a concept that has been broadly applied across vertebrates (17) and can be used to assess how disturbance can affect population growth via changes in vital rates.

The influence of disturbance source characteristics and environmental conditions emerging from this synthesis is also broadly applicable across vertebrate species, although the specific tools (e.g., the International Union for Conservation of Nature's (IUCN) Important Marine Mammal Areas) or environmental processes (e.g., El Niño Southern Oscillation) discussed may be specific to marine mammals or to marine or coastal environments. Nevertheless, similar spatial tools exist in terrestrial and freshwater habitats (e.g., the United Nations Environment Programme's and IUCN's World Database on Protected Areas, BirdLife International's Important Bird and Biodiversity Areas) and can be used to assess the overlap between a proposed activity and important habitats for critical life-history stages. Additionally, environmental conditions, such as interannual variability (18) and drought events (19), can influence female body condition and impact reproductive success in other vertebrates. Considering such conditions, when known, can guide activity planning that reduces overlap with sensitive periods. Ultimately, limiting or avoiding exposure to repeated or continuous disturbance in biologically important habitats and during

periods of reproductive sensitivity and low prey availability may reduce the potential for population-level effects.

1.9.2 Appendix B: PCoD model assumptions and limitations

Population Consequences of Disturbance (PCoD) models require a substantial amount of information to be adapted to a specific disturbance scenario. Even for populations where a large body of empirical data exists, many uncertainties remain. As a result, assumptions about model parameters (e.g., life-history traits) and underlying mechanisms (e.g., how disturbance impacts foraging rates) are made, which can influence model results. For example, PCoD model outcomes are sensitive to parameters related to prey or the environment, density dependence, exposure rates, energetics, the amount of time spent feeding (i.e., activity budgets), individual morphology, and the context-dependency of behavioural responses (20-23). Therefore, it is important that the uncertainties associated with model assumptions are documented, and that the effects of these uncertainties on model predictions are quantified (24-26). For example, uncertainty can be propagated in PCoD models using Monte Carlo simulations (27, 28). If uncertainty is not explicitly incorporated into the model, a sensitivity analysis can be performed *post hoc* to examine how changes in parameter values influence model results (20, 21, 29, 30). Model predictions can then be presented as a distribution of potential outcomes. This will ensure that the precautionary principle is applied when using PCoD model results to inform management and policy decisions (26).

In addition, most applications of the PCoD framework have focused on the behavioural-bioenergetic pathway (i.e., mediated by changes in energy acquisition or expenditure) (20, 28, 31), but some stressors may operate along other pathways. For

example, physiological responses, such as increased stress levels (32) or temporary reductions in hearing (33), can affect an individual's behaviour as well as lead to chronic effects on individual health and vital rates (24, 25). However, measuring physiological responses to disturbance is challenging for most marine mammal species because it requires extensive baseline measurements and repeated samples from individuals (25, 34). As a result, most PCoD models have not explicitly considered the physiological consequences of disturbance.

Most PCoD models have also only considered sources of disturbance in isolation. However, multiple sources of anthropogenic and environmental disturbance are likely to act concurrently in any one area. Similarly, PCoD models currently focus on a single species and do not include critical interspecific interactions, such as competition, that may affect the response to disturbance. Consequently, this requires a non-trivial extension of the PCoD framework to capture the effects of multiple ecological interactions and disturbance sources or stressors (25). A conceptual framework for the Population Consequences of Multiple Stressors has recently been considered (25), but research is just beginning. Future research will provide valuable information regarding the functional links between multiple ecological interactions and sources of disturbance and their potential population-level effects (see *Data gaps and future research priorities*).

Individual heterogeneity has also not been explicitly considered in most PCoD models but can affect the overall sensitivity of a population to a disturbance event. For example, recent work on northern elephant seals (*Mirounga angustirostris*) indicates

that a small number of females have high survival and thus produce a disproportionately large number of offspring, while other females with low survival make little contribution to the population (35). Thus, some females may be particularly robust and, as a result, a disturbance impacting these females may have a more limited effect on the population as a whole. Additionally, an individual's propensity to respond and the severity of the response may vary over time depending on factors such as body condition and current behavioural state (36, 37). Prior experience with a stressor may also lead to changes in responsiveness, including habituation or sensitization (see *Nature and context*) (38, 39). Thus, how and when an individual responds to disturbance will impact whether a disturbance event has a significant effect on the population.

Finally, the spatial and temporal scale of the data and the management or policy question being addressed can differ from the scale of the model, resulting in a scale mismatch. For example, marine mammal tracking data are often collected at fine scales (e.g., at a spatial scale of metres and temporal scale of seconds) but incorporating such data into a model to make fine-resolution predictions can become computationally challenging (e.g., due to computer memory and run time limitations), especially for long-lived migratory species with ranges that span hundreds to thousands of kilometres. As a result, PCoD models are often coarser than the data available (20, 30). This can affect the spatial and temporal resolution of the model outputs and, subsequently, the scale at which they can be applied to inform conservation and management decisions.

1.9.3 Appendix C: Tables and figures

Table C1. Summary of Population Consequences of Disturbance (PCoD) model publications that met our synthesis criteria (i.e., models that quantify the non-lethal effects of anthropogenic disturbance on marine mammal vital rates via the behavioural-bioenergetic pathway). Information is provided on species and citation, and if included in the models, life-history traits (M = movement ecology, R = reproductive strategy, S = body size, P = pace of life), disturbance source characteristics (B = overlap with biologically important habitats, D = duration and frequency, N = nature and context), and environmental conditions (V = natural variability in prey availability, C = climate change) are noted.

Species	References	Life-History Traits	Disturbance Source Characteristics	Environmental Conditions
Cetaceans				
<i>Balaenoptera acutorostrata</i>	(40)	M, R	D	
	(30)	M, R, S, P	B, D, N	V, C
	(20)	M, R	B, D, N	V
<i>Balaenoptera musculus</i>	(41)	M, S, R, P	B, N	V, C
	(27)	M, R, P	D	
<i>Eschrichtius robustus</i>	(28)	M, R	D	
	(42)	R, S, P	D	V
<i>Globicephala melas</i>	(43)	R, S, P	D	V
	(44)	M, R, S, P	N	
<i>Megaptera novaeangliae</i>	(45)	S, P		V
	(46)	R	B, D	
<i>Mesoplodon densirostris</i>	(47)	M, R, S, P	D, N	V
	(45)	S, P		V
<i>Orcinus orca</i>	(22)	M, R, S, P	N	V
<i>Phocoena phocoena</i>	(48)	M, R, S, P	D	V
	(49)	M, R, S, P	B, N	
	(50)	M, R, S, P	D	V

Species	References	Life-History Traits	Disturbance Source Characteristics	Environmental Conditions
	(51)	M, R, S, P	N	
<i>Physeter macrocephalus</i>	(52)	M, R, S, P	B, D, N	
	(53)	R, S, P	D	
<i>Tursiops aduncus</i>	(54)	R, S, P	D, N	V, C
	(55)	M, R, S	D, N	
<i>Tursiops truncatus</i>	(56)	M	B, D, N	V
Pinnipeds				
<i>Eumetopias jubatus</i>	(57)	R, S, P	D, N	V
<i>Halichoerus grypus</i>	(58)	R, S, P	D	V
<i>Leptonychotes weddellii</i>	(59)	R, P		V
	(60)	M, R	B, D	
<i>Mirounga angustirostris</i>	(61)	M, R	N	
	(31)	M, R, P	D	
<i>Mirounga leonina</i>	(62)	M, R, S, P	D	
<i>Phoca vitulina</i>				
<i>Pinnipedia</i>	(29)	R, S	D, N	

Table C2. Movement patterns and reproductive strategies exhibited by 20 families of marine mammals. An X indicates that the family generally exhibits that movement or reproductive pattern, recognizing that these categories are not mutually exclusive and there may be variation between individuals in a population (e.g., based on sex or age class) and different populations of the same species.

Order/Suborder, Family	Movement Patterns		Resident	Reproductive Strategies		References
	Migratory	Nomadic		Capital	Income	
Mysticeti						
Balaenidae (right whales and bowhead whale)	X			X		(63, 64)
Balaenopteridae (rorquals)	X	X		X ¹		(65, 66)
Eschrichtiidae (grey whale)	X			X		(67)
Neobalaenidae (pygmy right whale)	X ²			X ³		(68-70)
Odontoceti						
Delphinidae (dolphins)	X	X	X		X	(71-74)
Iniidae (Bolivian, Amazon, and Araguaian river dolphins)	X		X		X	(75-77)
Kogiidae (pygmy and dwarf sperm whales)	X ⁴	X ⁴	X ⁴		X	(78-81)
Monodontidae (beluga and narwhal)	X	X	X		X	(82-85)
Phocoenidae (porpoises)	X	X	X		X	(86-88)
Physeteridae (sperm whale)	X	X			X	(89, 90)
Platanistidae (Ganges and Indus river dolphins)	X		X		X	(91-93)
Pontoporiidae (La Plata river dolphin)			X		X	(94, 95)

Order/Suborder, <i>Family</i>	Movement Patterns			Resident	Reproductive Strategies		References
	Migratory	Nomadic	Capital		Income		
<i>Ziphiidae</i> (beaked whales)		X		X	X ⁵	X	(96-98)
Pinnipedia							
<i>Odobenidae</i> (walrus)	X					X ⁶	(99-101)
<i>Otariidae</i> (sea lions and fur seals)				X		X	(102)
<i>Phocidae</i> (true seals)	X				X ⁷		(103)
Fissipedia							
<i>Mustelidae</i> (sea otters)				X		X	(104)
<i>Ursidae</i> (polar bear)	X				X ⁸	X	(105-108)
Sirenia							
<i>Dugongidae</i> (dugong)	X		X			X	(109-111)
<i>Trichechidae</i> (manatees)	X			X		X	(112, 113)

Notes:

¹ Not all balaenopterids are “true” capital breeders. Some populations like the eastern North Pacific blue whale (*Balaenoptera musculus*) continue feeding in reproductive areas (114).

² Information on the movement ecology of the pygmy right whale (*Caperea marginata*) is limited and sightings have rarely been reported. Year-round strandings within its range suggest that pygmy right whales do not undertake the seasonal north-south migration characteristic of many mysticetes (68). However, seasonal inshore movements have been observed and may be related to the availability of prey in the spring and summer, with individuals recorded close to shore for up to 2 months (69, 70).

³ Information on the life history of the pygmy right whale (*Caperea marginata*) is limited. Pygmy right whales are similar in size to minke whales (*Balaenoptera acutorostrata*), a slightly larger mysticete that exhibits a capital breeding strategy (115). Thus, with limited information and using minke whales as a proxy, the pygmy right whale is described herein as a capital breeder.

⁴ Dwarf sperm whales (*Kogia sima*) and pygmy sperm whales (*Kogia breviceps*) are difficult to site and distinguish from one another during sightings surveys at sea and, as a result, are often categorized together as *Kogia* spp. (79). Much of what is known about the distribution of *Kogia* spp. has been inferred from stranding records (79). For example, in the northeast Atlantic Ocean, strandings occur in the fall and winter, which could indicate a seasonal presence in the region (79). Seasonal inshore-offshore

use has also been observed for dwarf sperm whales in the Bahamas (78). Data also suggest that a small resident population of dwarf sperm whales is present off Hawai'i (81). Given their pelagic distribution (79), some populations may also exhibit nomadic movement patterns.

⁵ Species in the family *Ziphiidae* are behaviourally income breeders but exhibit capital breeding tactics during gestation and lactation (56, 116).

⁶ Although female walrus forage during lactation, they rely on stored energy reserves during the first month of lactation (101).

⁷ Not all phocids are "true" capital breeders. Some species like Weddell (*Leptonychotes weddellii*), Mediterranean monk (*Monachus monachus*), Hawaiian monk (*Neomonachus schauinslandi*), ringed (*Pusa hispida*), and harbour (*Phoca vitulina*) seals include some degree of supplemental feeding during lactation (117-120). However, the energy expended during lactation for these species is primarily supplied by stored energy reserves (except for the Mediterranean monk seal) (103).

⁸ Female polar bears (*Ursus maritimus*) fast and rely on stored energy reserves during active gestation and early lactation (105, 106).

Table C3. Selected pace-of-life traits exhibited by females across 20 families of marine mammals, including growth (age at sexual maturity), reproduction (length of gestation, lactation, and the interbirth interval), and survival (maximum estimated or recorded lifespan, unless otherwise noted).

Order/Suborder, <i>Family</i>	Growth	Reproduction		Survival		References
	Age at Sexual Maturity (years)	Gestation (months)	Lactation (months)	Interbirth Interval (year(s))	Maximum Lifespan (years)	
Mysticeti						
<i>Balaenidae</i> (right whales and bowhead whale)	8-9 (right, mean) 25 (bowhead)	11-12 (right) 13-14 (bowhead)	6-12	3-4	70 (right, min) 140 (bowhead)	(63, 64, 121-124)
<i>Balaenopteridae</i> (rorquals)	5-10	10-12	3-12	1-3	50-95	(65, 125-128)
<i>Eschrichtiidae</i> (grey whale)	6-12	11-13	7-8	2	77	(67, 129)
<i>Neobalaenidae</i> (pygmy right whale)	Unknown (at lengths >5 m)	Unknown	5	Unknown	Unknown	(68)
Odontoceti						
<i>Delphinidae</i> (dolphins)	6-16	9-16	8-27	1-8	20-80	(130, 131)
<i>Iniidae</i> (Bolivian, Amazon, and Araguaian river dolphins)	6-10	12.3-13	18-70, 33.6 (mean)	2-7.7, 4.6 (mean)	35+	(75, 132)
<i>Kogiidae</i> (pygmy and dwarf sperm whales)	3-5	11-12	12-24	1-2	22	(79, 133)

Order/Suborder, Family	Growth		Reproduction			Survival		References
	Age at Sexual Maturity (years)	Gestation (months)	Lactation (months)	Interbirth Interval (year(s))	Maximum Lifespan (years)			
<i>Monodontidae</i> (beluga whale and narwhal)	8-13 (beluga) 8-9 (narwhal)	14-14.5 (beluga) 11-15 (narwhal)	12-24	3	60-80 (beluga) 101 (narwhal)			(82, 84, 134-136)
<i>Phocoenidae</i> (porpoises)	3-7	10-12	7-12	1-2	10-30+			(86, 137-141)
<i>Physeteridae</i> (sperm whale)	9	14-16	24-25	5	50 (min)			(89, 142)
<i>Platanistidae</i> (Ganges and Indus river dolphins)	≥10 (170 cm)	12	<12	Unknown	30-35			(143, 144)
<i>Pontoporiidae</i> (La Plata river dolphin)	2-5	10.5-11.2	9	1.5-2	21			(94, 145, 146)
<i>Ziphiidae</i> (beaked whales)	7-11	12-17	6-48	2 (min)	39			(147-152)
Pinnipedia								
<i>Odobenidae</i> (walrus)	4-12, 6 (mean)	15-16	24-36	2-4	44			(99, 153-155)
<i>Otariidae</i> (sea lions and fur seals)	2-8, 3 (mean)	8-9	4-36	1-3	20-30			(155-162)
<i>Phocidae</i> (true seals)	2-9, 4-6 (mean)	9	0.01-5	1	20-56			(155, 163-169)
Fissipedia								
<i>Mustelidae</i> (sea otters)	3	6	6	1	15-20			(104, 170)
<i>Ursidae</i> (polar bear)	4-5	6.3-8.5	24-30	2-3	25-30			(105, 106, 171, 172)

Order/Suborder, <i>Family</i>	Growth	Reproduction			Survival		References
	Age at Sexual Maturity (years)	Gestation (months)	Lactation (months)	Interbirth Interval (year(s))	Maximum Lifespan (years)		
Sirenia							
<i>Dugongidae</i> (dugong)	9-10	14	18	3-7	50-73	(109, 110, 173)	
<i>Trichechidae</i> (manatees)	2-4	11-14	12-24	2.5 (mean)	60	(112, 174, 175)	

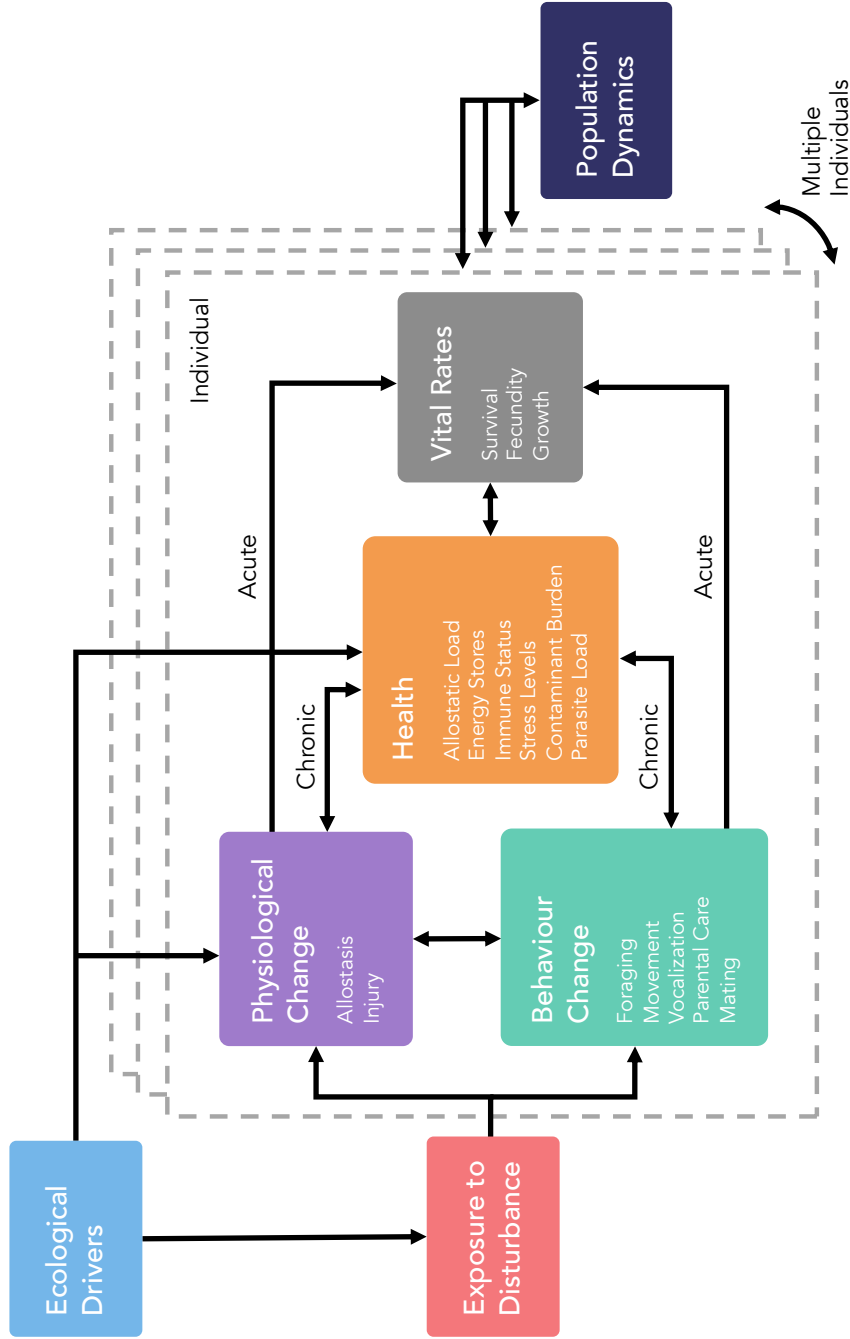


Figure C1. The Population Consequences of Disturbance (PCoD) framework. The boxes within the dashed gray boundary line represent the effects of exposure to a stressor and a range of ecological drivers on the vital rates of an individual animal. The effects are then integrated across all individuals in the population to project their effects on the population's dynamics. Figure adapted from Pirodda et al. (26).

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Chapter 2: Effects of reduced krill availability on humpback whales along the western Antarctic Peninsula

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2.1 Abstract

Climate-driven and human-induced changes in prey affect top predators' health and population dynamics globally. In the Southern Ocean, Antarctic krill are a vital component of the food web, supporting numerous marine predators and the region's largest commercial fishery. In recent years, the krill fishery has become more concentrated along the western Antarctic Peninsula, raising concerns about the effects of local krill depletion on baleen whales, which are not included in the current krill management strategy. To address this gap, we developed an individual-based model within a stochastic dynamic programming (SDP) framework to explore how changes in prey availability, mediated by climate change and krill fishing stressors, affect the population dynamics of humpback whales, one of the largest krill consumers in the region. Within the SDP framework, we simulated stressors using a Monte Carlo approach. We tracked individuals' reproductive and movement decisions over 25 years to quantify the effect of stressors on key population vital rates. Emergent model properties included migratory movements, seasonal fluctuations in body condition, and reproductive strategies, consistent with observed humpback whale behavior. Stressors had varying effects on pregnancy, birth, and weaning success rates depending on the severity of the krill reduction and whether both stressors were present. Across simulations, the effects were greatest during years when krill availability was already

poor due to natural variability. In multiple stressor scenarios, synergistic interactions had greater effects than in isolation, with some populations crashing before the end of the simulation. While the effects of climate change cannot be directly managed, potential effects may be mitigated by adaptively managing human activities in the region, such as krill fishing. This tool provides a general framework to predict the impact of multiple stressors on humpback whale population dynamics.

2.2 Introduction

Climate-driven and human-induced changes in prey affect top predator's health and population dynamics globally. Reductions in both prey abundance and quality compromise predator health and cause nutritional stress, which have been linked to reductions in reproductive success and survival (1-3). In addition, changes in the distribution of prey are causing some populations to deviate from seasonal foraging patterns, which has increased foraging effort and interactions with humans (4, 5). In the polar regions, particularly the western Antarctic Peninsula (AP), climate is changing more rapidly than elsewhere, altering the physical landscape due to melting sea ice and increasing human access (6-8). Sea ice plays a significant role in regulating the regional and global climate. It also provides critical nursery and feeding habitats for predators and their prey. As a result, changes in sea ice conditions will also have catastrophic ecological effects that affect a wide variety of species from the smallest crustaceans to the largest cetaceans (8, 9).

In the Southern Ocean, Antarctic krill (*Euphausia superba*; hereafter krill) are a vital component of the food web, supporting marine predators such as fish, penguins,

pinnipeds, and whales (10). Krill are also the target species for the largest commercial fishery in the region (11). Most krill are harvested in the southwest Atlantic (Area 48), which includes the AP (Subarea 48.1), an essential area for krill and krill consumers to feed and reproduce (10, 12). In recent years, krill catches have become more concentrated in this region, particularly along the western AP (13), raising concerns about the local depletion of krill and its potential effects on krill consumers (14-17). With proposed expansions to the krill fishery (18), there is an urgent need to better understand the behaviors and energy needs of krill consumers to inform management strategies that fully consider and adequately protect the structure and function of the Antarctic ecosystem (15, 16, 19).

The krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which has adopted an ecosystem-based, precautionary approach to management whereby catch limits and predator-prey interactions are modeled and monitored to account for the effects of harvesting on krill consumers (20). However, CCAMLR's current management approach does not include the largest Antarctic krill consumers, baleen whales (20). When the Commission was established, baleen whale populations were depleted to such levels that management primarily focused on land-based krill consumers. However, since the end of commercial whaling, most populations of baleen whales are increasing (21), with others recovering to pre-exploitation levels (22). Baleen whales play a critical ecological role in the Southern Ocean, promoting a thriving marine food web and increasing ecosystem productivity by fertilizing the ocean and moving nutrients within

the water column (23, 24). Thus, for CCAMLR's management strategy to be genuinely ecosystem-based and precautionary, baleen whales must now be included.

Humpback whales (*Megaptera novaeangliae*) (breeding stock G) are one such population experiencing rapid population growth following the cessation of whaling (22, 25). This breeding stock, which is managed by the International Whaling Commission, migrates annually from low-latitude, winter breeding areas off the western coast of South and Central America (from Peru to Costa Rica) to high-latitude, summer feeding areas along the western AP (Figure 2.1). As primarily capital breeders, humpback whales rely on stored energy acquired on the feeding grounds to finance the costs of migration and reproduction on the breeding grounds (26). For reproductive females, this includes storing additional energy or "capital" to support part of gestation and early lactation (26). As a result, reproductive success largely depends on access to abundant krill on the feeding grounds (25, 27), and declines in krill thus have particular relevance to this stock. Throughout the feeding season, the spatial distribution of humpback whales, as well as the krill fishing fleet, is tightly coupled to that of krill (28). In the late spring through summer months, krill are broadly distributed across the continental shelf in discrete patches (29). In the fall and early winter months, when most krill are caught by the fishery (13, 30), krill move into bays and fjords, forming large, dense aggregations before the formation of winter sea ice (31). During this period, when catch and effort are more concentrated in space and time, competition with the krill fishery will likely be greatest. Climate change may also affect krill growth and abundance in the region due to declining sea ice, warming temperatures, and ocean

acidification (32-34), with the western AP already experiencing localized declines in krill and poleward shifts in their distribution (35). As a result, krill fishing in a changing environment may lead to new, synergistic interactions that affect the predator-prey dynamics of humpback whales and krill in the region.

Here, we developed an individual-based model (IBM) within a stochastic dynamic programming (SDP) framework to explore how climate- and fishery-driven changes in krill availability affect the population dynamics of humpback whales that feed along the western AP. SDP has received increased attention in recent years as a method to implement the Population Consequences of Disturbance (PCoD) framework due to the flexibility it provides for exploring how an individual's current physiological state (e.g., energy stores, reproductive status) and changes in the environment (e.g., prey availability, the addition of a stressor) affect life-history rates (e.g., pregnancy rate, birth rate, weaning success rate), which can lead to cumulative population-level effects (e.g., population growth rate) (36, 37). In this model, reductions in krill availability were mediated by climate change and krill fishing. We modeled climate change as a stressor in isolation (i.e., single stressor) and in combination with krill fishing (i.e., multiple stressors) to examine their effects on reproductive success and survival. While the impact of climate change on krill and humpback whales cannot be directly managed, potential population consequences may be mitigated by adaptively managing human activities, such as krill fishing, in the region. As such, identifying periods when individuals may be most vulnerable to disturbance can inform management actions that ensure this previously over-exploited population continues to recover.

2.3 Methods

2.3.1 Model overview

Our SDP model was comprised of two steps: a backward iteration and a forward simulation (see *Appendix A: SDP conceptual diagram*). In the backward iteration, optimal behavioral and reproductive decisions that maximize an individual's fitness (e.g., reproductive success, survival) were identified. These optimal decisions, which are emergent properties of the model, were functions of time (t), the individual's physiological state (i.e., female body condition, x , reproductive state, r , and, when applicable, calf body condition, m), its location (l), and the external prey environment (i.e., krill regime, e). The output from the backward iteration was then summarized in decision matrices used in Monte Carlo forward simulations to predict an individual's fitness in the absence and presence of one or multiple stressors (38-40). The stressors modeled were assumed to be novel stimuli that were not part of the whale's evolutionary history (41-43); as such, this approach allowed us to model the mismatch in what a whale expected to encounter (based on the backward iteration) and the environment it actually experienced (in the forward simulation). Both behavioral and reproductive decisions were modeled on a daily time step.

The behavioral strategies considered for each time step depended on the whale's location (i.e., feeding grounds, breeding grounds, or migratory corridor). On the feeding and breeding grounds, a whale could stay in its current location or move into the migratory corridor to begin migration. Movement within the feeding and breeding grounds was modeled implicitly. Still, costs were incurred (see *A whale's physiological*

state, below), but there was no change in location (*l*) because the distribution of krill on the feeding grounds and humpback whales in both areas is poorly understood. However, movement within the migratory corridor was modeled explicitly to allow the timing of migration to be an emergent property of the model. As such, when in the migratory corridor, a whale could move forward (south) or backward (north). The migratory corridor was comprised of 59 cells based on the mean distance traveled by tagged individuals between the feeding and breeding grounds (6,700 km (44)) and a mean migration speed recorded for this species (4.65 km/hour (45)).

The reproductive strategies considered for each time step depended on the whale's current reproductive state. Over the course of her life, a female humpback whale could be in one of five reproductive states: (1) non-reproductive juvenile (i.e., not sexually mature), (2) non-reproductive adult (i.e., sexually mature, not pregnant and/or lactating), (3) pregnant, (4) lactating, or (5) pregnant and lactating (22, 25). Transitions from being pregnant and/or lactating to a non-reproductive adult or from being pregnant and lactating to pregnant could occur at any time if the optimal strategy were to terminate the pregnancy or wean the calf early. We modeled a female whale reaching sexual maturity at five years old and remaining reproductively active for 75 years (i.e., no senescence (46)), assuming an average maximum lifespan of 80 years (47, 48).

The model included biologically meaningful constraints specific to reproduction to address computer memory limitations and reduce model run times. Birth and implantation could only occur on the breeding grounds, with a fixed date of

August 1 and August 15, respectively, to allow for a gestation period of 11.5 months (49). Additionally, all lactating females were constrained to the breeding grounds for the first 50 days of their newborn calf's life to account for potential benefits such as thermoregulation (although this has been debated (50, 51)) and restrictions on its swimming abilities (52). Although the residence time for mothers and calves on the breeding grounds is unknown, 50 days represents the mean of the longest time between resights of mother-calf pairs offshore Hawaii (39 days (53)) and Ecuador (61 days (54)). Furthermore, lactation could occur for the first 10.5 months of a calf's life (47, 49), after which the calf is added to the population and begins to feed autonomously. If a calf was weaned early, it had to rely on stored energy reserves until it reached weaning age. Finally, in the final year of life, a female could only be in a non-reproductive adult or lactating state.

We used optimal behavioral and reproductive decisions from the backward iteration in Monte Carlo simulations to model the state dynamics of humpback whales under different stressor scenarios and predict the consequences of disturbance on reproductive success and survival (the forward simulation). We defined reproductive success as the number of female calves per mature female that were successfully weaned and added to the population, assuming a 50:50 sex ratio at weaning to determine whether the calf was female. The backward iteration and forward simulation, as well as all statistical analyses and visualizations, were coded in R (version 4.3.1) (55) using the following packages: *foreach* (56), *doParallel* (57), *abind* (58), *qs* (59),

popbio (60), dplyr (61), tidyverse (62), ggplot2 (63), cowplot (64), sf (65, 66), and rnaturalearth (67).

2.3.2 A whale's physiological state

We used body condition (percentage of blubber mass as a portion of total body mass) to characterize a female's physiological state, and that of her calf if she was lactating, at the start of each day. We set minimum (5% (68-70)) and maximum (45% (71-74)) thresholds for female and calf body condition. If body condition fell below the minimum threshold, we assumed the whale died from starvation. Changes in body condition from one time step (t) to the next ($t + 1$) depended on energetic costs and gains (if any) from foraging or, in the case of the calf, from nursing (see *Appendix B: Physiological equations and parameters*).

The potential energetic costs incurred on a given day fell into one of three categories: (1) metabolic costs (i.e., field metabolic rate, FMR), (2) growth costs, and (3) reproductive costs, including gestation and lactation. Metabolic costs reflected the energy requirements for maintenance and were calculated based on a whale's "ideal" body mass (estimated from a regression analysis of mass vs. length (47, 71, 72, 75-77)) and respiration rate (78-81), which depended on its current reproductive state (non-lactating or lactating) and activity level (informed by the whale's location: feeding ground, migratory corridor, or breeding ground). In addition, if a whale was migrating, its FMR during migration, mean swim speed (4.65 km/hour (45)), and total body mass were used to calculate the cost of locomotion (82). Growth costs were determined based on a whale's increase in body mass each day using the mass-length regression analysis

and lean tissue's energy density and deposition efficiency (83, 84). Finally, for pregnant whales, gestation costs included those associated with fetal tissue and the heat of gestation (85, 86). For lactating whales, lactation costs were determined by the energetic needs of the calf but were capped at the maximum amount of milk the female could deliver per day (125 kg (87)).

A whale could gain energy on the feeding grounds by feeding on krill. The amount of energy a whale could gain on a given day was a function of its forestomach capacity (88), the number of times the forestomach could be filled (88), the energy density of krill (4,575 kJ/kg (89)), and the energy remaining after fecal and urinary energy losses (i.e., metabolic efficiency; 85% (90, 91)). The number of times a whale's forestomach could be filled depended on the time available to feed (hours per day; see *Prey environment*) and the feeding rate (lunges per hour) (92). Feeding rate was a function of the whale's forestomach capacity, the size of its buccal cavity (93), the krill density encountered, and the prey-specific capture efficiency (90% (94)). A whale's forestomach capacity and the size of its buccal cavity were both functions of its body length.

If a whale met its energetic needs (and those of its offspring, when applicable) on a given day, she stored the remaining energy as blubber. However, if she did not acquire enough energy, she relied on her energy reserves to meet her energetic requirements (and those of her offspring, when applicable). Additionally, if the whale was lactating and did not have enough energy to support her calf, she ceased delivering

milk. Finally, if her body condition fell below the minimum threshold, she died of starvation.

2.3.3 Prey environment

The prey environment was modeled to reflect the seasonal and interannual variability of krill found in the environment. As such, on a given day, a whale had the probability $p_k(e, l, t, k)$ of encountering krill density k , which depended on the current krill regime, e , its location, l (on the feeding grounds or not; if not, $p_k(e, l, t, k) = 0$), and time, t , since prey densities also varied seasonally.

Discrete krill biomass estimates (kg/m^3), their encounter probabilities, and seasonal availability were characterized using information from frequency distributions of mean biomass in Lascara et al. (95). Initial runs of the model revealed unrealistic reproductive outputs, leading us to scale these biomass estimates by 65% to better reflect the krill densities targeted by whales in the region (31, 96) (Table 2.1). We defined seasons in the model with respect to the feeding season: early (November–January), mid (February–April), late (May–July), and post (August–October). This varies slightly (by one month) from how seasons are defined in Lascara et al. (95), with spring, summer, fall, and winter corresponding to early, mid-, late, and post-feeding seasons. This approach was taken to capture the dense aggregations of krill available late in the feeding season, which whales appear to feed on into July (15).

Long-term abundance anomaly estimates for krill in Steinberg et al. (97) were used to inform the magnitude of interannual variability in the model. We created three krill regimes (i.e., low, medium, and high); the scaled biomass estimates from Lascara

et al. (95) represented the medium krill regime, which were then scaled by +60% and -40% to create the high and low krill regimes, respectively. The probability of a year being a high or low krill regime was 0.2, while the probability of a medium krill regime was 0.6. A shift between krill regimes could occur on October 31 (the transition between the post-feeding and early feeding seasons) of each simulated year (see *Appendix C: Krill densities and regimes in the backward iteration* for additional details). Under baseline conditions in the forward simulation, the krill regimes were presented as a repeated pattern of a five-year cycle (i.e., medium, high, medium, medium, low) based on krill recruitment patterns described in Steinberg et al. (97). Therefore, in addition to seasonal variability, a whale also experienced interannual fluctuations in krill, which was modeled in the backward iteration to capture a whale's behavioral and reproductive adaptations to these periodic regime shifts in the forward simulation.

Feeding was limited to krill densities $\geq 0.01 \text{ kg/m}^3$ based on estimates from Videsen et al. (98), which suggests a humpback whale requires about 10 krill/m³ to recoup the cost of a lunge (assuming 1 krill = 1 gram); thus, densities below this value would not be energetically efficient. Feeding was also limited in the number of hours available for a whale to feed per day. Along the western AP, humpback whales transition from feeding during all hours early in the feeding season to only at night later in the season in response to the availability of dense aggregations of krill in the upper reaches of the water column (92). We used hourly feeding rate data across the feeding season from Nichols et al. (92) to account for this seasonal change in foraging effort.

In the model, whales could feed for 24 hours at the beginning of the feeding season (January), which linearly declined to 16 hours near the end of the feeding season (June); then, from July through December, the time available to feed linearly increased from 16 to 24 hours.

2.3.4 Additional mortality

In nature, humpback whales can die from causes other than starvation, including disease, predation, and interactions with humans (e.g., vessel collision). To account for these processes in the model, we included a yearly survival rate of 0.875 for calves and 0.96 for juveniles and adults in the backward iteration and forward simulation (99). Additionally, a fetus can be aborted irrespective of the female's energetic status. To account for this process, we included a fetus's daily probability of survival based on an overall estimate of perinatal loss (13.5%) reported for North Atlantic right whales (*Eubalaena glacialis*) (100), which has been used as a conservative estimate of abortion rate in other SDP models (43).

2.3.5 Backward iteration: SDP equations

The backward iteration starts at terminal time, T , which is the last day of the female's life and, if she is lactating, the final day she can wean her calf. If the female is lactating at T , her terminal fitness is described by the function:

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

where γ determines the steepness of the curve and m_{50} is the body condition at which the calf has a 50% chance of surviving to 10.5 months old, when it can be added to the population (88). If the female is not lactating at T , her terminal fitness equals 0 because she has no future reproductive opportunities.

Then, moving backward in time from T , one day at a time, the behavioral and reproductive decisions that maximize a whale's future expected reproductive success are computed and recorded, which depend on the value of the state variables x , m (when applicable), l , e , and t . These calculations are described below; for additional details, see *Appendix D: SDP equations*. If two or more strategies had the same fitness value, the corresponding behavioral and reproductive strategies were recorded and determined in the forward simulation. For behavioral ties on the breeding or feeding grounds, a whale stayed in its current location. In contrast, in the migratory corridor, a whale continued moving in the same direction (forward or backward) as the previous day. For reproductive ties, a decision was randomly chosen from all potential optimal reproductive strategies.

Behavioral decisions

On a given day, a whale must make a behavioral decision related to movement, and the choices available depend on its current location. On the feeding and breeding grounds, a whale can choose to stay in its current location or begin migration. When in the migratory corridor, it can choose to move forward or backward.

Thus, the expected fitness of a non-lactating whale in reproductive state r is:

$$< F_r > = \max\{V_{b_1}(x', l', e, t + 1), V_{b_2}(x'', l'', e, t + 1)\} \quad (2)$$

where $V_{b_1}(x', l', e, t + 1)$ and $V_{b_2}(x'', l'', e, t + 1)$ are the fitness values of behavioral choice b_1 and b_2 , respectively, and x' and x'' are the female's future expected body conditions after accounting for the costs and gains, if any, of the associated behavioral choice l' and l'' . Thus, $< F_r >$ is a whale's maximum expected fitness taken over the possible behavioral strategies given the current value of the state variables x , l , e , and t .

For lactating whales, fitness for a given reproductive state r is:

$$< F_r > = \max\{V_{b_1}(x', m', l', e, t + 1), V_{b_2}(x'', m'', l'', e, t + 1)\} \quad (3)$$

where the state variable m represents the calf's body condition, and m' and m'' are the calf's future expected body conditions after accounting for the costs and gains, if any, of the associated behavioral choice l' and l'' . See *Appendices B through D* for how fitness was calculated for the possible behavioral strategies given the current state variables.

Reproductive decisions

Reproductive state 1: non-reproductive juvenile whales. If a calf survives to 10.5 months old and is added to the population, it becomes a juvenile whale and remains in this reproductive state until it reaches sexual maturity. As a result, the fitness of a juvenile whale is:

$$F_1(x, l, e, t) = < F_1 > \quad (4)$$

Reproductive state 2: non-reproductive adult whales. Once a juvenile whale reaches sexual maturity (t_m), she becomes a non-reproductive adult female:

$$F_1(x, l, e, t_m) = < F_2 > \quad (5)$$

The fitness function for a non-reproductive adult female is analogous to that of a juvenile female:

$$F_2(x, l, e, t) = < F_2 > \quad (6)$$

However, if she is on the breeding grounds (l_b) at the time of implantation (t_i), she can implant and become pregnant or remain a non-reproductive adult. This decision depends on comparing the fitness values for a non-reproductive adult (F_2) and pregnant (F_3) whale:

$$F_2(x, l_b, e, t_i) = \max\{< F_2 >, < F_3 >\} \quad (7)$$

If a non-reproductive adult is not on the breeding grounds on the day of implantation, she remains in her current state.

Reproductive state 3: pregnant whales. A pregnant whale can become a non-reproductive adult at any time during gestation if her pregnancy is terminated, which depends on comparing the fitness values for a non-reproductive adult (F_2) and pregnant (F_3) whale:

$$F_3(x, l, e, t) = \max\{< F_2 >, < F_3 >\} \quad (8)$$

A pregnant whale can successfully give birth if she is on the breeding grounds on the day of birth (t_b), and at that time, can give birth and nurse the calf or abandon it. This

decision depends on comparing the fitness values for a non-reproductive adult (F_2) and lactating (F_4) whale:

$$F_3(x, l_b, e, t_b) = \max\{< F_2 >, < F_4 >\} \quad (9)$$

If a pregnant whale is not on the breeding grounds on the day of birth, she gives birth, but the calf does not survive, and she then becomes a non-reproductive adult.

Reproductive state 4: lactating whales. A lactating whale can wean her calf at any time between birth and the end of the lactation period, and her fitness is calculated as:

$$F_4(x, m, l, e, t) = \max\{< F_2 > + \varphi(m), < F_4 >\} \quad (10)$$

where the fitness of weaning the calf early is calculated as the fitness of the non-reproductive adult state plus the probability of the calf surviving to 10.5 months old and being added to the population given its current body condition ($\varphi(m)$).

A lactating whale can become pregnant at the time of implantation while on the breeding grounds. This decision depends on comparing the fitness values of the non-reproductive adult (F_2), pregnant (F_3), lactating (F_4), and pregnant/lactating (F_5) states:

$$F_4(x, m, l_b, e, t_i) = \max\{< F_2 > + \varphi(m), < F_3 > + \varphi(m), < F_4 >, < F_5 >\} \quad (11)$$

At the end of the lactation period (t_w), a lactating whale's fitness is calculated as:

$$F_4(x, m, l, e, t_w) = \{< F_2 > + \varphi(m)\} \quad (12)$$

Reproductive state 5: pregnant and lactating whales. A pregnant and lactating whale's pregnancy can be terminated at any time during gestation, or her calf can be weaned early. Her fitness is calculated as:

$$F_5(x, m, l, e, t) = \max\{< F_2 > + \varphi(m), < F_3 > + \varphi(m), < F_4 >, < F_5 >\} \quad (13)$$

At the end of the lactation period, a pregnant and lactating whale can become a non-reproductive adult if the pregnancy is terminated, or she can remain pregnant. Her fitness is calculated as:

$$F_5(x, m, l, e, t_w) = \max\{< F_2 > + \varphi(m), < F_3 > + \varphi(m)\} \quad (14)$$

2.3.6 Forward simulation: simulated stressor scenarios

In the forward simulation, we used matrices of optimal reproductive and behavioral decisions from the backward iteration in Monte Carlo simulations to model the state dynamics of female humpback whales and assess vital rates under baseline conditions and changes in response to stressor scenarios.

We created a stable-age structured population of 200 whales to assess the consequences of stressors on population dynamics. Starting parameters (i.e., body condition, reproductive state, and location) for simulated whales were identified by running a trial simulation of 1000 whales from weaning until death under a medium krill regime. The forward simulation ran for a normalization period of five years, beginning on August 1, the day a pregnant female gives birth; thus, the initial population size was greater than 200 (see *Appendix E: Creating a stable-age distribution and identifying starting conditions for the forward simulation*). A

normalization period of five years was chosen to ensure that model outputs would not be impacted by initial model parameterization. The resulting population (including age, body condition, reproductive state, and location) was then used as the starting population in subsequent simulated scenarios.

Each scenario was simulated for 25 years and repeated 50 times. Simulated scenarios included baseline conditions (with no reductions in krill biomass), as well as climate change and krill fishing stressors. For the climate change scenarios (i.e., single stressor scenarios), krill was reduced by 10%, 25%, and 50% year-round, and an additional low krill year was added to the end of the baseline, five-year krill regime (making it a six-year krill regime) (35, 101). These reductions in krill were chosen as they are within the range of observed reductions in biomass density for the region (35). For scenarios with the combined effects of climate change and krill fishing (i.e., multiple stressors scenarios), krill densities were reduced by 10%, 25%, and 50% in March through June of each year due to krill fishing (when the spatiotemporal overlap between the krill fishery and humpback whales is greatest) and were also reduced by 10%, 25%, and 50% year-round due to climate change; all possible combinations were simulated.

To assess the effect of the stressor scenarios on female vital rates, we used Cohen's d , which is the difference between means in the undisturbed and disturbed scenarios scaled by their pooled standard deviation (41, 102). Positive values indicate an adverse effect of disturbance on vital rates, with values of 0.2, 0.5, and 0.8 indicating small, medium, and large effects, respectively (102). In the analysis, we focused on key

vital rates such as pregnancy rate (the percentage of sexually mature females that become pregnant), birth rate (the percentage of sexually mature females that give birth), weaning success rate (the percentage of female calves born that successfully wean and are alive at 10.5 months old), and population growth rate (the annual percent increase in population abundance), which provide insight into population dynamics and are also measurable in the field.

2.3.7 Sensitivity analysis

We conducted sensitivity analyses on five model parameters to identify which had the largest influence on simulation results. We individually varied each parameter, resulting in 10 sensitivity analyses. For each sensitivity analysis, we reran the backward iteration and 50 replicates of the forward simulation under baseline conditions and compared results using Cohen's *d*. See *Appendix F: Sensitivity analysis* for the analyzed parameters and results.

2.4 Results

2.4.1 Baseline conditions

On average, females gave birth to their first calf at age 6 (mean = $6.14 \pm \text{SD} = 0.4$ years), the year after becoming sexually mature, with a maximum delay until age 11. Pregnancy rates were high at the beginning of gestation, with an average of 88.97% ($\pm 4.3\%$) of sexually mature individuals becoming pregnant; however, the number of females that remained pregnant decreased as gestation progressed, with only 44.96% ($\pm 4.62\%$) of sexually mature females giving birth the following year. All lactating

females became pregnant while nursing, but few carried the pregnancy term ($7.89\% \pm 3.95\%$), regardless of whether the current calf survived to 10.5 months old and was added to the population (e.g., a female could have abandoned the calf and kept the pregnancy). Of those who were both pregnant and lactating at the start of gestation, $5.48\% (\pm 4.76\%)$ successfully weaned their calf while also pregnant, and fewer than 10% of those individuals gave birth the following year ($9.45\% \pm 19.36$). The average weaning date was April 11, 65 days before the weaning deadline (June 15). However, successfully weaned calves were weaned, on average, several weeks later on May 19, and the average weaning success rate was $71.64\% (\pm 13.37\%)$. At the end of the 25-year simulation, the mean population size was $1072 (\pm 65)$ individuals, resulting in a mean population growth rate of $5.9\% (\pm 2.54\%)$ per year.

Migratory behavior emerged from the model, with sexually mature whales migrating between feeding and breeding grounds. Non-reproductive adult females arrived on the feeding grounds between November 1 and November 19. Generally, they left the feeding grounds between June 2 and June 17, with some staying until August 2. Similarly, pregnant females arrived on the feeding grounds on November 1 and left on June 2. Lactating females (non-pregnant and pregnant) arrived on the feeding grounds nearly three weeks later (November 19), and they always weaned their calf before migrating to the breeding grounds. Juveniles did not complete migration; instead, they generally left the feeding grounds on June 17, with some staying until August 2, and returned on November 1 without making it to the breeding grounds.

Body condition exhibited dramatic seasonal fluctuations in response to migration, particularly during low krill years (Figure 2.2). Overall, whales were in poorer body condition during low krill years than in medium and high krill years (Figure 2.3A). As a result, poorer body condition in low krill years led to nursing females abandoning their calves earlier on average, leading to lower weaning success rates and birth rates following low krill years (Figure 2.3B). Irrespective of the prey environment, body condition on the day of implantation strongly influenced whether a whale became pregnant, whereby females who became pregnant were in better body condition ($36.45\% \pm 4.52\%$) than those who did not ($29.45\% \pm 2.2\%$). Pregnancy rates exhibited interannual variability in response to krill availability. In the middle of the feeding season, we found that, on average, $62.21\% (\pm 2.62\%)$ of mature females were pregnant during low krill years. In contrast, on average, $74.15\% (\pm 6.38\%)$ and $78.43\% (\pm 2.09\%)$ of mature females were pregnant during medium and high krill years, respectively. Pregnancy rates were also low following low krill years ($66.36\% \pm 3.06\%$), and the highest pregnancy rates followed high krill years ($79.9\% \pm 2.01\%$).

2.4.2 Stressor scenarios

Stressors had varying effects on pregnancy, birth, and weaning success depending on the severity of the krill reduction and whether multiple stressors were present (Figure 2.4). For the single stressor, climate change scenarios, year-round reductions in krill and an increased frequency of low krill years negatively affected pregnancy, birth, and weaning success rates. When krill was reduced by 10% and 25%,

pregnancy, birth, and weaning success rates fell by 5-20%; when krill was reduced by 50%, rates dropped by 40-60%, resulting in a population growth rate of -4.31% ($\pm$ 14.19%) (Figure 2.5; Table G2). For the multiple stressors scenarios, the combined effect of climate change and krill fishing had increasingly catastrophic effects on pregnancy, birth, and weaning success rates as the reduction in krill increased, with krill reductions by 50% for both climate change and krill fishing leading to the population crashing before the end of the 25-year simulation (Figure 2.5C; Table G3).

See *Appendix G: Tables of life-history parameters and Cohen's d values* for additional results from the modeled scenarios.

2.5 Discussion

We developed an IBM-SDP model to explore how reduced krill availability, mediated by climate change and krill fishing stressors, affects the population dynamics of humpback whales that feed along the western AP. Our model captured several aspects of the life history of humpback whales (Table G1). While no model can fully capture the complexities of a population's life history, these emergent properties can be compared with empirical data for western AP humpback whales and other populations. They can also help fill in the gaps in a population's life history, especially since collecting empirical data to calculate vital rates such as birth and weaning success rates for large whales is challenging. Our modeling effort also highlights critical knowledge gaps that can inform future research directions.

In the model, we found that most sexually mature females (mean = 89%) became pregnant in a given year, likely because the beginning of gestation is

energetically inexpensive; however, as gestation progressed, pregnancy rate decreased (mean = 73%), with fewer mature females being pregnant in the middle of the feeding season (February 1). Recognizing that existing pregnancy rate estimates do not discern between sexually immature and mature whales, we recalculated pregnancy rate to include all females older than one year (rather than just sexually mature females older than five years). We found that the pregnancy rate at the beginning of gestation was 60.35% ($\pm 3.52\%$), and in the middle of the feeding season was 49.3% ($\pm 5.94\%$). These findings are similar to pregnancy rate estimates of humpback whales observed in Antarctic whaling areas IV and V from 1950 to 1956 (mean = 47.99%, range = 36.19% to 71.88%) (103) and are also consistent with more recent estimates in Pallin et al. (25) for humpback whales on their western AP feeding grounds between December and March (mean = 51.97%, range = 29.50% to 86.22%).

While birth rate estimates are not available for breeding stock G, empirical estimates for other humpback whale populations range from 36% to 44% (104). Our findings are generally consistent with these estimates, with an average of 45% of mature females giving birth each year and a mean inter-birth interval of 2.41 (± 0.5) years under baseline conditions. Annual reproduction was also an emergent property of the model. Early in the feeding season, we found that 60% of simulated females nursing a calf were also pregnant, which is comparable to empirical data provided by Pallin et al. (22) for a similar time of year (mean = 54.5%). However, how many of these annual pregnancies result in successful births the following year is unknown for this population. On the Hawaiian breeding grounds, Glockner-Ferrari and Ferrari (105)

reported that 14% of females calved in consecutive years (although ascertainment bias is likely because the study was focused on mothers and calves). In contrast, on the feeding grounds, Robbins (106) and Clapham and Mayo (107) found that only 2-6.3% of females returned with calves to the Gulf of Maine in consecutive years. Similarly, we found that few whales gave birth in consecutive years, with less than 8% of nursing females carrying the pregnancy to term.

In the model, a calf depended on its mother for nutrients and nursed for a maximum of 10.5 months (47, 49), after which it was considered independent and fed autonomously. The timing and process of calf independence for humpback whales is not fully known. Still, observations of calves independently feeding suggest that the weaning process may begin at five to six months of age (108). Empirical evidence suggests that many mother-calf pairs separate after the feeding season (108, 109), while some separate on the feeding grounds (110, 111), with few remaining together for the following feeding season (110). In the model, weaning occurred, on average, in mid-April, approximately two months before the weaning deadline; however, for calves that successfully survived to 10.5 months old and were added to the population, weaning occurred, on average, one month later in mid-May. We also found that, under baseline conditions, females always weaned their calves prior to the start of their northern migration. For females who were pregnant and lactating, weaning occurred at least two weeks prior to the weaning threshold to ensure an on-time arrival to the breeding grounds to give birth. In contrast, for lactating females, weaning occurred before or on the last day milk could be provided, after which they migrated a few days later. These

results may be affected by some of the simplifying assumptions in the model regarding weaning, especially since calves may be gradually transitioning from entirely depending on their mother for nutrients to feeding independently during those last few months together. Additionally, calves may benefit from migrating with their mother regardless of whether they are nursing (e.g., reduced predation; their mother knows the migration route to the breeding grounds). In the model, the relationship between mothers and calves is based solely on energetics and, thus, does not capture other factors that may keep the pair together. As a result, the model may underestimate the weaning success rate (mean = 72%) and, therefore, our result should be viewed as a conservative estimate.

The simulated population's annual average population growth rate was 5.9%, which is generally consistent with the empirically-derived growth rate for breeding stock G (5.07%) (112). The estimated annual growth rate for this breeding stock is considered low compared to other populations experiencing a rapid recovery post-whaling (10% for the Western Australia population (113), 7.4% for the Southwestern Atlantic population (114)); however, Félix et al. (112) suggest that the number of whales in breeding stock G could be an underestimate, especially since mixing occurs between humpback whale stocks in Antarctic waters (115, 116). Growth rate may be influenced by anthropogenic factors such as the high rate of entanglement on the breeding grounds (117, 118) and vessel collisions (119), as well as ecological factors such as an increase in predation by killer whales (120) and climate change (121). The western AP is experiencing one of the fastest rates of regional climate change (8, 122),

resulting in decreased seasonal ice cover and a reduction of krill (35, 123), which has been shown to affect pregnancy rates for breeding stock G (25). Additionally, density-dependent factors, which were not included in the model, could occur. Our population growth rate estimate is the result of calibrating the model using empirical data on the reproductive rates of breeding stock G (e.g., pregnancy rate, rate of being simultaneously pregnant and lactating) and other humpback whale populations (e.g., birth rate, annual calving rate), and does not include the effects of these additional external stressors; therefore, it should be considered a conservative estimate.

Migration was also an emergent property of the model, and its timing was generally driven by both reproductive and energetic benefits. There were some instances when non-reproductive adults skipped a reproductive event, particularly when they were in poor body condition and occasionally when they did not complete migration. Juveniles also did not complete migration; instead, they stayed on the feeding grounds until it was no longer energetically beneficial. In the model, a whale's FMR was influenced by its body mass (i.e., tidal volume was a function of "ideal" body mass) and its respiration rate, which depended on whether the individual was a calf or juvenile/adult, whether it was lactating or not, and its location (i.e., feeding grounds, migratory corridor, or breeding grounds). Location-specific respiration rates were estimated from the literature (see Table A1), with a whale's respiration rate being higher on the feeding grounds than in the migratory corridor or on the breeding grounds. As such, these movement decisions were likely an artifact of how the model was parameterized. For example, when it became too energetically costly to stay on the

feeding grounds, juveniles moved into the migratory corridor to begin their migration north; however, they always turned around before making it to the breeding grounds.

A growing body of evidence suggests that not all individuals in this and other humpback whale populations undertake an annual migration to the breeding grounds (124-126). Nevertheless, the migratory movements that emerged from the model suggest that there must be more than a reproductive incentive driving whales to migrate and prolong their time on the breeding grounds, especially in areas where little to no feeding has been observed. The reason why humpback whales and other baleen whales migrate is not fully understood and may not be driven by a single factor. In addition to reproduction, some additional hypotheses for migration include reducing the thermal stress on calves (127), avoiding killer whale predation on calves (51), resource tracking (128), the need to undergo an epidermal molt (129), social learning and development (130), and/or it is an evolutionary holdover (131). Resource tracking is assumed to be a driver of migration for eastern North Pacific blue whales (43, 88, 132); however, the extent to which humpback whales feed outside of the feeding grounds is unknown, but it is believed to be low (133).

Information about humpback whales' migratory movements and foraging behavior is critical to understanding how individuals may respond to stressors that impact their energetics. Along the western AP, humpback whales exhibit high feeding rates throughout the day at the beginning of the feeding season, with feeding rates declining and becoming more concentrated at night later in the season (92). Despite these reduced feeding rates, Bierlich et al. (134) found that humpback whales continued

to gain substantial body mass late into the feeding season. Under baseline conditions, some juvenile, non-reproductive adult, and pregnant whales reached the maximum body condition threshold (45%) set in the model (Figure H1), generally between mid-March and mid-April, depending on the whale's reproductive status. This timing aligns with the “first” arrival dates observed by Avila et al. (135) for humpback whales on the breeding grounds offshore Colombia (~May/June); however, instead of migrating, simulated whales stayed on the feeding grounds until it was reproductively beneficial to migrate, essentially continuing to “top off” their energy reserves until it was time to migrate.

The rate at which humpback whales gain energy reserves may be mediated by seasonal changes in krill density (136) and/or quality (i.e., lipid content) (137). In the model, we used krill density estimates from Lascara et al. (95), as they provided seasonal estimates that covered the entire year. Since the Lascara et al. (95) estimates were collected at a larger, regional spatial scale, even our re-scaled density estimates (see *Prey environment*, above) may not fully capture the densities consumed by individual whales, the probability of such densities occurring in the environment, or how krill coalesce and swarm differently from spring into fall. Regarding krill quality, the model used a mean energy density estimate for Antarctic krill (138), which could have led to whales reaching the maximum body condition threshold earlier in the feeding season than would have occurred if krill lipid content increased as the feeding season progressed. As fine-scale prey data become available, they can be readily incorporated into the model to better capture the nuances of energy gain throughout the

feeding season. Nevertheless, our model still reproduced key life-history characteristics of humpback whales, lending value even without such fine-scale data.

Similar to the findings in Pirotta et al. (43) for simulated blue whales (*Balaenoptera musculus*), we found that the combined effects of multiple stressors resulted in greater impacts on vital rates than a stressor in isolation (139). For the multiple stressor scenarios, it is important to note that the krill fishing stressor only considered impacts on whales via energetics and did not consider other potential adverse effects such as entanglement (140). Additionally, by restricting the krill fishing stressor to March through June, simulated whales had more time to replenish their energy reserves, thus providing some energetic buffer before the onset of krill fishing later in the feeding season. If the krill fishing stressor had coincided with the arrival of whales on the feeding grounds, when feeding rates are much higher (92), we would have observed greater effects on these vital rates, with females prioritizing their health and foregoing an existing reproductive attempt. This highlights the importance of understanding the timing of arrival on the feeding grounds and the quality of the prey environment, as it can affect whether an individual can buffer against reduced prey availability. In the model, most whales arrived on the feeding grounds in November of each year and thus had three to four months to gain energy reserves before krill fishing commenced and continued through the rest of the feeding season.

Across all simulations, effects were greatest during years when krill availability was already poor. During low krill years, females were in poorer body condition. As a result, fewer whales were able to carry their pregnancy to term, which led to lower birth

rates, and for whales that gave birth, calves were weaned earlier, which led to lower weaning success rates. These effects were further exacerbated when reductions in krill due to climate change in isolation or combined with krill fishing coincided with naturally occurring poor krill years. Incorporating targeted restrictions on human activities during these energetically stressful periods could mitigate effects on vital rates. To test this, we simulated a “mitigation” scenario, where krill was reduced by 25% due to krill fishing and climate change, with no krill fishing during low krill years. We found that when krill fishing did not occur during low krill years, the population fared better overall, with a population growth rate of 3.8% compared to 2.6% when no mitigation was implemented. As such, the environmental context in which human activities operate must be considered when developing strategies to mitigate negative consequences on populations.

In the Antarctic, changes in sea ice coverage negatively affect many ice-dependent species (8, 33). For example, krill larvae and juveniles depend on sea ice for growth and survivorship, and declining sea ice along the western AP may result in poor recruitment events (33, 34). Ocean acidification could also affect the growth, recruitment, and survival of krill, with high levels of carbon dioxide in the water column affecting embryonic development and the regular formation of new exoskeletons (34). Additionally, warming sea temperatures may also affect krill biomass, with recent work showing localized declines in krill along the AP and Scotia Sea, as well as a southward shift in their distribution, over the last four decades (35). These changes in the Antarctic region have also led to an increased human presence. In

addition to krill fishing, the western AP is experiencing a dramatic increase in tourism (141), which brings threats related to noise (142) and vessel strikes (119). Understanding how these stressors interact with the existing pressures of climate change and krill fishing to cause population effects is critical to developing targeted mitigations that protect humpback whales and other wildlife throughout the region. Models such as the one we developed provide a general framework within which to achieve that.

2.6 Conclusions

Our model provides a general framework to predict the impact of multiple stressors on humpback whale population dynamics. Simulated stressors had varying effects on pregnancy, birth, weaning success, and population growth rates depending on the severity of the krill reduction and whether both stressors were present. For the single stressor scenarios, year-round reductions in krill due to climate change had an adverse impact on key vital rates regardless of the severity of the krill reduction. In contrast, in the multiple stressors scenarios, we found that the combined effects of climate change and krill fishing were greater than climate change in isolation, with some populations crashing before the end of the simulation. Finally, across all simulations, we found that effects on vital rates were greatest during years when krill availability was already poor and that removing the krill fishing stressor during these periods could reduce the impact on population dynamics.

This model captures the complex feeding patterns, reproductive strategies, and migratory movements of western AP humpback whales within an IBM-SDP

framework. Although the model reproduced many of the life-history characteristics of humpback whales, its emerging properties are ultimately driven by how the model was parameterized, thus highlighting data gaps and directions for future research. For example, more data are needed to better understand the krill densities targeted by humpback whales (96) and how these may change within and across years in response to environmental variability (97). Such information would also extend the model to include a spatial structure in the feeding grounds. A spatially explicit model could be used to identify when and where whales may be most vulnerable to reductions in krill and inform mitigations that reduce interactions between whales and the krill fishery (16). Furthermore, data are needed on the timing and length of migration for females in different reproductive states, including potential drivers of migratory movements, to better understand the consequences on an individual's energetics and vulnerability to stressors.

IBM-SDP models provide a framework to explore the ecology of long-lived species and quantify how vital rates may shift in response to climate-driven and human-induced changes in prey. While the effects of climate change on these populations cannot be directly managed, tools such as the one presented here can help plan human activities to minimize the overlap with biologically important areas during energetically vulnerable and reproductively sensitive times (143).

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2.8 Figures

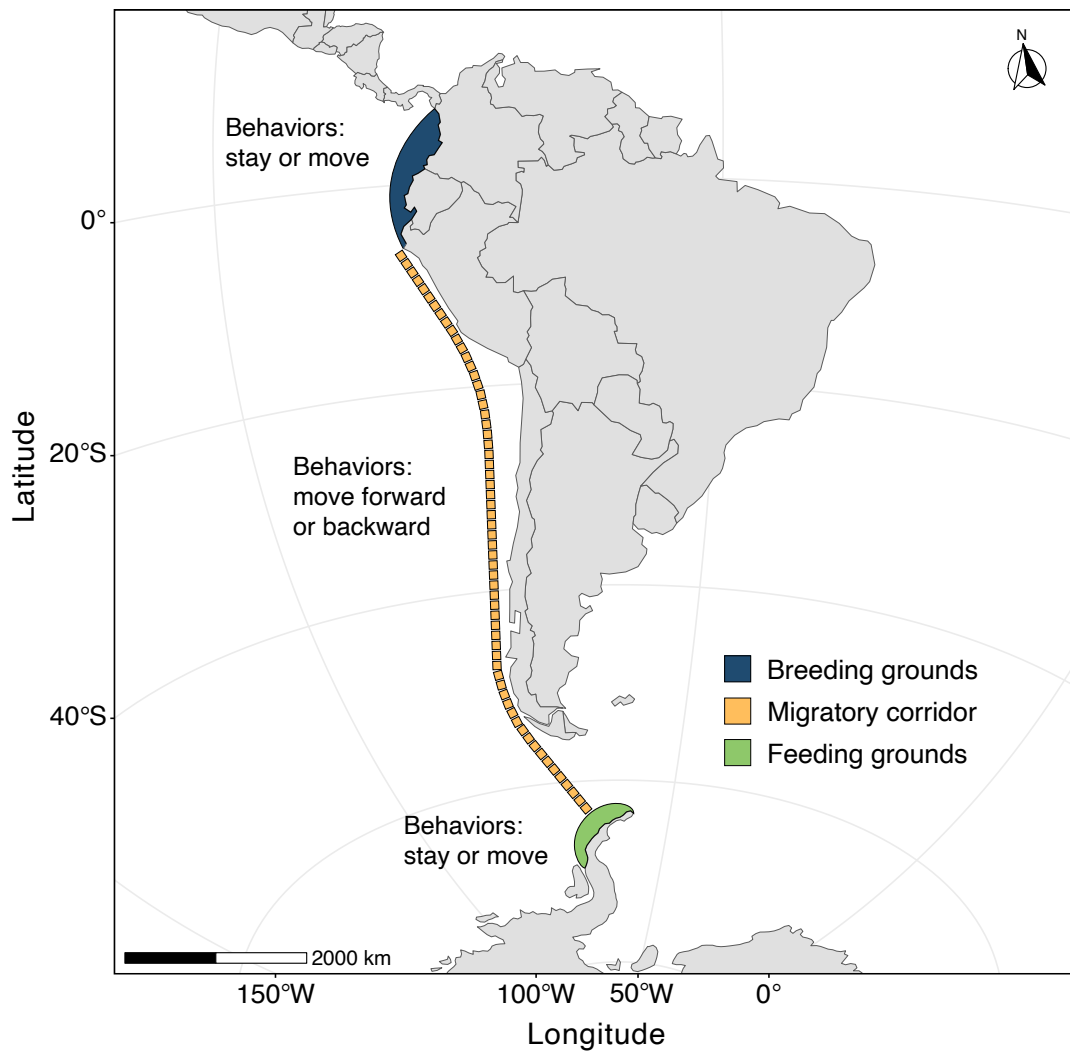


Figure 2.1. Map of the study area, including the breeding grounds, feeding grounds, and 59 locations that made up the migratory corridor. Possible behavioral choices for each region are also provided.

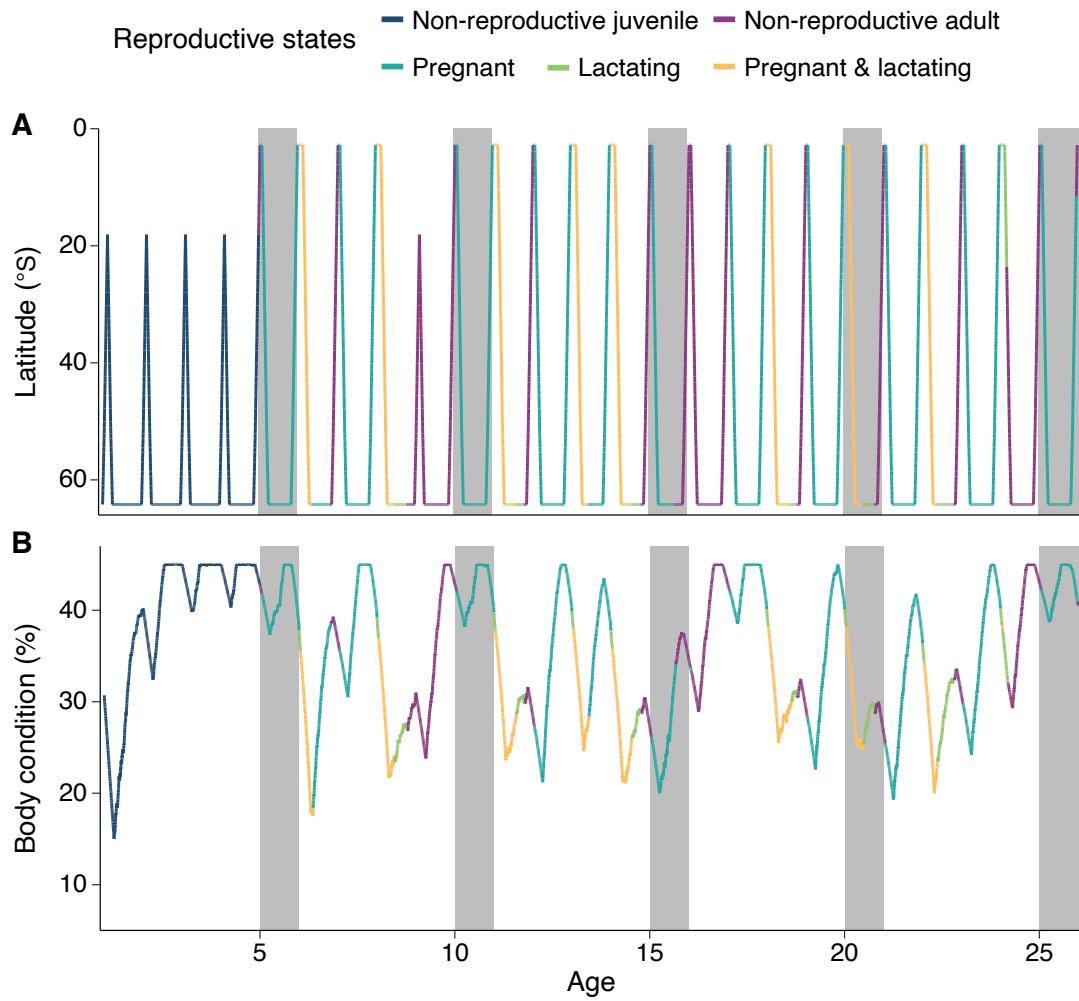


Figure 2.2. An example of the time series of (A) location and (B) body condition for one simulated whale, colored by reproductive state, under baseline conditions. Gray vertical rectangles represent low krill years.

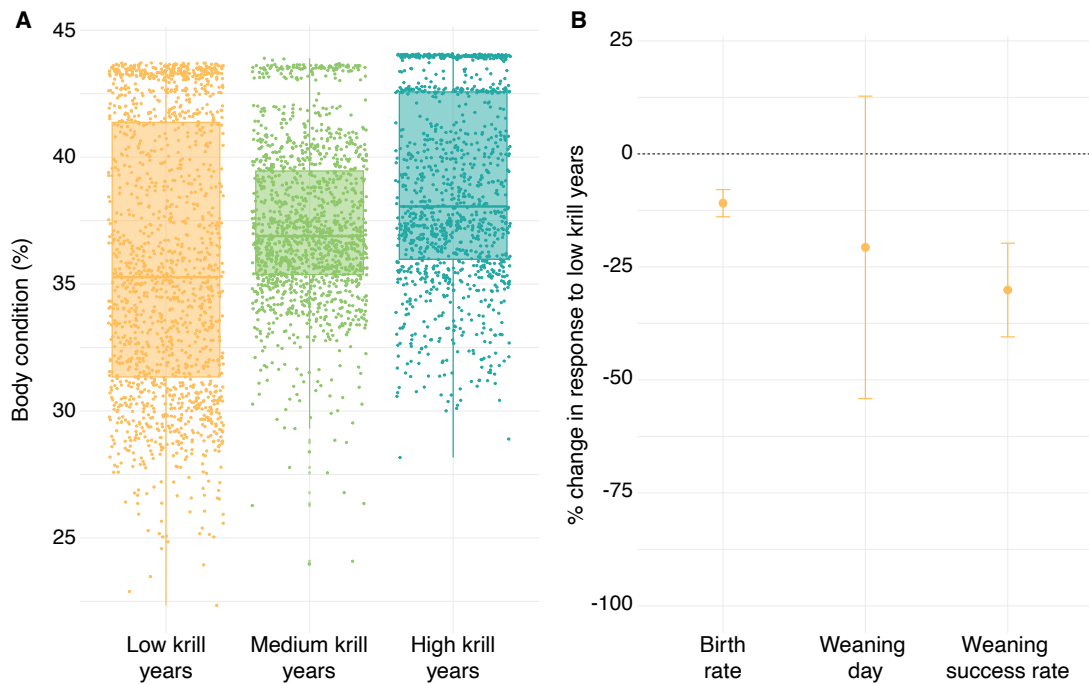


Figure 2.3. (A) Mean body condition of whales for one simulation across low, medium, and high krill years under baseline conditions. (B) Mean percent change (for the same simulation in (A)) in birth rate following a low krill year, and weaning day (including both unsuccessful and successful weanings) and weaning success rate during a low krill year, compared to medium and high krill years (dashed line); error bars represent the standard deviation.

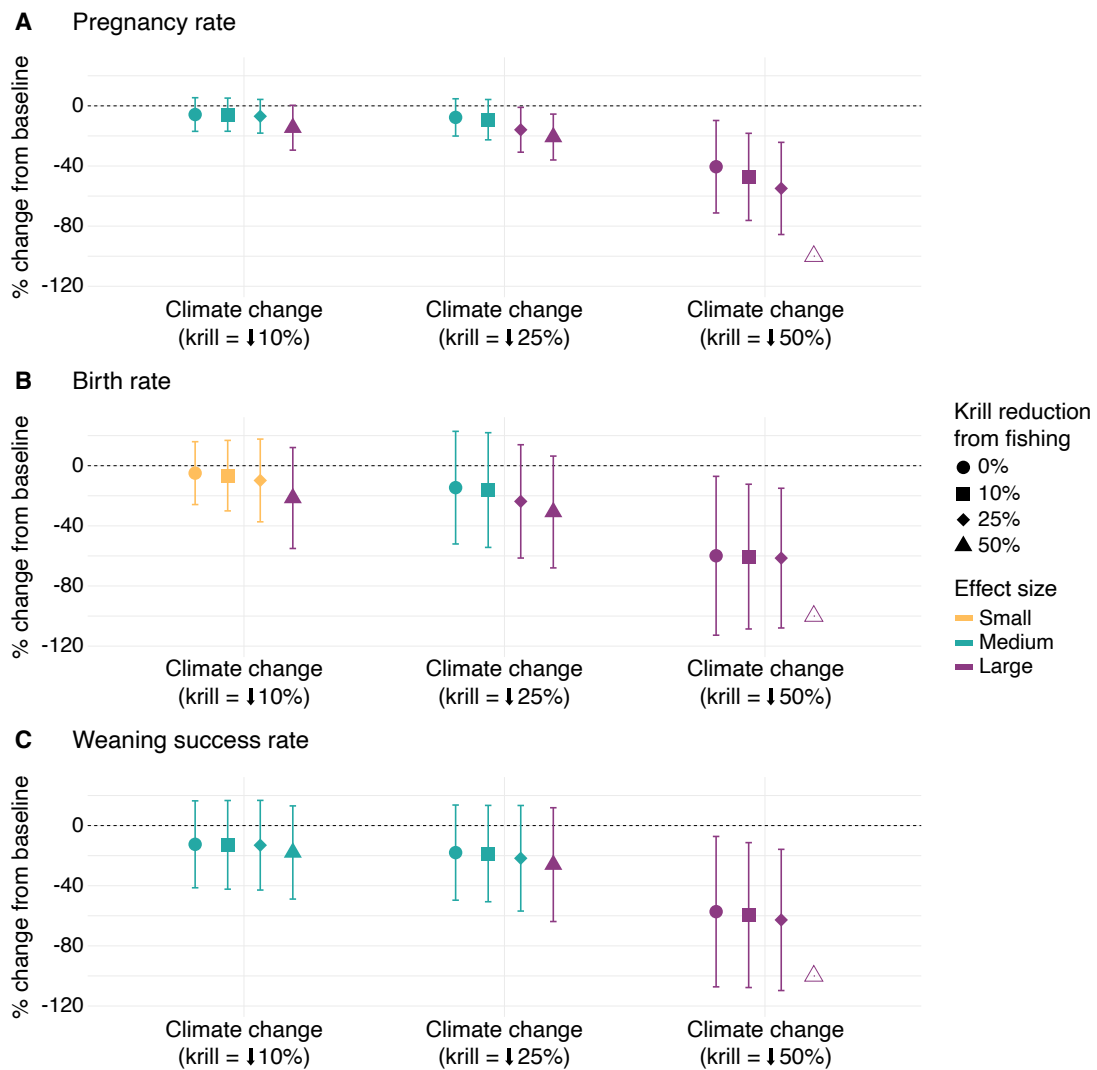


Figure 2.4. The influence of simulated stressors on (A) pregnancy rate (on February 1, in the middle of the feeding season), (B) birth rate, and (C) weaning success rate. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor), error bars represent the average standard deviation within a population as a percent change around the mean, and the colors represent the effect size based on Cohen's *d*. The x-axis represents the simulated stressor scenarios, where the value in parentheses represents the percent reduction in krill due to climate change and the shape represents the percent reduction in krill due to krill fishing. A hollow shape means the population crashed before the simulations ended.

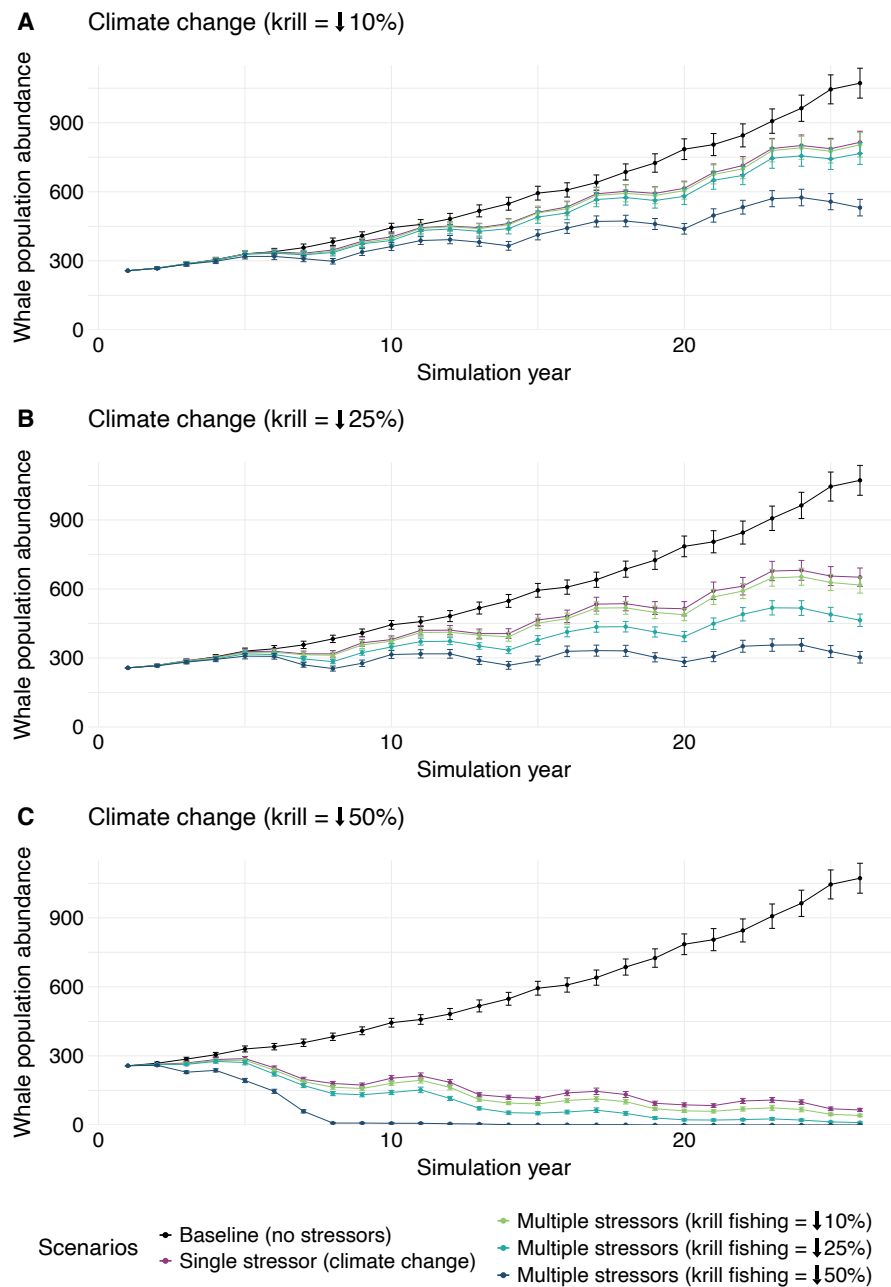


Figure 2.5. Humpback whale population trajectories under three climate change scenarios, with the percent reduction in krill due to climate change noted in parentheses. The colored trajectories represent baseline (no stressors), single stressor (climate change), and multiple stressors (climate change and krill fishing) scenarios; the error bars represent the standard deviation. For the multiple stressors scenarios, the percent reduction in krill due to krill fishing is noted in the legend in parentheses.

2.9 Supplementary material

2.9.1 Appendix A: SDP conceptual diagram

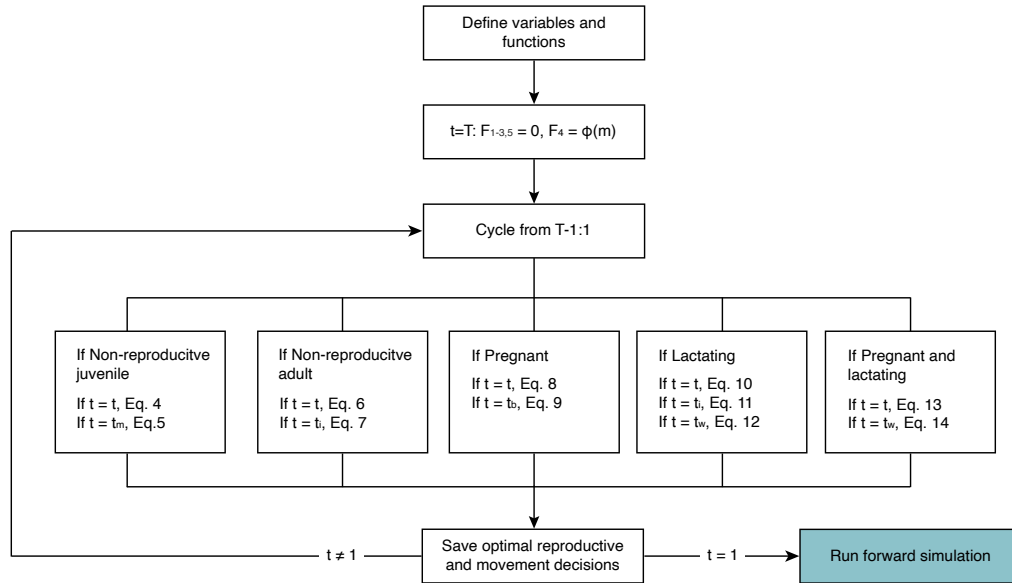


Figure A1. Conceptual diagram of the backward iteration of the SDP model. The listed equations can be found in the main text.

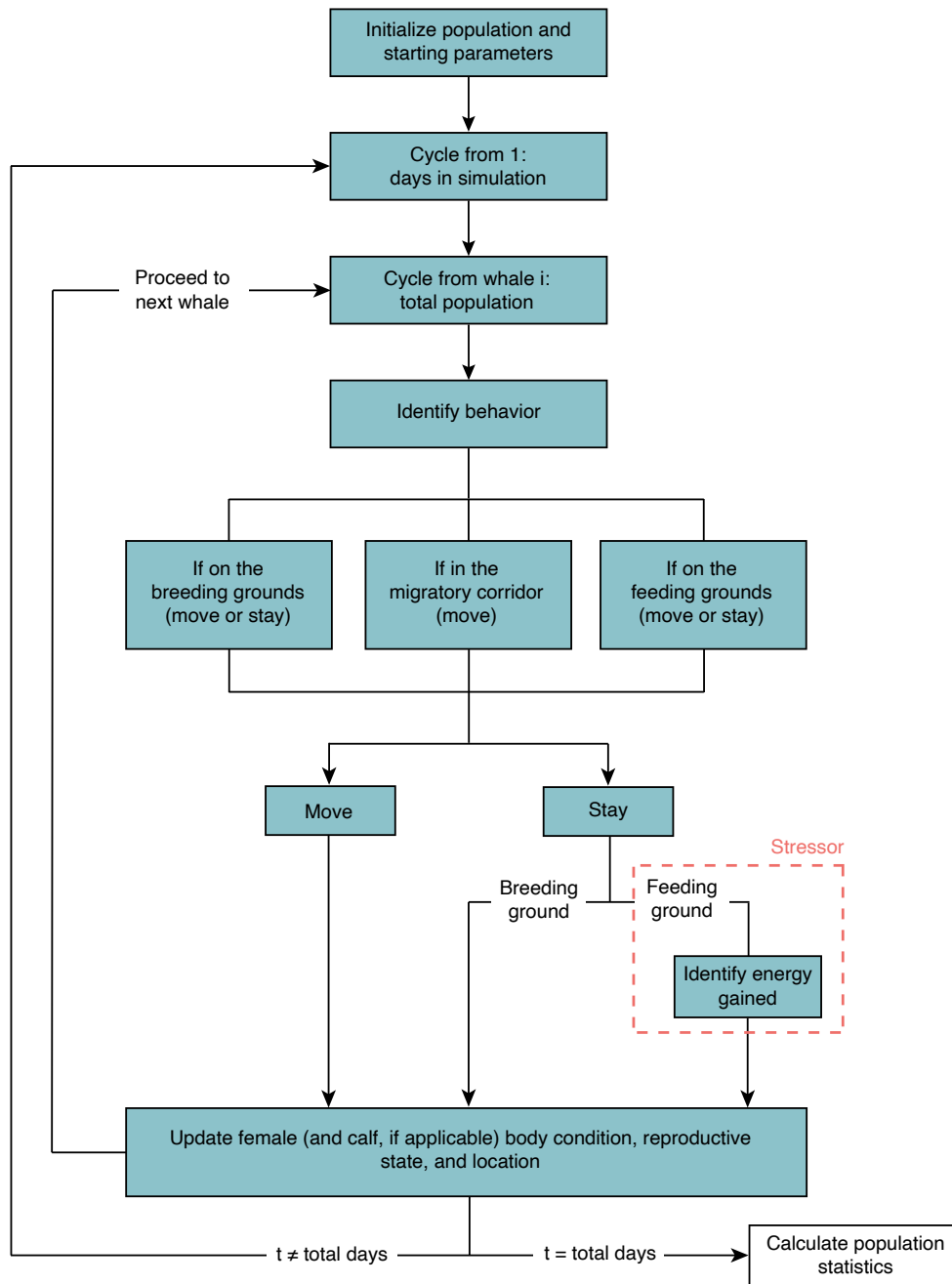


Figure A2. Conceptual diagram of the forward simulation of the SDP model.

2.9.2 Appendix B: Physiological equations and parameters

Ideal body mass (M) and length (L). A whale's ideal body mass (kg) on a given day (i.e., time t) was estimated from a regression analysis of total mass vs. length from data gathered from harvested fetuses (equation 1) as well as a near-term fetus and mature males and females (equation 2) (1-3):

$$\text{Fetus} \quad M(t) = 16.667 \times L(t)^{2.8034} \quad (1)$$

$$\text{Calf/juvenile/adult} \quad M(t) = 12.875 \times L(t)^{3.0365} \quad (2)$$

where $L(t)$ is the length of a whale at time t in meters. The weight of fluid losses was incorporated into the total mass, as necessary, as suggested by Lockyer (1). Body length on a given day, $L(t)$, was determined using a combination of age-length growth functions for fetuses, calves, juveniles, and adults obtained from the literature and reported below (4-6). For the calf/juvenile age-length function, a *scalar* = 0.276 was used to align the endpoint of the calf/juvenile length function and start point of the adult length function.

$$\text{Fetus} \quad L(t) = (3.5684 \times \text{month}^2 - 3.2984) \times 0.01 \quad (3)$$

$$\text{Calf/juvenile} \quad L(t) = (11.448 + \text{scalar}) \times (1 - e^{-0.977 \times (\text{year} + 0.459)}) \quad (4)$$

$$\text{Adult} \quad L(t) = (45.21 \times 1 - e^{-0.205 \times (\text{year} + 4.936)}) \times 0.3048 \quad (5)$$

For simplicity, we assumed that energy is stored only as blubber, and during periods of fasting or starvation, a whale meets its energy needs by breaking down stored blubber. The weights of blubber and non-blubber tissues (i.e., lean mass) from the literature were used to estimate the proportion of blubber (0.28) and lean mass (0.72) for an average female (1, 2). At birth, the proportion of blubber and lean mass for calves

was 0.31 and 0.69, respectively, with lean mass linearly increasing to 0.72 of a calf's ideal mass at weaning (1, 2, 7).

Female and calf body conditions were expressed as the percentage of blubber mass as a portion of total mass at time t . Lower (5%) and upper (45%) limits were placed on female and calf body conditions, where a body condition $\leq 5\%$ meant that the whale died of starvation. The lower limit refers to the percentage of essential fat estimated for pigs (8, 9) and has also been used in previous bioenergetic models (7, 10). The upper limit for females was calculated from historical whaling data for humpback whales (1, 2), whereas the upper limit for calves is based on the maximum blubber proportion recorded in recently weaned phocid pups (also, fat masses larger than this are expected to impair a calf's swimming performance) (11-13). A lower limit was also placed on the body condition required to support lactation (16%, used in previous bioenergetic models and also corresponds to estimates of ideal fat content (7, 14)); as such, if a female's reserves fell below this threshold, she did not deliver milk to her calf. For ease of derivation of the SDP equations, female and calf body conditions varied in increments of 2.5%.

Cost of growth (C_{growth}). The daily cost of growth (kJ/day) was determined based on a whale's daily increase in mass using the body length and mass functions described above and the following equation (15):

$$C_{growth}(t) = \Delta W(t) \times (e_{lean} + (e_{lean} \times (1 - DE_{lean}))) \quad (6)$$

where $\Delta W(t)$ is the whale's change in body mass from the previous day in kg, e_{lean} is the energy density of lean tissue in kJ/kg, and DE_{lean} is the deposition efficiency of lean mass. To calculate the energy density of lean tissue, the following equation was used (16):

$$e_{lean} = (p_{protein} \times e_{protein}) + (p_{lipid} \times e_{lipid}) \quad (7)$$

where $p_{protein} = 0.2175$ is the proportion of lean mass that is protein (17, 18), $p_{lipid} = 0.065$ is the proportion of lean mass that is lipid (17, 18), $e_{protein} = 23,430$ kJ/kg is the energy density of protein (19), and $e_{lipid} = 39,700$ kJ/kg is the energy density of lipid (19). The deposition efficiency of lean mass was calculated as (16):

$$DE_{lean} = \frac{(p_{protein} \times DE_{protein}) + (p_{lipid} \times DE_{lipid})}{p_{protein} + p_{lipid}} \quad (8)$$

where $DE_{protein} = 0.47$ is the deposition efficiency of protein (8) and $DE_{lipid} = 0.82$ is the deposition efficiency of lipid (20). These deposition efficiency of protein was determined by taking the mean of the minimum and maximum values reported in Malavear (8).

Field metabolic rate (FMR). Mass-specific FMR (kJ/day) was estimated from direct measurements of breaths/minute or breaths/hour for calves, juveniles, and adults on the feeding grounds, during migration, and on the breeding grounds (Table A1).

Table A1. Respiration rates in breaths/minute (presented as mean (SD)) and sources used to calculate respiration rate in breaths/day (mean) for a humpback whale throughout its lifetime depending on location and age class.

Age class	Respiration rate (breaths/minute)	Respiration rate (breaths/day)	Source
Breeding ground			
Juvenile	0.4 (0.04)	570.8	(21)
Adult (non-reproductive/pregnant)	0.4 (0.04)	570.8	(21)
Adult (lactating)	0.7 (0.2)	932.5	(22)
Calf	1.6 (0.4)	2169.1	(22)
Migrating			
Juvenile	0.5 (0.1)	692.8	(21)
Adult (non-reproductive/pregnant)	0.5 (0.1)	692.8	(21)
Adult (lactating)	0.6 (0.1)	841.1	(21)
Calf	1.3 (0)	1873	(21)
Feeding ground			
Juvenile/adult	1.24 (1.06)	1020.8	(23, 24) ¹
Calf	1.1 (0)	1584	(21)

Note: ¹ Juvenile and adult respiration rate on the feeding grounds includes the pooled results of feeding and non-feeding behaviors.

To convert respiration rates to breaths/day, we sampled from a lognormal distribution of breaths per minute, inverted the values to get breath-hold time, and summed the breath-hold times and number of breaths until reaching 24 hours. This process was reiterated as a Monte Carlo simulation 20,000 times to reduce uncertainty and provide a more realistic distribution of respiration rate (25, 26). Daily FMR was calculated using the following equation:

$$FMR(t) = 200 \times \%O_2 \times R \times V_t \quad (9)$$

where 200 is the amount of heat produced in kJ/L O₂ consumed (19), %O₂ = 11% is the mean extraction efficiency per breath based on direct measurements from young

gray whale calves in captivity and at the breeding lagoons (25-27), R is the respiration rate in breaths per day, and V_t is the tidal volume in liters. Tidal volume was estimated as a function of body mass based on different cetacean species, including *Tursiops* spp., pilot whales, gray whales, fin whales, and sei whales (28), as:

$$V_t = 0.074 \times M(t)^{0.90} \quad (10)$$

where $M(t)$ is ideal body mass in kg.

Cost of transport ($C_{transport}$ or COT). During migration, a whale's daily mass-specific COT (kJ/kg/km) was calculated using the following equation (29):

$$C_{transport}(t) = \frac{FMR(t)}{S \times M(t)} \quad (11)$$

where $FMR(t)$ is in kJ/s, S is swimming speed in km/s, and $M(t)$ is body mass in kg. The swim speed used was 4.65 km/hour (30). COT was then used to determine the daily cost of migration as follows:

$$C_{migration} = C_{transport}(t) \times d \times M(t) \quad (12)$$

where $d = 111.67$ km is the distance traveled per day during migration and $M(t)$ is body mass in kg. This approach was used instead of FMR alone to account for a whale's change in total body mass throughout migration.

Energy gained from feeding (E_{gained}). On the feeding grounds, a whale could gain energy by feeding on krill (kJ/day), and the amount of energy gained depended on the whale's physiology and environmental conditions (e.g., available krill biomass, krill regime).

The total energy gained on a given day (kJ/day) was calculated as:

$$E_{gained} = n_{filled} \times f_{capacity} \times ED \times M \quad (13)$$

where n_{filled} is the number of times the forestomach can be filled, $ED = 4,575$ kJ/kg is the energy density of Antarctic krill (31), and $M = 0.85$ is the metabolic efficiency. Metabolic efficiency was estimated from existing values of fecal efficiency (93%) from minke whales (*Balaenoptera acutorostrata*) (32) and predicted values of urinary efficiency (92%) reported in the literature (33-35).

The number of times a whale's forestomach could be filled was calculated as:

$$n_{filled} = \begin{cases} \frac{h_{forage}(t)}{t_j} & \text{if } t_j > t_c \\ \frac{h_{forage}(t)}{t_c} & \text{if } t_j \leq t_c \end{cases} \quad (14)$$

where $h_{forage}(t)$ is the maximum number of hours available for feeding at time t , t_j is the time it takes to fill the forestomach in hours, and $t_c = 3$ hours, which is the time it takes to clear the forestomach (36).

The time available to feed per day depended on the time of year. Along the western Antarctic Peninsula, humpback whales transition between two behavioral modes of diel foraging effort in response to intra-seasonal availabilities of dense krill in the upper water column. In the summer, whales are observed feeding during all hours, while in the fall, whales are observed mostly feeding at night (37, 38). Using information from Nichols et al. (37), simulated whales could feed for 24 hours at the beginning of the feeding season (January) which linearly declined to 16 hours at the

end of feeding season (June); then, from July through December, the time available to feed linearly increased from 16 to 24 hours.

The time it took to fill the forestomach (hours) was calculated as:

$$t_j = \frac{f_{capacity}}{l \times k \times V_{engulf} \times C} \quad (15)$$

where $f_{capacity}$ is the forestomach capacity in kg, l is the number of lunges per hour, k is the krill density encountered, V_{engulf} is the volume of water that can be engulfed per lunge, and $C = 0.9$ is the capture efficiency of krill (39, 40).

A whale's forestomach capacity (kg) was calculated as (7, 36):

$$f_{capacity} = 0.47 \times L(t)^{2.78} \quad (16)$$

where $L(t)$ is the length of the whale at time t in meters.

Lunge rate was determined by calculating the number of lunges it took to fill the forestomach (assuming a whale feeds until it is full), which was a function of the volume of water engulfed per lunge, the krill density encountered, and the capture efficiency of krill.

The volume of water engulfed per lunge (m^3) was calculated as (41):

$$V_{engulf} = \frac{7.063 \times L(t)^{3.255}}{1027} \quad (17)$$

where $L(t)$ is the length of the whale at time t in meters and 1027 kg/m^3 accounts for the density of seawater (40).

Cost of gestation ($C_{\text{gestation}}$). For pregnant females, the daily cost of gestation (kJ/day) was calculated as (adapted from (26)):

$$C_{\text{gestation}}(t) = \frac{\Delta m_f(t)}{m_b} \times (e_b + e_p + h_g) \quad (18)$$

where $\Delta m_f(t)/m_b$ is the proportional change in a fetus's body mass on that day (given $\Delta m_f(t)$ is the change in body mass from the previous day and m_b is a calf's body mass at birth in kg), e_b is the energy content of a newborn calf in kJ, e_p is the energy content of the placenta and other tissues associated with pregnancy in kJ, and h_g is the heat of gestation in kJ. The energy content of the placenta and other tissues assumed a full-term fetus is 80.7% of the total cost of reproductive tissue (14, 42, 43). The energy content in a newborn calf was calculated based on the relative contribution of lipid, protein, and other tissues to its body mass using the following equation (26):

$$e_b = (m_b \times p_{\text{lipid}} \times e_{\text{lipid}}) + (m_b \times p_{\text{protein}} \times e_{\text{protein}}) \quad (19)$$

where m_b is the calf's body mass at birth in kg, p_{lipid} and p_{protein} are the proportions of lipid and protein found in the fetus, $e_{\text{lipid}} = 39,700$ kJ/kg is the energy density of lipid (19), and $e_{\text{protein}} = 26,600$ kJ/kg is the energy density of protein (19). Empirical measurements of p_{lipid} and p_{protein} are not available for newborn humpback whales; therefore, we used a percent lipid mass estimate of 5% ($p_{\text{lipid}} = 0.05$) found in ringed seal neonates (44) and a percent protein mass estimate of 12.6% ($p_{\text{protein}} = 0.126$) calculated for gray whale neonates (26), both of which have been used in previous

bioenergetic models for gray whales (25, 26, 45). The heat of gestation (kJ) was determined using the following equation (46):

$$h_g = (4,400 \times m_b^{1.2}) \times 4.184 \quad (20)$$

where m_b is the calf's body mass at birth in kg and multiplying by 4.184 converts kcal to kJ.

Cost of lactation ($C_{lactation}$). For lactating females, the daily cost of lactation (kJ/day) depends on the amount of milk delivered to the calf, which is a function of the calf's needs and the female's current condition, and was calculated as follows (7):

$$C_{lactation} = D_{milk}(t) \times \frac{e_{milk}}{E} \quad (21)$$

where $D_{milk}(t)$ is the amount of milk delivered to the calf in kg at time t , $e_{milk} = 19,400$ kJ/kg is the energy content in the female's milk (47), and $E = 0.9$ is the mammary gland efficiency of milk production (18). The amount of milk delivered to the calf on a given day was determined using the following logic: if the female's lipid reserves (after accounting for her own energetic needs) were less than or equal to the blubber mass threshold required to support lactation (16% (7, 14)), no milk was delivered to the calf; if the female's lipid reserves were greater than the lactation threshold but less than the maximum amount of milk that can be delivered on a given day (125 kg (47)), she delivered what she could spare as milk; and if the female's lipid reserves were greater than the amount of milk that could be delivered on a given day, she delivered the maximum amount of milk to the calf and stored the excess energy as

blubber. On days when the calf's energetic needs were not completely met, the calf relied on its own reserves.

Changes in body condition (x). A whale's body condition was calculated as the percentage of its blubber mass as a portion of total body mass. Changes in its blubber mass, and subsequently body condition, from one time step (time = t) to the next (time = $t + 1$) depended on energetic costs and gains (if any) from foraging or, in the case of the calf, from nursing. Thus, for a whale with blubber mass $b(t)$ in kg, its updated blubber mass $b(t + 1)$ in kg would be calculated as:

$$b(t + 1) = b(t) - \frac{(C_{total}(t) + E_{gained}(t))}{e_{lipid}} \quad (22)$$

where $C_{total}(t)$ are the whale's total daily energetic costs in kJ, $E_{gained}(t)$ are the energetic gains in kJ, and $e_{lipid} = 39,700$ kJ/kg is the energy density of lipid (19).

The whale's updated body condition (%) would then be calculated as:

$$x(t + 1) = \frac{b(t + 1)}{b(t + 1) + (l \times M(t + 1))} \times 100 \quad (23)$$

where $b(t + 1)$ is the whale's updated blubber mass, l is the proportion of body mass that is lean, $M(t + 1)$ is a whale's ideal body mass on day $t + 1$.

Table A2. Physiological parameters used in the SDP model.

Parameter	Description	Value	Unit	Reference
x_{max}	Max female body condition threshold	45	%	(1, 2)
x_{min}	Min female body condition threshold	5	%	(7-9)
$x_{lactation}$	Female body condition threshold for lactation	16	%	(7, 14)
m_{max}	Max calf body condition threshold	45	%	(11-13)
m_{min}	Min calf body condition threshold	5	%	(7-9)
m_{50}	Calf body condition threshold at which survival probability is 50%	28	%	(1, 2)
$p_{s,a}$	Daily probability of survival for juveniles and adults	$0.96^{1/365}$	...	(48)
$p_{s,c}$	Daily probability of survival for calves	$0.87^{1/365}$	...	(48)
$p_{s,f}$	Daily probability of survival for fetuses	$0.865^{1/365}$	...	(49)
e_{lipid}	Energy density of lipid	39,700	kJ/kg	(19)
$e_{protein}$	Energy density of protein	26,600	kJ/kg	(19)
DE_{lipid}	Deposition efficiency of lipid	0.82	...	(8)
$DE_{protein}$	Deposition efficiency of protein	0.47	...	(8)
p_{lipid}	Proportion of lipid found in fetus	0.05	...	(44)
$p_{protein}$	Proportion of protein found in fetus	0.126	...	(26)
t_c	Time to clear forestomach	3	hours	(36)
M	Metabolic efficiency	0.85	...	(32, 33)
M_{max}	Max amount of milk delivered per day	125	kg/day	(47)
e_{milk}	Milk energy content	19,400	kJ/kg	(47)
E	Mammary gland efficiency	0.9	...	(18)

2.9.3 Appendix C: Krill densities and regimes in the backward iteration

Calculating fitness across krill densities. In the model, the feeding grounds were comprised of discrete densities of krill (kg/m^3) that varied both seasonally and interannually, as well as in their probability of being encountered. Therefore, on a given day, a whale had the probability $p_k(e, l, t, k)$ of encountering krill density k , which depended on the krill regime (e), location (l) of the whale (on the feeding grounds or not; if not, $p(e, l, t, k) = 0$) and time (t). Therefore, for a whale in reproductive state r with body condition x (and calf body condition m , when lactating) on the feeding grounds, we calculated the fitness associated with the behavioral decision to stay on the feeding grounds and feed as follows:

$$V_{r,feed}(x, l, e, t + 1) = p_{s,a} \times \left(\sum_k p_k(e, l, t, k) \times F_r(x', l, e, t + 1) \right)$$

where $p_{s,a}$ is the daily survival probability for juveniles and adults (48) and $\sum_k p_k(e, l, t, k) \times F_r(x', l, e, t + 1)$ describes an averaging across all possible sources of stochasticity. To do this, we took the weighted average of encountering each krill density based on the probability of encountering that density.

Transitioning between krill regimes. We modeled the transition between three krill regimes, representing high, medium, and low krill conditions, to capture humpback whales' adaptation to the interannual variability of krill. For baseline environmental conditions, we assumed a repeated pattern of 5-year cycle (i.e., medium, high, medium, medium, low) based on krill recruitment patterns in Steinberg et al. (50). The probability of a year being a high krill regime was $\rho_h = 0.2$, a medium krill regime

was $\rho_m = 0.6$, and a low krill regime was $\rho_l = 0.2$. The shift between the regimes could occur on day 92 (October 31) of each simulated year or $t_e(a) = 92 + a \times 365$ in model time, where a is the whale's age in years.

For a whale in reproductive state r with body condition x in location l (and calf body condition m , when lactating) on day $t \neq t_e(a)$:

$$\begin{aligned} F_{r,h}(x, l, e, t) &= \max\{V_{r,h,b}(x, l, e, t + 1)\} \\ F_{r,m}(x, l, e, t) &= \max\{V_{r,m,b}(x, l, e, t + 1)\} \\ F_{r,l}(x, l, e, t) &= \max\{V_{r,l,b}(x, l, e, t + 1)\} \end{aligned}$$

where $F_{r,h}(x, l, e, t)$, $F_{r,m}(x, l, e, t)$, and $F_{r,l}(x, l, e, t)$ represent the fitness values of behavioral choice b under high, medium, and low krill regimes, respectively. However, on day $t = t_e(a)$:

$$\begin{aligned} F_r(x, l, e, t) &= \max\{\rho_h \times V_{r,h,b}(x, l, e, t + 1) + \rho_m \times V_{r,m,b}(x, l, e, t + 1) \\ &\quad + \rho_l \times V_{r,l,b}(x, l, e, t + 1)\} \end{aligned}$$

where a whale's fitness is the weighted average of behavioral choice b under high, medium, and low krill regimes.

2.9.4 Appendix D: SDP equations

State functions

Calf	If stay/move (not weaned): $b' = b - \frac{(FMR(t) + C_{growth}(t) - D_{milk}(t)) \times DE_{lipid}}{e_{lipid}}$ If stay/move (weaned but prior to t_{wean}): $b' = b - \frac{(FMR(t) + C_{growth}(t)) \times DE_{lipid}}{e_{lipid}}$
Non-reproductive juvenile or adult	If stay (feeding): $b' = b - \frac{(FMR(t) + C_{growth}(t) - E_{gained}) \times DE_{lipid}}{e_{lipid}}$ If stay (breeding): $b'' = b - \frac{(FMR(t) + C_{growth}(t)) \times DE_{lipid}}{e_{lipid}}$ If move: $b''' = b - \frac{((C_{transport}(t) \times d \times M(t)) + C_{growth}(t)) \times DE_{lipid}}{e_{lipid}}$
Pregnant	If stay (feeding): $b' = b - \frac{(FMR(t) + C_{growth}(t) + C_{gestation}(t) - E_{gained}) \times DE_{lipid}}{e_{lipid}}$ If stay (breeding): $b'' = b - \frac{(FMR(t) + C_{growth}(t) + C_{gestation}(t)) \times DE_{lipid}}{e_{lipid}}$ If move: $b''' = b - \frac{((C_{transport}(t) \times d \times (M(t) + m_f(t))) + C_{growth}(t) + C_{gestation}(t)) \times DE_{lipid}}{e_{lipid}}$

Lactating

If stay (feeding): $b' = b - \frac{(FMR(t) + C_{growth}(t) + C_{lactation}(t) - E_{gained}) \times DE_{lipid}}{e_{lipid}}$

If stay (breeding): $b'' = b - \frac{(FMR(t) + C_{growth}(t) + C_{lactation}(t)) \times DE_{lipid}}{e_{lipid}}$

If move: $b''' = b - \frac{((C_{transport}(t) \times d \times M(t)) + C_{growth}(t) + C_{lactation}(t)) \times DE_{lipid}}{e_{lipid}}$

Pregnant & lactating

If stay (feeding): $b' = b - \frac{(FMR(t) + C_{growth}(t) + C_{gestation}(t) + C_{lactation}(t) - E_{gained}) \times DE_{lipid}}{e_{lipid}}$

If stay (breeding): $b'' = b - \frac{(FMR(t) + C_{growth}(t) + C_{gestation}(t) + C_{lactation}(t)) \times DE_{lipid}}{e_{lipid}}$

If move: $b''' = b - \frac{((C_{transport}(t) \times d \times (M(t) + m_f(t))) + C_{growth}(t) + C_{gestation}(t) + C_{lactation}(t)) \times DE_{lipid}}{e_{lipid}}$

Reproductive state	r
Non-reproductive juvenile	1
Non-reproductive adult	2
Pregnant	3
Lactating	4
Pregnant & lactating	5

Fitness functions

Non-reproductive juvenile or adult	If stay (feeding): $V_{r,feed}(x, l, e, t + 1) = p_{s,a} \times (\sum_k p_k(e, l, t, k) \times F_r(x', l, e, t + 1))$
	If stay (breeding): $V_{r,breed}(x, l, e, t + 1) = p_{s,a} \times F_r(x'', l, e, t + 1)$
	If move forward: $V_{r,forward}(x, l, e, t + 1) = p_{s,a} \times F_r(x''', l + 1, e, t + 1)$
	If move backward: $V_{r,backward}(x, l, e, t + 1) = p_{s,a} \times F_r(x''', l - 1, e, t + 1)$
Pregnant	If stay (feeding): $V_{r,feed}(x, l, e, t + 1) = p_{s,a} \times p_{s,f} \times (\sum_k p_k(e, l, t, k) \times F_r(x', l, e, t + 1))$
	If stay (breeding): $V_{r,breed}(x, l, e, t + 1) = p_{s,a} \times p_{s,f} \times F_r(x'', l, e, t + 1)$
	If move forward: $V_{r,forward}(x, l, e, t + 1) = p_{s,a} \times p_{s,f} \times F_r(x''', l + 1, e, t + 1)$
	If move backward: $V_{r,backward}(x, l, e, t + 1) = p_{s,a} \times p_{s,f} \times F_r(x''', l - 1, e, t + 1)$
Lactating	If stay (feeding): $V_{r,feed}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times (\sum_k p_k(e, l, t, k) \times F_r(x', m', l, e, t + 1))$
	If stay (breeding): $V_{r,breed}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times F_r(x'', m', l, e, t + 1)$
	If move forward: $V_{r,forward}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times F_r(x''', m', l + 1, e, t + 1)$
	If move backward: $V_{r,backward}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times F_r(x''', m', l - 1, e, t + 1)$

Pregnant & lactating	If stay (feeding): $V_{r,feed}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times p_{s,f} \times (\sum_k p_k(e, l, t, k) \times F_r(x', m', l, e, t + 1))$
	If stay (breeding): $V_{r,breed}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times p_{s,f} \times F_r(x'', m', l, e, t + 1)$
	If move forward: $V_{r,forward}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times p_{s,f} \times F_r(x''', m', l + 1, e, t + 1)$
	If move backward: $V_{r,backward}(x, m, l, e, t + 1) = p_{s,a} \times p_{s,c} \times p_{s,f} \times F_r(x''', m', l - 1, e, t + 1)$

Terminal fitness and calf survival functions

Terminal fitness function	No calf: $\phi(x) = 0$
	Calf: $\phi(x, m) = \varphi(m)$

Calf survival function	$\varphi(m) = \frac{m^\gamma}{m^\gamma + m_{50}^\gamma}$
------------------------	--

Optimal movement decision

Non-reproductive juvenile or adult, or pregnant	Feeding ground: $\langle F_r \rangle = \max \{V_{r,feed}(x, l, e, t + 1), V_{r,backward}(x, l, e, t + 1)\}$
	Breeding ground: $\langle F_r \rangle = \max \{V_{r,breed}(x, l, e, t + 1), V_{r,forward}(x, l, e, t + 1)\}$
	Migratory corridor: $\langle F_r \rangle = \max \{V_{r,forward}(x, l, e, t + 1), V_{r,backward}(x, l, e, t + 1)\}$

Lactating or pregnant & lactating

Feeding ground: $\langle F_r \rangle = \max \{V_{r,feed}(x, m, l, e, t + 1), V_{r,backward}(x, m, l, e, t + 1)\}$

Breeding ground: $\langle F_r \rangle = \max \{V_{r,breed}(x, m, l, e, t + 1), V_{r,forward}(x, m, l, e, t + 1)\}$

Migratory corridor: $\langle F_r \rangle = \max \{V_{r,forward}(x, m, l, e, t + 1), V_{r,backward}(x, m, l, e, t + 1)\}$

Optimal reproductive decision

When $r = 1$ $F_1(x, l, e, t) = \langle F_1 \rangle$

When $r = 2$ $F_2(x, l, e, t) = \langle F_2 \rangle$

If $t = t_{implant}$: $V_2(x, l, e, t) = \max \{\langle F_2 \rangle, \langle F_3 \rangle\}$

When $r = 3$ $F_3(x, l, e, t) = \max \{\langle F_2 \rangle, \langle F_3 \rangle\}$

If $t = t_{born}$: $V_3(x, l, e, t) = \max \{\langle F_2 \rangle, \langle F_4 \rangle\}$

When $r = 4$ $F_4(x, m, l, e, t) = \max \{\langle F_2 \rangle + \varphi(m), \langle F_4 \rangle\}$

If $t = t_{implant}$: $V_4(x, m, l, e, t) = \max \{\langle F_2 \rangle + \varphi(m), \langle F_3 \rangle + \varphi(m), \langle F_4 \rangle, \langle F_5 \rangle\}$

If $t = t_{wean}$: $V_4(x, m, l, e, t) = \langle F_2 \rangle + \varphi(m)$

When $r = 5$ $F_5(x, m, l, e, t) = \max \{\langle F_2 \rangle + \varphi(m), \langle F_3 \rangle + \varphi(m), \langle F_4 \rangle, \langle F_5 \rangle\}$

If $t = t_{wean}$: $V_5(x, m, l, e, t) = \max \{\langle F_2 \rangle + \varphi(m), \langle F_3 \rangle + \varphi(m)\}$

2.9.5 Appendix E: Creating a stable-age distribution and identifying starting conditions for the forward simulation

A stable-age distribution was created using the dominant eigenvector of a Leslie matrix comprised of an annual survival probability for juveniles and adults (0.96 (48)) and an annual fecundity (0.202). Fecundity was estimated based on a mean birth interval (2.38 (48)) and accounted for a 50:50 sex ratio at birth and the survival rate of an adult female (48, 51). As in the SDP model, whales became sexually mature at 5 years old and could live to be 80 years old. The Leslie matrix and eigenvector were calculated using the popbio package in R (version 4.3.1) (52, 53).

To determine an individual's starting body condition, reproductive state, and location, we ran a forward simulation for a population of 1000 whales from weaning until death under a medium krill regime. We recorded an individual's body condition, reproductive state, and location on day 1 (August 1) of each simulated year to create distributions of body condition based on age and reproductive state, and to calculate the proportion of mature individuals that are either in a non-reproductive adult, pregnant, lactating, or pregnant and lactating state for each age class. When assigning reproductive states, immature females (< 5 years old) were identified as juveniles; for mature whales, an individual's reproductive state was assigned based on age-specific probabilities of being in a non-reproductive adult or lactating state (on day 1, sexually mature whales cannot be pregnant or pregnant and lactating). Then, a starting body condition was sampled from a distribution of body conditions based on the individual's

age and reproductive state. Finally, a starting location was sampled from a distribution of locations based on the individual's reproductive state.

With a stable-age structured population of 200 individuals, each with a starting body condition, reproductive state, and location, we ran a second forward simulation for a normalization period of 5 years, beginning on day 1 (August 1) of each simulated year, the day a pregnant female gives birth; thus, the initial population size was greater than 200. A normalization period of 5 years was chosen to ensure that model outputs would not be impacted by initial model parameterization. The resulting population (including age, body condition, reproductive state, and location) was then used as the starting population in subsequent simulations for baseline and stressor scenarios.

2.9.6 Appendix F: Sensitivity analysis

Table F1 provides a list of model parameters tested in the sensitivity analysis. Table F2 provides a list of key vital rates (i.e., pregnancy, birth, weaning success, and population growth rates) and their values from the original model. Details of how each model parameter affected model results under baseline conditions are reported below with summary tables (Tables F3 through F7). Each summary table lists the four key vital rates, their value using the adjusted model parameter, and the Cohen's d value to assess the effect of the adjustment on the associated vital rate. Positive values indicate an adverse effect while negative values indicate a positive effect on vital rates, with values of ± 0.2 , ± 0.5 , and ± 0.8 indicating small, medium, and large effects, respectively. The values for the vital rates in the summary tables are presented as mean (SD).

Table F1. List of model parameters tested in the sensitivity analysis.

Model parameter/description	Original value	Sensitivity combinations
Maximum threshold for female body condition	45%	40%, 50%
Age threshold for mother/calf to leave breeding grounds	50 days	$\pm 50\%$
Multiplier for medium krill density	0.65	$\pm 25\%$
Shape parameter of the fitness function	8	$\pm 25\%$
Scale parameter of the fitness function	0.28	$\pm 25\%$

Table F2. List of key vital rates and their values from the original model.

Life-history parameter	Mean	SD
Pregnancy rate (%) ¹	72.62	7.57
Birth rate (%)	44.96	4.62
Weaning success rate (%)	71.64	13.37
Population growth rate (%)	5.9	2.54

Notes: ¹Calculated on day 185 (February 1) of each simulated year and includes only sexually mature whales (≥ 5 years old).

Maximum threshold for female body condition. Reducing the maximum body condition threshold had large and small adverse effects on weaning success and population growth rates, respectively. With a smaller reserve to store energy, fewer females were successfully weaned and added to the population, with those who were pregnant and lactating often choosing to wean and abandon their calves early (September 28 ± 36 days) to maintain their pregnancy. Of the females who were both pregnant and lactating, regardless of whether the calf was successfully weaned, 17.51% ($\pm 9.00\%$) gave birth the following year, which is higher than in the original model ($7.89\% \pm 3.95\%$). For females who successfully weaned a calf, weaning occurred later, on average (June 7 ± 9 days), than in the original model (May 19 ± 10 days). Of the females who were both pregnant and lactating and successfully weaned their calf, $0.19\% \pm 0.95\%$ gave birth the following year. In contrast, increasing the maximum body condition threshold led to an adverse effect on pregnancy rate and a positive effect on weaning success rate. With a larger reserve to store energy, more females successfully weaned their calves, with females who were both pregnant and lactating often choosing to abort their pregnancy to ensure their calf was weaned successfully,

with fewer females successfully weaning a calf while pregnant ($1.12\% \pm 2.30\%$). For females who successfully weaned their calves, weaning occurred later, on average (May 30 ± 9 days), than in the original model. Of the females who were both pregnant and lactating and successfully weaned their calf, $10.06\% \pm 21.52\%$ of them gave birth the following year.

Table F3. Summary table for the sensitivity analysis for the maximum threshold for female body condition.

Life-history parameter	Max = 40%	Cohen's <i>d</i>	Max = 50%	Cohen's <i>d</i>
Pregnancy rate (%)	71.13 (8.91)	0.18	67.76 (6.74)	0.68
Birth rate (%)	44.38 (13.85)	0.06	44.87 (8.61)	0.01
Weaning success rate (%)	52.95 (22.65)	1.00	76.71 (14.77)	-0.36
Population growth rate (%)	4.37 (5.31)	0.37	6.38 (3.26)	-0.16

Age threshold for mother/calf to leave breeding grounds. Shifting the age threshold to day 25 (August 25) meant mothers and calves could leave the breeding grounds earlier. As expected, this had a large effect on pregnancy and birth rates since females who were lactating or pregnant and lactating could reach the feeding grounds earlier and did not have to rely on their energy reserves for an extended period. Subsequently, this allowed more females who were simultaneously pregnant and lactating to maintain both their calf and pregnancy, which led to an increased rate of weaning success while pregnant ($22.24\% \pm 16.69\%$) and birth the following year ($37.16\% \pm 25.21\%$). This led to a small, positive effect on the population growth rate. Shifting the age threshold to day 75 (October 15) meant that mothers and calves left

the breeding grounds later, and females had to rely on their energy reserves for an extended period. This resulted in large effects on pregnancy rates and birth rates, with females choosing to abort their pregnancy and keep nursing their calf or abandon both their pregnancy and calf. Subsequently, this led to a lower weaning success rate and population growth rate.

Table F4. Summary table for the sensitivity analysis for the age threshold (for the calf, in days) for a mother/calf to leave the breeding grounds.

Life-history parameter	Day = 25	Cohen's <i>d</i>	Day = 75	Cohen's <i>d</i>
Pregnancy rate (%)	81.20 (4.90)	-1.35	59.50 (5.150)	2.03
Birth rate (%)	50.44 (7.18)	-0.91	39.81 (8.43)	0.76
Weaning success rate (%)	73.69 (13.26)	-0.15	66.66 (17.26)	0.32
Population growth rate (%)	6.91 (2.83)	-0.38	4.74 (3.41)	0.39

Multiplier for medium krill regime. To be expected, when the multiplier was reduced, the krill densities available in a given month, season, or year were lower, which led to a decrease in all four key vital rates. This also meant fewer whales were both pregnant and lactating in a given year, with it being very rare that a female successfully weaned a calf while pregnant ($0.13\% \pm 0.40\%$) and gave birth the following year ($0.67\% \pm 3.00\%$). In contrast, when the multiplier increased, meaning the krill densities available were higher, the population's vital rates increased. This also meant that more females were both pregnant and lactating in a given year, with $19.07\% \pm 12.53\%$ of females successfully weaning a calf while pregnant and $26.44\% \pm 30.09\%$ of the females who successfully weaned a calf giving birth the following year.

Table F5. Summary table for the sensitivity analysis for the multiplier for the medium krill regime.

Life-history parameter	Multiplier = 0.4875	Cohen's <i>d</i>	Multiplier = 0.8125	Cohen's <i>d</i>
Pregnancy rate (%)	67.02 (5.83)	0.83	82.95 (5.72)	-1.54
Birth rate (%)	40.43 (13.24)	0.46	50.76 (7.26)	-0.95
Weaning success rate (%)	64.90 (24.18)	0.34	76.69 (7.54)	-0.47
Population growth rate (%)	4.82 (5.01)	0.27	7.20 (2.05)	-0.56

Shape parameter of the fitness function. In the model, the shape parameter influenced the steepness of the fitness function. Varying this parameter by $\pm 25\%$ from the original value had negligible effects on most vital rates except for a small effect on pregnancy rate when the shape parameter was larger. In this case, as the steepness of the function increased, the calf's probability of survival for a given condition also increased. As a result, females generally weaned their calves earlier, with an average wean date on April 6 (± 80 days), with those who were successfully weaned being weaned, on average, on May 14 (± 7 days). With calves weaned earlier, more females who were both pregnant and lactating were able to maintain their pregnancy, resulting in an increased rate of weaning success while pregnant ($11.89 \pm 10.99\%$).

Table F6. Summary table for the sensitivity analysis for the shape parameter of the fitness function.

Life-history parameter	Shape = 6	Cohen's <i>d</i>	Shape = 10	Cohen's <i>d</i>
Pregnancy rate (%)	71.61 (7.55)	0.13	74.47 (6.15)	-0.27
Birth rate (%)	44.12 (5.38)	0.17	45.75 (4.84)	-0.17
Weaning success rate (%)	69.02 (13.91)	0.19	72.89 (13.40)	-0.09
Population growth rate (%)	5.53 (2.73)	0.14	6.17 (2.67)	-0.10

Scale parameter of the fitness function. In the model, the scale parameter of the fitness function is the proportion of blubber mass at which the calf has a 50% chance of surviving and being added to the population. Therefore, a value higher than what was used in the original model meant that the calf had to be in better body condition at 10.5 months old (when it can be added to the population) and vice versa when this value was lower. When this value was higher, there were medium effects on pregnancy, birth, and weaning success rates and small effects on population growth rate. The decrease in pregnancy and birth rates was generally mediated by females who were both pregnant and lactating aborting their pregnancy to dedicate energy to their calf or abandoning both their pregnancy and calf. As a result, there were lower rates of weaning success while pregnant ($0.18\% \pm 0.50\%$) and birth following a successful weaning ($3.52\% \pm 13.84\%$). When this parameter was reduced, there was a minimal effect on weaning success rate but a small effect on population growth rate and large effects on pregnancy and birth rates. As a result, females generally weaned their calves earlier, with an average wean date on March 16 (± 74 days), with successfully weaned calves being weaned, on average, on simulation April 20 (± 5 days). With calves

weaned earlier, more females who were both pregnant and lactating were able to maintain their pregnancy, resulting in an increased rate of weaning success while pregnant ($28.49\% \pm 20.08\%$) and birth following a successful weaning ($14.13\% \pm 16.08\%$).

Table F7. Summary table for the sensitivity analysis for the scale parameter of the fitness function.

Life-history parameter	Scale = 0.21	Cohen's <i>d</i>	Scale = 0.35	Cohen's <i>d</i>
Pregnancy rate (%)	79.56 (5.50)	-1.05	67.38 (8.570)	0.65
Birth rate (%)	49.40 (6.13)	-0.82	42.27 (6.59)	0.47
Weaning success rate (%)	74.02 (11.38)	-0.19	65.08 (14.80)	0.47
Population growth rate (%)	6.65 (2.66)	-0.29	4.96 (2.95)	0.34

2.9.7 Appendix G: Tables of life-history parameters and Cohen's *d* values

Table G1. Calculated life-history parameters under baseline conditions (no stressors).

Life-history parameter	Mean	SD
Age at first birth (years)	6.14	0.4
Interbirth interval (years)	2.41	0.5
Weaning month/day for successfully weaned calves	May 19	10 days
Pregnancy rate (%) ¹ (August 16)	88.97	4.3
Pregnancy rate (%) ² (February 1)	72.62	7.57
Birth rate (%)	44.96	4.62
Weaning success rate (%)	71.64	13.37
First year survival rate (%)	95.83	3.13
Population growth rate (%)	5.9	2.54
Pregnant and lactating (%) ³ (August 16)	100	0
Pregnant and lactating (%) ⁴ (February 1)	60.31	25.3
Successful weaning while pregnant (%) ⁵	5.48	4.76
Birth after a successful weaning (%) ⁶	9.45	19.36
Recruitment rate (%) ⁷	80.07	6.74
Death rate (%)	3.36	0.74
Population growth rate (%)	5.9	2.54

Notes: ¹ Calculated on day 16 (August 16, the day after a whale can implant) of each simulated year and includes only sexually mature whales (≥ 5 years old); ² calculated on day 185 (February 1) of each simulated year and includes only sexually mature whales (≥ 5 years old); ³ calculated on day 16 of each simulated year and captures the percentage of whales that are lactating that are also pregnant; ⁴ calculated on day 185 of each simulated year and captures the percentage of lactating whales that are also pregnant; ⁵ percentage of whales that successfully weaned a calf while pregnant; ⁶ percentage of whales that gave birth after successfully weaning a calf while pregnant in the previous year; ⁷ percentage of calves in a given cohort (i.e., calves born in the same year) who reached sexual maturity and successfully gave birth.

Table G2. Selected life-history parameters under the climate change stressor scenarios. Pregnancy rate was calculated on day 185 (February 1) of each simulated year.

Life-history parameter	Mean	SD	Cohen's <i>d</i>
Climate change (10%)			
Pregnancy rate (%)	68.43	8.12	0.53
Birth rate (%)	42.74	9.40	0.30
Weaning success rate (%)	62.71	20.71	0.51
Population growth rate (%)	4.81	4.50	0.30
Climate change (25%)			
Pregnancy rate (%)	67.04	9	0.67

Birth rate (%)	38.4	16.84	0.53
Weaning success rate (%)	58.76	22.67	0.69
Population growth rate (%)	3.96	6.29	0.4
Climate change (50%)			
Pregnancy rate (%)	43.22	22.33	1.76
Birth rate (%)	18.03	23.75	1.57
Weaning success rate (%)	30.63	35.83	1.52
Population growth rate (%)	-4.31	14.19	1

Table G3. Selected life-history parameters under the combined climate change and krill fishing stressor scenarios. In the climate change (50%) and krill fishing (50%) stressor scenario, the population crashed before the 25-year simulation completed, as indicated by the dashes in the columns. Pregnancy rate was calculated on day 185 (February 1) of each simulated year.

Life-history parameter	Mean	SD	Cohen's <i>d</i>
Climate change (10%), krill fishing (10%)			
Pregnancy rate (%)	68.36	8.01	0.55
Birth rate (%)	41.99	10.54	0.36
Weaning success rate (%)	62.46	21.12	0.52
Population growth rate (%)	4.76	4.79	0.3
Climate change (10%), krill fishing (25%)			
Pregnancy rate (%)	67.59	8.14	0.64
Birth rate (%)	40.55	12.37	0.47
Weaning success rate (%)	62.28	21.36	0.53
Population growth rate (%)	4.57	5.01	0.33
Climate change (10%), krill fishing (50%)			
Pregnancy rate (%)	62.06	10.83	1.13
Birth rate (%)	35.3	15.09	0.87
Weaning success rate (%)	58.82	22.2	0.7
Population growth rate (%)	3.11	6.06	0.6
Climate change (25%), krill fishing (10%)			
Pregnancy rate (%)	65.95	9.74	0.76
Birth rate (%)	37.68	17.15	0.58
Weaning success rate (%)	58.3	22.95	0.71
Population growth rate (%)	3.74	6.37	0.45
Climate change (25%), krill fishing (25%)			
Pregnancy rate (%)	61.07	10.83	1.24
Birth rate (%)	34.29	16.94	0.86
Weaning success rate (%)	56.06	25.15	0.77
Population growth rate (%)	2.6	6.92	0.63
Climate change (25%), krill fishing (50%)			
Pregnancy rate (%)	57.56	11.08	1.59

Birth rate (%)	31.12	16.72	1.13
Weaning success rate (%)	53.03	27.11	0.87
Population growth rate (%)	0.95	7.98	0.84
Climate change (50%), krill fishing (10%)			
Pregnancy rate (%)	38.32	21.04	2.17
Birth rate (%)	17.78	21.64	1.74
Weaning success rate (%)	28.99	34.52	1.63
Population growth rate (%)	-6.01	14.58	1.14
Climate change (50%), krill fishing (25%)			
Pregnancy rate (%)	32.74	22.26	2.4
Birth rate (%)	17.33	20.89	1.83
Weaning success rate (%)	26.68	33.64	1.76
Population growth rate (%)	-10.48	18	1.27
Climate change (50%), krill fishing (50%)			
Pregnancy rate (%)	-	-	-
Birth rate (%)	-	-	-
Weaning success rate (%)	-	-	-
Population growth rate (%)	-	-	-

2.9.8 Appendix H: Additional figures

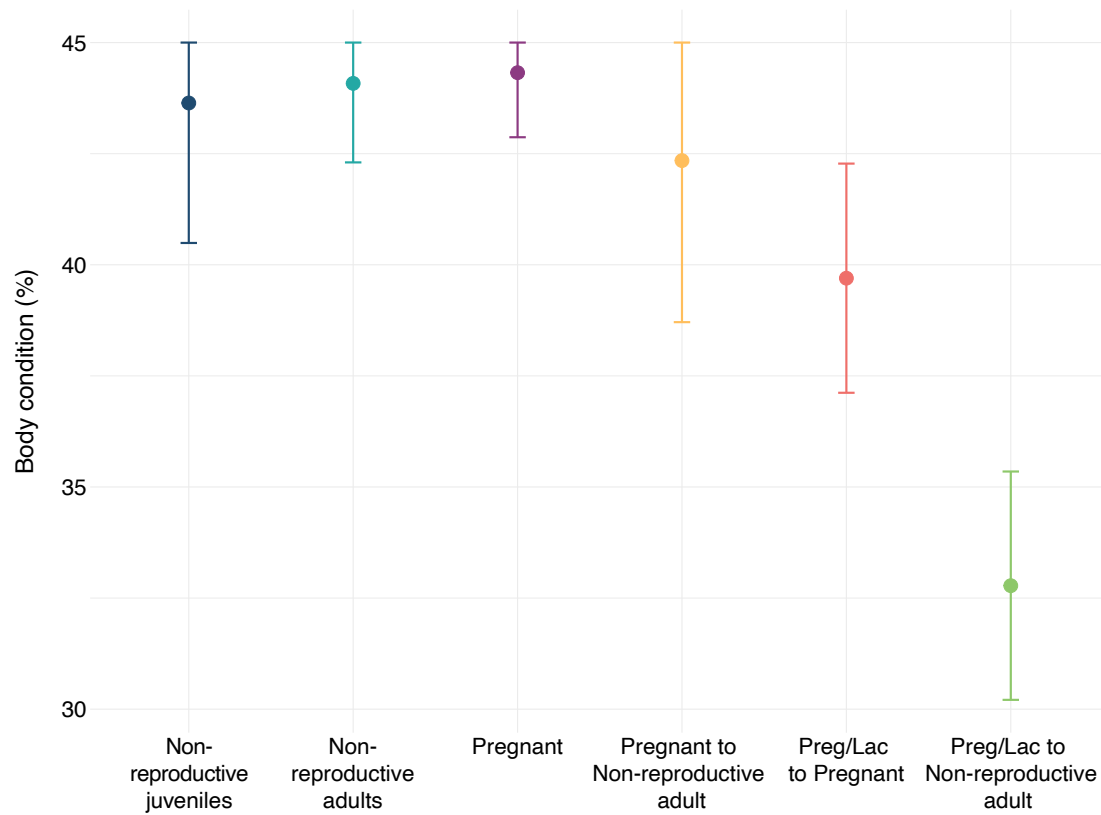


Figure H1. Body condition at the end of the feeding season as a function of reproductive state; the error bars represent the standard deviation (max body condition = 45%). For non-reproductive juvenile, non-reproductive adult, and pregnant states, whales arrived on and departed from the feeding grounds in the same reproductive state. Pregnant to non-reproductive adult, pregnant and lactating (preg/lac) to pregnant, and preg/lac to non-reproductive adult represent reproductive state transitions that occurred on the feeding grounds, where the first reproductive state was a whale's state the day it arrived on the feeding grounds and the second reproductive state was the whale's state the day it departed the feeding grounds. Other reproductive states or transitions (e.g., lactating, lactating to non-reproductive adult) did not occur on those days (arriving on or departing from the feeding grounds) and, therefore, are not included in the figure.

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Chapter 3: Spatial and temporal sensitivities of an endangered humpback whale population to anthropogenic stressors in the California Current Ecosystem

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3.1 Abstract

Changes in prey abundance, composition, and distribution influence predators' foraging ecology, potentially exacerbating the effects of human stressors on population dynamics. In the California Current Ecosystem, seasonal and interannual variability in krill and fish availability affect humpback whale distribution. These factors consequently mediate a whale's exposure to existing (e.g., naval sonar, shipping, fishing, wildlife tourism) and proposed (e.g., offshore wind farms) anthropogenic stressors. In this study, we developed a spatially explicit, dynamic state model to investigate the influence of environmental variability on prey choice and humpback whale distribution, the spatial and temporal sensitivities of whales on their California and Oregon feeding grounds, and how a stressor's temporal features influence a population's fitness. We simulated stressors using a Monte Carlo approach and tracked individuals' reproductive and movement decisions to quantify the effect of stressors on population vital rates. Emergent model properties included interannual shifts in diet, movement patterns, and seasonal changes in body condition. The spatial use patterns of simulated whales were driven by seasonal and interannual variability, which influenced the effects of stressors on vital rates. Overall, stressors located offshore the central and north central coasts of California and southern and central Oregon had the

greatest impact on vital rates. Specifically, the most sensitive locations and times were offshore the Big Sur coast in spring, the greater Monterey Bay area in summer, and offshore San Francisco and the Greater Farallones region in fall. However, adjusting the temporal features of a stressor reduced impacts on vital rates, especially when the stressor was in important feeding locations during energetically vulnerable and reproductively sensitive times. Models such as the one we present in this study can provide a general framework to identify sensitive feeding times and areas for vulnerable populations, as well as a quantitative basis for comparing different stressor scenarios associated with our expanding offshore footprint.

3.2 Introduction

Human activities have had widespread and pervasive impacts on our oceans (1), leading to habitat degradation and even species extinction (2-4). These impacts are continually evolving, either due to the expansion of existing uses (e.g., shipping, fishing) or the emergence of new ones (e.g., ocean mining, offshore industrial development), and they are likely to be exacerbated by climate change pressures, such as ocean warming and acidification (5). If current trajectories persist, many ocean ecosystems may be pushed past a critical tipping point of sustainability (6, 7). With our offshore footprint projected to expand in the future (6), we must understand the spatial and temporal extent of anthropogenic stressors and their effects on the ocean and marine wildlife. This information can help managers make more informed decisions to sustain healthy oceans and protect vulnerable wildlife populations while ensuring our oceans can continue supporting human uses.

Baleen whales are important in the function and structure of marine ecosystems through nutrient cycling, ocean fertilization, and carbon sequestration (8, 9). Throughout most of the 19th and 20th centuries, commercial whaling severely depleted global populations of baleen whales (10). It is estimated that large whale populations were reduced by 60% to 90%, with total whale biomass reduced by 85% (11, 12). In the North Pacific Ocean, pre-whaling abundance for humpback whales (*Megaptera novaeangliae*) is estimated to be around 15,000 individuals, which was reduced to as few as 1,000 individuals when commercial whaling for this species was banned in the region in 1966 (13). Today, humpback whales are managed as distinct population segments (DPSs) based on genetics and movement data (14-16), with four DPSs occurring in the North Pacific Ocean (i.e., Central America, Mexico, Hawaii, and Western North Pacific). Although humpback whale abundance has been increasing, three DPSs are listed as threatened or endangered under the United States Endangered Species Act (i.e., Mexico DPS: threatened, Central America DPS: endangered, Western North Pacific DPS: endangered) (17). While commercial whaling is no longer a threat, these DPSs are exposed to a variety of human activities that can cause injury and mortality (e.g., entanglement, vessel strike) and result in disturbance (e.g., noise) (18).

The Central America humpback whale DPS is one population that has been slow to recover (17). This population breeds off the coasts of Central America and, more recently, southern Mexico (19) and feeds within the California Current Ecosystem (CCE), mainly offshore California and Oregon, with only a few individuals identified in the northern Washington and southern British Columbia feeding areas (20-24). In

this region, humpback whales predominantly feed on krill (e.g., *Euphausia pacifica*, *Thysanoessa spinifera*) and small schooling fish such as northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and Pacific herring (*Clupea pallasii*) (25, 26). In the CCE, these prey species experience short-term, regional upwelling and longer-term, basin-wide processes (e.g., El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO)) that affect their distribution and abundance (27-29). In turn, this variability in krill and fish availability affects humpback whale distribution (30) and, consequently, mediates their exposure to existing (e.g., naval sonar, shipping, fishing, wildlife tourism) and proposed (e.g., offshore wind farms) human activities (23, 31-33). As capital breeders, humpback whales primarily subsist on the stored energy gained on their feeding grounds while fasting during migration and on the breeding grounds. For reproductive females, this includes storing additional energy or “capital” to support reproduction. Thus, human activities that decrease energy intake and/or increase energy expenditure could adversely affect reproductive success and, subsequently, population dynamics. In addition, there are growing concerns regarding the combined effects of human activities and anthropogenic climate change that may affect prey availability (26, 34-36), which could further impact the recovery of this population.

Determining when human activities and changing environmental conditions (i.e., stressors) cause biologically significant effects on a population can be challenging. For example, when stressors lead directly to the death of an individual, the consequences on the population are relatively clear and quantifiable; however, non-

lethal effects, such as short-term changes in behavior and physiology, are more difficult to characterize and link to negative consequences for the population (37). To address this, the Population Consequences of Disturbance (PCoD) framework was developed to conceptualize how short-term, individual responses to stressors can lead to long-term, population-level effects (38). One way to link individual responses to population-level impacts is by using a process-based approach for modeling individuals' energy budgets, whereby changes in the external environment (e.g., prey availability) affect an individual's internal state (e.g., energy stores) and, subsequently, growth, reproduction, and survival (i.e., vital rates) (38-41). Stressors can affect energy budgets both directly (e.g., extraction of prey) and indirectly (e.g., displacement from important feeding areas), and the magnitude of the impact can be influenced by the individual's life history (e.g., movement patterns, reproductive state), the characteristics of the stressor (e.g., spatial and temporal properties), and the environmental conditions (e.g., seasonal changes, climatic oscillations) (36). As a result, considerable data may be required on a species' biology and the prey environment, which are often challenging to collect. However, process-based models can overcome this hurdle as they rely on a mechanistic understanding of the links between disturbance and population-level effects (42, 43), which, in this case, are primarily mediated by effects on an individual's movement and foraging behavior. They are also helpful in identifying which model inputs most significantly impact model outcomes, as well as prioritizing specific data needs that can ultimately increase the model's utility in mitigating negative effects.

In this study, we build on the individual-based, stochastic dynamic programming (IBM-SDP) model in Keen et al. (44) developed for a humpback whale population that feeds along the western Antarctic Peninsula. In that model, movement within the feeding grounds was implicitly modeled to explore temporal sensitivities to climate- and fishery-driven changes in krill on humpback whale population dynamics. In this model, we create a spatially explicit feeding ground with two prey types (i.e., krill and fish) for humpback whales in the CCE that considers both the spatial and temporal distribution of individuals and their prey in relation to simulated stressors. This approach is particularly valuable for a population whose foraging habitat spans thousands of kilometers and multiple ecological zones and legislative jurisdictions. For this model implementation, we focus on a subset of the Central America DPS that breeds offshore Costa Rica and feeds offshore California and Oregon; however, this model can be adapted to capture the behaviors of whales that utilize other breeding and feeding areas in the CCE where comparable information is available. Here, we use the IBM-SDP model to explore (1) the influence of environmental variability on prey choice and whale distribution, (2) when and where individuals are most sensitive to disturbance on the feeding grounds, and (3) how a stressor's temporal features influence a population's fitness (i.e., reproductive success and survival). By synthesizing this information in a cohesive IBM-SDP framework, model outputs can inform planned human activities that minimize overlap with individuals during energetically vulnerable and reproductively sensitive times.

3.3 Methods

3.3.1 Model overview

The IBM-SDP model in Keen et al. (44) was comprised of two steps: a backward iteration and a forward simulation (45-47). In the backward iteration, SDP equations were solved backward, starting at terminal time T , the final day of a female humpback whale's life, through its first day of independence (after successfully weaning from its mother), to identify the optimal behavioral and reproductive decisions that maximize her expected lifetime reproductive success (assuming an average maximum lifespan of 80 years (48, 49)) based on one or more state variables. These optimal behavioral and reproductive decisions were then used in Monte Carlo forward simulations to predict the individual- and population-level consequences of simulated stressors. In this model, the simulated stressors were assumed to be novel stimuli (i.e., not part of the whale's evolutionary history) and, therefore, were only included in the forward simulation. This allowed us to model the mismatch in what a whale expected to encounter based on the backward iteration and the altered environment it experienced when stressors were presented in the forward simulation. In this model, lifetime reproductive success was defined as the number of female calves per mature female that were successfully weaned and added to the population; as such, we assumed a 50:50 sex ratio at weaning to determine whether the calf was female. The backward iteration and forward simulation, as well as all statistical analyses and visualizations, were coded in R (version 4.3.1) (50) using the following packages: *foreach* (51),

doParallel (52), abind (53), qs (54), popbio (55), dplyr (56), tidyverse (57), ggplot2 (58), cowplot (59), sf (60, 61), and rnatrleearth (62).

3.3.2 Behavioral and reproductive decisions

Using the methods of Keen et al. (44), we modeled a female whale's behavioral and reproductive decisions at a daily time step. These decisions, which were emergent properties of the model, were functions of her body condition (x) and, when applicable, calf body condition (m), as well as her reproductive state (r), location (l), and the environmental regime (e) (see *Prey environment*, below). Regarding female and calf body condition (percentage of blubber mass as a portion of total body mass), we set minimum (5% (39, 63, 64)) and maximum (45% (65-68)) thresholds. If body condition fell below the minimum threshold, we assumed the whale died from starvation. Changes in body condition from one time step to the next depended on energetic costs and gains from foraging (in the case of a calf, from nursing) and were driven by an underlying bioenergetic model (see Keen et al. (44) for equations and parameters used in the bioenergetic model).

The behavioral strategies considered for each time step depended on the whale's location (i.e., feeding grounds, migratory corridor, or breeding grounds). The feeding grounds were divided into 14 foraging locations ranging from the United States-Mexico border to the Oregon-Washington border and from the coast to 100 km offshore (Figure 3.1). When a whale was on the feeding grounds, it could stay in its current location, move to an adjacent foraging location, or, if in the southernmost foraging location, begin migration. The migratory corridor was comprised of 39 locations based on the

distance traveled by tagged individuals between their feeding grounds and Costa Rica breeding grounds (~4,500 km (20-22, 69)) and a mean migration speed recorded for this species (4.65 km/hour (70)). When in the migratory corridor, a whale could move forward (south) or backward (north). The breeding grounds were comprised of a single location, and movement within this area was modeled implicitly (i.e., costs were incurred, but there was no change in location, *l*) because the distribution of humpback whales on their breeding grounds is not well known.

The reproductive strategies considered for each time step depended on the whale's current reproductive state. Over the course of her life, a female humpback whale could be in one of four reproductive states: (1) non-reproductive juvenile (not sexually mature, i.e., less than five years old), (2) non-reproductive adult (sexually mature, i.e., five years of age or older, not pregnant or lactating), (3) pregnant, or (4) lactating (71, 72), with a whale remaining reproductively active for 75 years (i.e., no senescence (73)). Some reproductive strategies also depended on location and time; for example, birth and implantation could only occur on the breeding grounds, with a fixed date of January 1 and January 15, respectively, to allow for a gestation period of 11.5 months (74). Additionally, in her final year of life, a whale could only be in a non-reproductive adult or lactating state. However, transitions from being pregnant or lactating to a non-reproductive adult could occur at any time if the pregnancy was terminated or the calf was weaned early.

SDP models can be time and memory intensive; therefore, we included biologically meaningful constraints specific to reproduction to make the model more

tractable (39, 44, 75). In addition to a fixed time of birth and implantation (explained above), all lactating whales and their newborn calves were constrained to the breeding grounds for the first 50 days after parturition to account for potential benefits to the calf (e.g., thermoregulation, but see (76, 77)) and its limited swimming abilities (78). Furthermore, a calf could receive milk from its mother for the first 10.5 months of life (48, 74), after which the calf was added to the population and fed autonomously; however, if a calf was weaned early, it had to rely on its own energy reserves until it reached 10.5 months.

3.3.3 Prey environment

The temporal and spatial variability of prey in the environment was simulated using a California Current implementation of the Regional Ocean Modeling System (ROMS) coupled to the NEMUCSC biogeochemical model (79) and an IBM for sardine and anchovy (80-82) for the period 1990-2010. The NEMUCSC model describes nutrient, phytoplankton, and zooplankton dynamics, which are advected and diffused in space by solving a transport equation based on the regional circulation calculated with ROMS. The ROMS-NEMUCSC-IBM model output was generated prior to SDP calculations and provided monthly surface biomass estimates of krill (mmolN/m^3) and total sardine and anchovy abundance (millions of individuals, combined into a single “fish” category) at 3-km^2 and 10-km^2 horizontal resolution, respectively, from 31° to 47° N and 115° to 130° W. These prey types represent the dominant prey consumed by humpback whales in this region (i.e., offshore California and Oregon) (25, 26). To estimate krill abundance (number of individuals) from krill

biomass, we assumed 1 mmolN was roughly equal to 1 gram of wet weight (the approximate weight of an individual krill) (80) and that the surface biomass estimates of krill were representative of the upper 40 m of the water column. Krill abundance was then scaled from the number of krill per m² to the number of krill within a 3-km² grid cell. Finally, these spatially referenced grid cells for krill and fish were separated into one of fourteen foraging locations based on the center coordinates of each grid cell.

Abundance estimates were normalized for each prey type (krill and fish) to represent the proportion of local abundance within a foraging location relative to the maximum abundance across all foraging locations. These relative abundances were then separated into three environmental regimes (see below), fit to a beta distribution, and converted to discrete distributions with 10 equally spaced values (i.e., energy classes) from 0 to 1. We used these relative abundance estimates to represent the proportion of maximum energy that a whale could gain on a given day. This was a function of the whale's forestomach capacity (influenced by the whale's body length), how quickly it could be cleared (3 hours (83)), and the number of times it could be filled per day, as well as the energy density of krill (3,628 kJ/kg, which assumes a diet comprised of 80% *T. spinifera* and 20% *E. pacifica*) or fish (6,000 kJ/kg) (84), and the amount of energy remaining after fecal and urinary energy losses (i.e., metabolic efficiency; 85%) (85, 86) (see *Appendix A: Energy gained from feeding*). Based on initial model iterations, populations crashed before the end of the 21-year simulation. Using surface estimates of krill biomass may be one reason for this mismatch,

potentially underestimating their total abundance within a 3-km² grid cell and their relative abundance in the SDP model's prey environment. As such, relative abundance values for both prey types were scaled by 1.36 to best approximate the growth rate of the population (87); however, a whale could not exceed the maximum energy gained on a given day based on its physiological capacity, as described above.

The interannual variability of the prey environment in the CCE is influenced by several modes of climate variability with different periodicities (e.g., ENSO, with a 3- to 7-year periodicity (88); NPGO, with a 10- to 30-year periodicity (89); PDO, with a 20- to 30-year periodicity (90)). Warm and cool phases of the NPGO have previously been shown to influence the diets of humpback whales in the CCE (26); however, with the number of years of simulated prey data available, we could not fully capture this multidecadal periodicity. Instead, three environmental regimes were created that represent the three states of ENSO—El Niño (warm phase), neutral, La Niña (cool phase)—a dominant mode of inter-annual variability in the region (88). Based on previous ENSO events, we created a repeated pattern of a seven-year cycle (i.e., neutral, El Niño, neutral, neutral, neutral, El Niño, La Niña) to represent baseline conditions in the model. Thus, the probability of a year being an El Niño year was 2/7, a neutral year was 4/7, and a La Niña year was 1/7. In the model, the shift between environmental regimes could occur on ordinal day 365 (December 31) of each simulated calendar year (where ordinal day 1 is January 1).

Therefore, in the backward iteration of the model, a whale's fitness was calculated based on whether it fed on krill or fish. A whale's prey-specific fitness was

calculated across all possible sources of stochasticity, where we took the weighted average of encountering each energy class based on the probability of encountering that energy class. The energy class and probability of encounter depended on the current environmental regime (e), the whale's location (l) (if not on the feeding grounds, the probability of finding krill or fish was zero), and time (t). The prey type that yielded the highest fitness was recorded and used to determine which prey type a whale fed on in the forward simulation. If there was a fitness tie in the backward iteration (i.e., both prey types resulted in the same expected fitness), the prey type was picked at random in the forward simulation. The energy class encountered on a given day in the forward simulation was then determined by sampling from the prey-specific probability distribution used in the backward iteration.

3.3.4 Simulated scenarios and responses to stressors

Using the approach of Keen et al. (44), we created a stable-age structured population with a starting population size of 200 whales. We ran a forward simulation under baseline conditions for a normalization period of seven years (the length of a simulated ENSO cycle) to ensure that model outputs would not be impacted by initial model parameterization. The resulting population (including age, body condition, reproductive state, and location) was used as the starting population in subsequent simulated scenarios. Each simulated scenario was repeated 50 times.

Simulated scenarios included baseline conditions (with no stressors), general stressors that varied by foraging location and season (spring, summer, and fall), and construction stressors that mimicked installation schedules for offshore wind turbines

(Table 3.1). In the general stressor scenarios, the stressor occurred in a specific season and location, and the stressor occurred in every year of the simulation; all possible combinations were simulated for 21 years. In the construction stressor scenarios, we simulated one- and three-year wind turbine installation schedules to explore the potential effects of varying the temporal features of a stressor on humpback whale vital rates. Offshore California, wind lease areas primarily overlap with foraging locations 4 (central California wind lease area) and 9 (northern California wind lease area). For these simulations, we focused on foraging location 4, where there are three wind leases covering 240,898 acres or ~10% of a foraging location (91). We chose to simulate the stressor during the most sensitive season (based on outcomes of the general stressor scenarios) as well as during a four-month window when turbine installation is most likely. For these scenarios, the proportion of the location exposed and the frequency of the stressor varied. For example, scenarios 43-49 and 57 represent a schedule where construction in the three lease areas occurs all in one year, whereas scenarios 50-56 and 58 represent a schedule where construction occurs in one lease area per year over three years, with the latter resulting in a smaller area disturbed but a longer period exposed (see “Frequency” and “Proportion disturbed” columns in Table 3.1). Construction stressors were introduced in the second ENSO cycle (years 8-14) and simulated for 35 years to capture population vital rates before, during, and for a few ENSO cycles after the stressor occurred. To account for the three phases of ENSO in the model, the timing of the stressor was varied to cover all environmental combinations.

For all stressor scenarios, on a given day t , a specific proportion of each foraging location was exposed to the stressor. This proportion was used as a probability in a Bernoulli draw to determine whether a feeding whale in that location was exposed to the stressor (75). Each whale was characterized by a probability of responding to a stressor when exposed, which was drawn from a beta distribution, $\beta(5, 5)$, at the start of the simulation or when the whale was added to the population (75). If the feeding whale responded to the stressor, it would change its behavior and select the next best behavioral strategy; however, if the whale did not respond, it would stay in its current location and feed, although it would experience a reduction in the location's overall productivity (95%) (75). This reduction is meant to represent how a stressor could affect a whale's energy acquisition and expenditure, including spatial avoidance and indirect effects on prey.

To quantify the effect of each stressor scenario on vital rates, we used Cohen's d , which calculates the difference between means in the baseline and stressor scenarios scaled by their pooled standard deviation (40, 92). Only positive values indicate an adverse effect of a stressor on vital rates, with values of $d < 0.2$ indicating a negligible effect, $0.2 \geq d < 0.5$ indicating a small effect, $0.5 \geq d < 0.8$ indicating a medium effect, and $d \geq 0.8$ indicating a large effect (92). In the analysis, we focused on key vital rates such as pregnancy, birth, weaning success, and population growth rates. Pregnancy and birth rates were calculated based on the percentage of mature females that became pregnant or gave birth per year, respectively. Weaning success rate was calculated as the percentage of female calves born per year that were successfully weaned and alive

at 10.5 months of age. Finally, population growth rate was calculated as the annual percent increase in population abundance. These vital rates were chosen because they can be readily calculated from field data and provide insight into the effects of stressors on population dynamics.

3.3.5 Sensitivity analysis

We conducted sensitivity analyses on five model parameters to identify which had the largest influence on simulation results. We individually varied each parameter, resulting in 10 sensitivity analyses. For each sensitivity analysis, we reran the backward iteration and 50 replicates of the forward simulation and compared results using Cohen's *d*. See *Appendix B: Sensitivity analysis* for the analyzed parameters and results.

3.4 Results

3.4.1 Baseline conditions

On average, 32.98% ($\pm 5.06\%$) (i.e., mean $\pm$ SD) of mature females in a population became pregnant, and 26.83% ($\pm 5.75\%$) gave birth in a given year, with an average calving interval of 3.94 (± 0.51) years. Females typically became pregnant and gave birth to their first calf at age 6 (6.13 ± 0.38 years), a year after reaching sexual maturity; however, some females delayed their first birth until age 10. Calves were weaned, on average, on ordinal day 254 (September 11), over two months before the weaning deadline (ordinal day 319 or November 15); however, the subset of calves that were weaned successfully were weaned, on average, several weeks later on ordinal day

291 (October 18). Of the calves born in a given year, an average of 57.02% ($\pm 16.21\%$) were successfully weaned and were added to the population at 10.5 months old, contributing to a mean population growth rate of 1.73% ($\pm 2.1\%$) per year.

The interannual variability of the prey environment had dramatic effects on female body condition and, subsequently, vital rates. For example, when comparing mean body condition near the end of the feeding season (ordinal day 319 or November 15) across environmental regimes, whales were in better body condition in La Niña years than in neutral years or El Niño years (Figure 3.2A). This resulted in higher weaning success rates during La Niña years ($70.8\% \pm 13.11\%$) compared to El Niño years ($44.67\% \pm 15.86\%$). Subsequently, pregnancy rates were highest following a La Niña year ($40.19\% \pm 4.27\%$) and lowest following an El Niño year ($28.92\% \pm 2.82\%$), while birth rates were highest two years after a La Niña year ($34.91\% \pm 3.79\%$) and lowest two years after an El Niño year ($23.73\% \pm 4.29\%$).

The environmental regime also influenced whales' diets (Figure 3.2B) and where they spent their time feeding (Figure 3.3). During El Niño years, a whale's diet was comprised of, on average, 64.19% krill and 35.81% fish, whereas during La Niña years, their diet was comprised of, on average, 82.19% krill and 17.81% fish. During neutral years, their diet was comprised of, on average, 74.58% krill and 25.42% fish. Fish were consumed exclusively in the southern and central part of their feeding grounds, in locations 1 and 3 through 8 (offshore California, between 32.5°N and 40.4°N), whereas krill were consumed in locations 4 through 13 (offshore central California through Oregon, between 35.5°N and 45.4°N). During El Niño years, whales

utilized more of their foraging grounds, feeding as far north as location 13 (offshore northern Oregon, between 44.5°N and 45.4°N), whereas during La Niña years, whales primarily fed in locations 3 through 7 (offshore central and north central California, between 34.5°N and 39.4°N), and during neutral years, whales fed in locations 3 through 6 (offshore central and north central California, between 34.5°N and 38.4°N); some prey were consumed in location 1 (offshore southern California, between 32.5°N and 33.4°N), but it was very rare ($< 0.0021\%$, on average), and whales did not spend time feeding in locations 2 (offshore southern California, between 33.5°N and 34.4°N) and 14 (offshore northern Oregon, between 45.5°N and 46.4°N).

Migratory behavior also emerged from the model. Non-reproductive adults arrived on the feeding grounds between ordinal day 41 (February 10) and 91 (April 1) and generally left the feeding grounds on ordinal day 341 (December 7); however, following El Niño years, some non-reproductive adults chose not to migrate and overwintered on the feeding grounds. Pregnant females arrived on the feeding grounds on ordinal day 55 (February 24) and left on ordinal day 326 (November 22). Lactating females arrived on the feeding grounds over four weeks later (ordinal day 91) and typically overwintered on the feeding grounds after weaning their calves. Similar to some non-reproductive adults and lactating whales, juveniles did not participate in an annual migration and remained on the feeding grounds until reaching sexual maturity.

3.4.2 General stressor scenarios

The general stressor scenarios had varying effects on vital rates depending on when and where the stressor occurred (Figure 3.4 and Figure 3.5). The greatest overall effect on vital rates occurred in location 4 (offshore central California, between 35.5°N and 36.4°N) in the spring, where the stressor had a small effect on pregnancy rates and a large effect on birth and weaning success rates (Figure 3.4A), leading to a mean population growth rate of -4.16% ($\pm 2.17\%$) per year (Figure 3.5A). In summer, stressors in location 5 (offshore central California, between 36.5°N and 37.4°N) had the greatest impact on vital rates, particularly birth and weaning success rates (Figure 3.4B), with a mean population growth rate of -3.88% ($\pm 4.95\%$) per year (Figure 3.5B). In fall, location 6 (offshore north central California, between 37.5°N and 38.4°N) was the most vulnerable location for the population, where the stressor had large effects on birth and weaning success rates (Figure 3.4C), contributing to a mean population growth rate of -2.08% ($\pm 3.68\%$) per year (Figure 3.5C).

2.4.3 Construction stressor scenarios

The effect of the construction stressor on vital rates depended on the temporal characteristics of the stressor, including the time of year (Figure 3.6A). When the construction stressor occurred in spring (the most sensitive period for location 4 in the general stressor scenarios), the greatest effect on population growth rate occurred in year 10 for the one-year scenario ($1.2\% \pm 3.90$ per year) and years 10-12 for the three-year scenario ($0.66\% \pm 5.73\%$ per year), with the stressor spread out across three years

having a greater overall impact on the population (Figure 3.6B). When the stressor occurred during the four-month period when construction is most likely, there was no impact on vital rates, including population growth rate; thus, when installation occurred during this period, it did not matter whether construction occurred all in one year or if it was spread out across three years (Figure 3.6B).

See *Appendix C: Tables of life-history parameters and Cohen's d values* for additional results from the modeled scenarios.

3.5 Discussion

We developed a spatially explicit, dynamic state model to investigate the influence of environmental variability on prey choice and humpback whale distribution, the spatial and temporal sensitivities of whales on their California and Oregon feeding grounds, and how a stressor's temporal features influence a population's fitness. For endangered populations, like the one modeled here, tools like this can help predict the effect of future stressors and inform mitigation strategies that reduce or eliminate adverse effects. While many of the model's emergent properties reflect the behaviors of wild humpback whales, no model can fully capture a population's complex life history. However, results can highlight future research directions that can improve the model's utility and, ultimately, its predictive power.

In the CCE, humpback whales have a complex population structure, comprising three DPSs (i.e., Central America, Mexico, and Hawaii), with some overlap in their feeding areas (e.g., Central America and Mexico DPSs). As a result, it can be challenging to discern between populations on their feeding grounds and calculate

population-specific vital rates. For the Central America DPS, estimates for vital rates such as birth, pregnancy, and weaning success rates are not well known. Thus, to calibrate the model and identify the prey scalar, we used a recent population growth rate estimate for Central America whales of $1.6\% \pm 2.0\%$ (87) (this number excludes whales that breed offshore southern Mexico and were only recently added to this DPS (19)). This parameterization resulted in average pregnancy ($32.98\% \pm 5.06\%$) and birth ($26.83\% \pm 5.75\%$) rates that are lower than those estimated from empirical data for other populations (mean pregnancy rate: 52% (breeding stock G) (72), mean birth rate: 36% to 44% (93)); however, the annual population growth rate for this population is also much lower than reported for other populations (10% for the Western Australia population (94), 7.4% for the Southwestern Atlantic population (95)), likely contributing to its endangered status. While the exact reason for this population's slow recovery post commercial whaling is unknown, it may be limited by its slow life history (e.g., slow growth rate, long gestation period, high maternal investment, low fecundity (36, 96-98)) and high level of site fidelity to both breeding and feeding areas (14, 15, 22, 69, 99, 100). In addition, density-dependent effects may be slowing this DPS's recovery, which has been suggested as a reason for the low population growth rate in eastern North Pacific (ENP) blue whales (*Balaenoptera musculus*) (101). This population also continues to be exposed to a diverse suite of stressors (e.g., naval sonar, shipping, fishing, wildlife tourism) with new, potential stressors proposed for the future (e.g., offshore wind farms). While existing stressors and their associated impacts (e.g., entanglement, vessel strike) were not explicitly modeled here, they could be

incorporated into future model iterations to quantify the effects of one or multiple stressors on the population's vital rates.

Migration was an emergent property of the model, with a whale's reproductive state and body condition influencing when it moved between the feeding and breeding grounds. Non-reproductive juvenile whales always chose to forgo migration and overwinter on the feeding grounds, where prey was available year-round. However, once sexually mature, they did opt to migrate to the breeding grounds. In the model, not all sexually mature whales participated in an annual migration, with body condition being a primary driver of whether a whale chose to migrate. For example, sexually mature whales who migrated had a mean body condition of 42.14% ($\pm 1.78\%$), whereas those who did not migrate had a mean body condition of 24.93% ($\pm 8.39\%$). In reality, although body condition may influence whether an individual migrates, the reasons for migration are not fully understood. Some hypotheses focus on mothers protecting their calves from thermal stress and predation (77, 102), while others include resource tracking (75, 103), the need for individuals to undergo an epidermal molt (104), social learning and development (105), and/or it is an evolutionary holdover (106). While it is not known what proportion of the population overwinters in the CCE, sightings and passive acoustic data indicate that humpback whales are present year-round offshore California (107-109). It is possible that overwintering on the feeding grounds could increase if prey availability becomes a limiting factor due to climate change. In addition, as other whale populations, including other humpback whale DPSs, increase in the CCE, resources could become limiting, leading to competition that may

necessitate nutritionally stressed whales to spend more time on the feeding grounds to meet their energy demands.

The spatial distribution of whales throughout their foraging environment was also an emergent property of the model. Simulated whales spent approximately 75% of their feeding time in locations 4, 5, and 6 (between 35.5°N and 38.4°N), which extends from offshore Cambria, through Monterey Bay and the Gulf of the Farallones, to just north of Bodega Bay. The predominant use of these locations by simulated whales is consistent with empirical observations and overlaps with biologically important areas identified for this species on the West Coast of the United States (24). Location 2 (between 33.5°N and 34.4°N), which includes the Santa Barbara Channel, is also known as a popular location for humpback whales, particularly in spring (107, 110). However, simulated whales did not feed in this location; instead, they bypassed this area for more northerly foraging locations. This mismatch may be because the resolution of the ROMS-NEMUCSC-IBM model may not fully resolve the semi-permanent eddy in the Santa Barbara Channel, which influences prey distribution, abundance, and availability in the region (111, 112). As such, prey abundance in location 2 may be underestimated, thus underrepresenting the importance of this foraging location relative to other locations in the SDP model.

Empirical observations and habitat density models also indicate interannual and seasonal shifts in the north-south distribution of humpback whales along the coast (107, 110, 113, 114). In the model, preference for specific foraging locations was influenced by the environmental regime. During El Niño years, simulated whales primarily

utilized foraging locations between location 6 (offshore San Francisco to just north of Bodega Bay) and location 12 (offshore central Oregon). In contrast, during La Niña and neutral years, simulated whales primarily used foraging locations offshore central and north central California, with whales spending most of their time in location 4 (~80%) during La Niña years and most of their time split between location 4 (~44%) and location 6 (~36%) during neutral years. Seasonality also played a role in how simulated whales utilized their feeding grounds. For example, during neutral years, location 4 was a popular feeding area for whales in the spring (~86%), with its popularity decreasing into the summer (~29%) and fall months (~5%). In addition to their movements up and down the coast, empirical data show that humpback whales move between inshore and offshore feeding areas in response to environmental variability (107, 108, 115). Although the size of the individual foraging locations in this implementation of the model was too coarse to capture this cross-shore movement, foraging locations could be resized in the future, depending on the resolution of the prey data available, to capture the distribution of simulated whales at finer scales.

In the model, diet (krill vs. fish) varied both geographically and in response to environmental variability. We found that fish were overwhelmingly consumed in the southern and central regions of the feeding grounds, while krill were mostly consumed throughout the whales' range. This is generally consistent with the regional variability of krill and anchovies reported in Szesciorka et al. (33) and with the stomach contents of humpback whales described in historical whaling records (25). These records also noted considerable variation between years in the prey types found in whales'

stomachs. In the model, we found that krill were, on average, the dominant prey type consumed by simulated whales; however, more fish were consumed during El Niño years than in neutral and La Niña years. More recently, prey switching in response to environmental variability has also been supported using stable isotope analysis, with Fleming et al. (26) finding more krill in the diet of humpback whales during positive phases of the NPGO (cool sea surface temperatures (SSTs) and strong upwelling, similar to La Niña conditions) and more fish in their diet during negative phases of the NPGO (warmer SSTs and decreased upwelling, similar to El Niño conditions). While prey switching by humpback whales may reflect changes in the availability of their prey in response to changing environmental conditions, it may also be influenced by the size or density of a patch and its distribution, which was not included in our model. Humpback whales, like other baleen whales, require dense aggregations of prey for energetically efficient foraging (116, 117). Thus, while krill may be more abundant overall in a particular model location, they may be patchier and more diffuse in the water column, which may reduce the energetic efficiency of feeding on that prey type. Similarly, although fewer fish may be in a particular model location, they may be more densely aggregated and thus more energetically beneficial to feed on. While much research has focused on humpback whales feeding on krill in the CCE (118-120), comparable data for humpback whales feeding on fish are limited. As fine-scale prey data becomes available for fish, particularly at the scale at which a whale feeds (121, 122), these data can be incorporated into the model to better capture the nuances of prey patch dynamics and the thresholds for prey switching in the CCE.

The results from the stressor scenarios highlight the need for the careful planning of human activities to avoid locations and times critical for humpback whales on their feeding grounds (36, 123, 124). For example, we found that location 5 (from offshore Monterey to just south of San Francisco) was an important foraging location for whales in spring, summer, and fall, with stressors having varying effects on vital rates depending on the season. However, while location 4 (from offshore Cambria to just south of Monterey Bay) was critical to feeding humpback whales in the spring and summer, stressors that occurred in that location in fall had negligible effects on vital rates. Thus, by leaving important feeding habitats undisturbed, whales could meet their energy needs even when other locations on their feeding grounds were disturbed (36). The construction stressor scenarios also highlighted the importance of timing when planning a disturbance event. For example, when the construction stressor was placed in location 4 in the spring, a critical time for whales in this location, the overall mean population growth rate decreased. However, when the stressor occurred outside of this critical time, there was no effect on the mean population growth rate. It is interesting to note that construction scenarios that avoided stressors in spring did overlap with part of summer, which the model also identified as an important time for whales in location 4. Even though stressors occurred during this important time, there were negligible effects on vital rates. A potential reason for this may be because other locations provided comparable feeding habitats, allowing a whale to still meet its energy needs. We also found that the temporal features of a stressor influenced the extent to which vital rates were impacted, especially when it occurred in important foraging locations

during critical times (36). For example, when the construction stressor occurred exclusively in spring, the population fared better when the stressor occurred all in one year than across multiple years, even though the multi-year stressor had a smaller spatial footprint. However, when the stressor did not occur in spring, the temporal features of the stressor had negligible effects on the population's vital rates. It is important to note that the modeled prey environment does not account for the spatial distribution of prey within a feeding location (as discussed above), and where a stressor is placed within a foraging location will impact whether whales are exposed and their vital rates are impacted (125, 126). As a result, this should be accounted for in future implementations of the model.

Climate change will likely alter the predator-prey dynamics and distributional patterns observed today. In the CCE, climate change is projected to affect the phenology and dynamics of coastal upwelling, increase SST and near-surface stratification, and alter nutrient supply (127-129). In turn, this will affect the abundance, composition, and distribution of prey available to humpback whales and other predators in the region (26, 115). Due to their flexible foraging strategy, humpback whales in the CCE may be more resilient to changing climate conditions than other species that specialize on a single prey type (e.g., ENP blue whales) (130). While the impacts of climate change on predator-prey dynamics were not included in this model, they could be integrated into future modeling efforts to predict how the spatial and temporal sensitivities of humpback whales to stressors may shift in response to a changing climate. For example, in response to warming conditions, whales may extend the

northern part of their primary feeding habitat, which has been observed for whales in the western North Atlantic Ocean (131). As such, the spatial extent of the model could be extended to cover feeding grounds offshore Washington, southern British Columbia, and further north, which would require a nontrivial extension of the ROMS-NEMUCSC-IBM model or acquisition of comparable data to capture the seasonal and interannual variability of krill, anchovies, and sardines. In addition, with a northward extension of the model's spatial extent, it would also be advisable to include herring as an additional prey type in the model.

Ecosystem responses to climate change are likely to be complex and challenging to predict; however, empirical observations may provide some insight into how this population may respond to changing conditions. For example, the unprecedented marine heatwave in the eastern North Pacific Ocean from 2014-2016, coupled with a strong El Niño event in 2015-2016, led to a sharp decline in the survival and reproductive success of humpback whales in southeastern Alaska (132). During this period, offshore California, humpback whales shifted their distribution to match the inshore shift of anchovies, subsequently leading to a spike in whale entanglements in 2015-2016 (115). Additionally, there were also fewer sightings of humpback whales and calves on their Costa Rica breeding grounds (133), which could mean that whales may be finding more thermally favorable breeding areas at intermediate latitudes or overwintering on their feeding grounds. As a result, these distributional shifts in response to changing conditions could expose whales to new stressors or exacerbate the effects of existing ones, potentially further slowing the recovery of this vulnerable

population. This model can serve as a general framework to explore how human activities will interact with climate change pressures to inform the placement and timing of planned activities and ensure management and conservation goals for this population are achieved.

3.6 Conclusions

Our model expands on the IBM-SDP model in Keen et al. (44) to consider both the spatial and temporal distribution of whales and their prey in relation to simulated stressors when evaluating the consequences of disturbance. Simulated general stressors had varying effects on vital rates depending on where and when the stressor occurred. Stressors located offshore the central and north central coasts of California and offshore southern and central Oregon had the greatest impact on vital rates. Specifically, the most sensitive locations and times were offshore the Big Sur coast in spring, the greater Monterey Bay area in summer, and offshore San Francisco and the Greater Farallones region in fall. The construction stressor scenarios highlighted how adjusting the temporal features of a stressor can reduce impacts on vital rates, particularly in important foraging locations, as well as the importance of timing when planning human activities.

The model also highlighted specific data needs that can ultimately increase its utility for making predictions about the effects of stressors on humpback whales in the CCE. For example, data are needed on the timing of migration for females in different reproductive states, as well as their length of stay and movements on their breeding grounds, to better understand the consequences on their energetics and vulnerability to

stressors. Additionally, data are needed to better characterize the prey environment at the spatial and temporal scales exploited by humpback whales, including how it changes within and across years in response to environmental variability. This information would also allow the model's foraging locations to be resized to provide finer-scale predictions of spatial sensitivities. Furthermore, extending the model's spatial extent to include northern feeding areas could provide a better understanding of how whales may shift their distribution and exposure to stressors in a changing climate.

Models such as the one presented here can offer a general framework for identifying sensitive feeding times and areas for vulnerable populations, thus providing a quantitative basis for comparing different stressor scenarios associated with our expanding offshore footprint. While this model focused on a subset of the Central America DPS that breeds offshore Costa Rica and feeds offshore California and Oregon, it can be adapted to represent the behaviors of whales that use other breeding and feeding areas in the CCE where comparable information is available. Such additions would allow for a more comprehensive understanding of spatially and temporally sensitive areas throughout the CCE to inform the planning of human activities and minimize impacts.

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3.8 Tables and figures

Table 3.1. Simulated stressor scenarios implemented in the forward simulation. General stressor scenarios were simulated for 21 years, and construction stressor scenarios were simulated for 35 years.

Scenario	Stressor	Duration	Frequency	Foraging location(s)	Proportion disturbed
1-14	General	Spring (Mar-May)	Every year	1-14	0.1
15-28	General	Summer (Jun-Aug)	Every year	1-14	0.1
29-42	General	Fall (Sept-Nov)	Every year	1-14	0.1
43-49	Construction	Spring (Mar-May)	1 year	4	0.1
50-56	Construction	Spring (Mar-May)	3 years	4	0.033
57	Construction	Jul-Oct	1 year	4	0.1
58	Construction	Jul-Oct	3 years	4	0.033

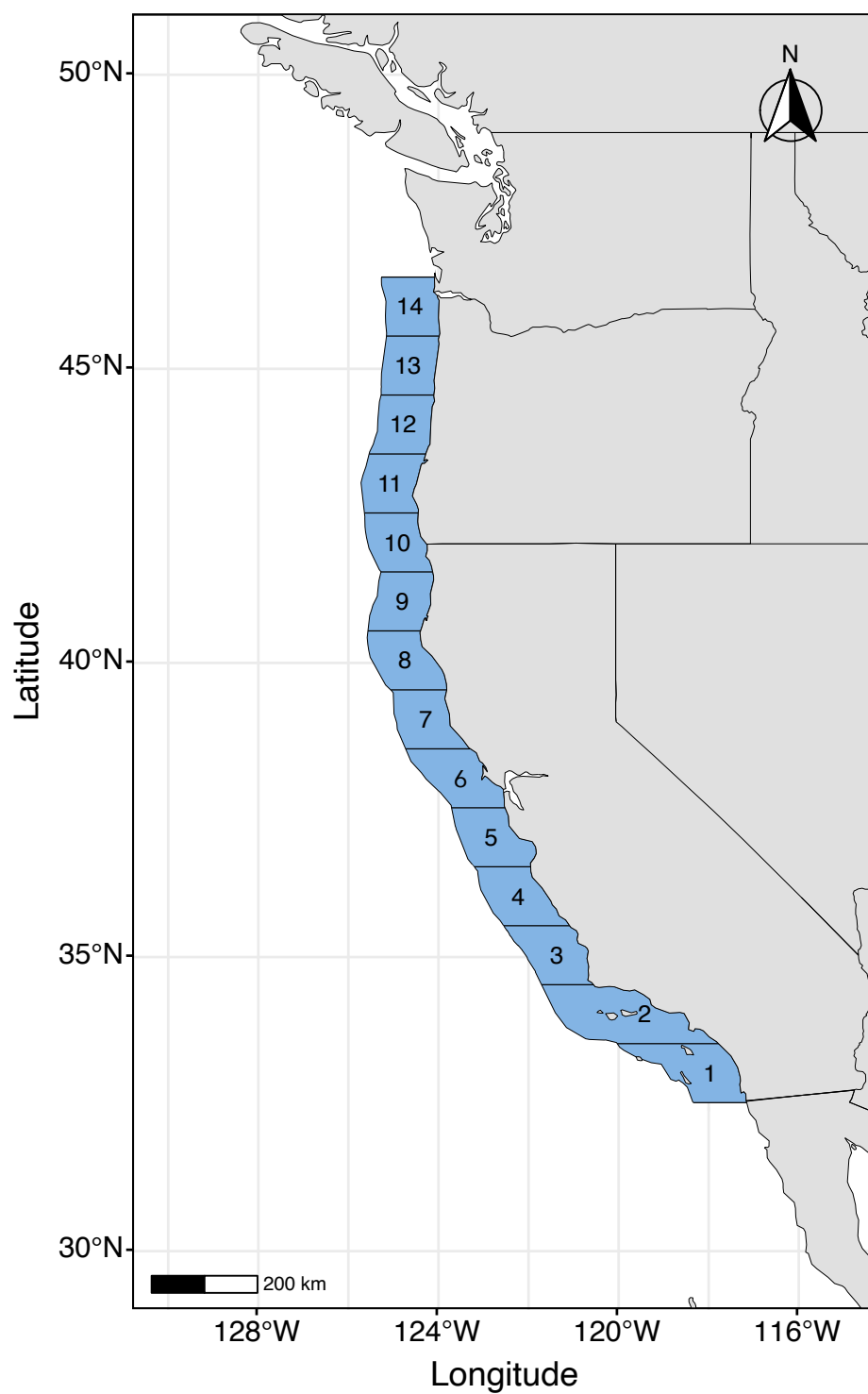


Figure 3.1. Map of the feeding grounds and 14 foraging locations.

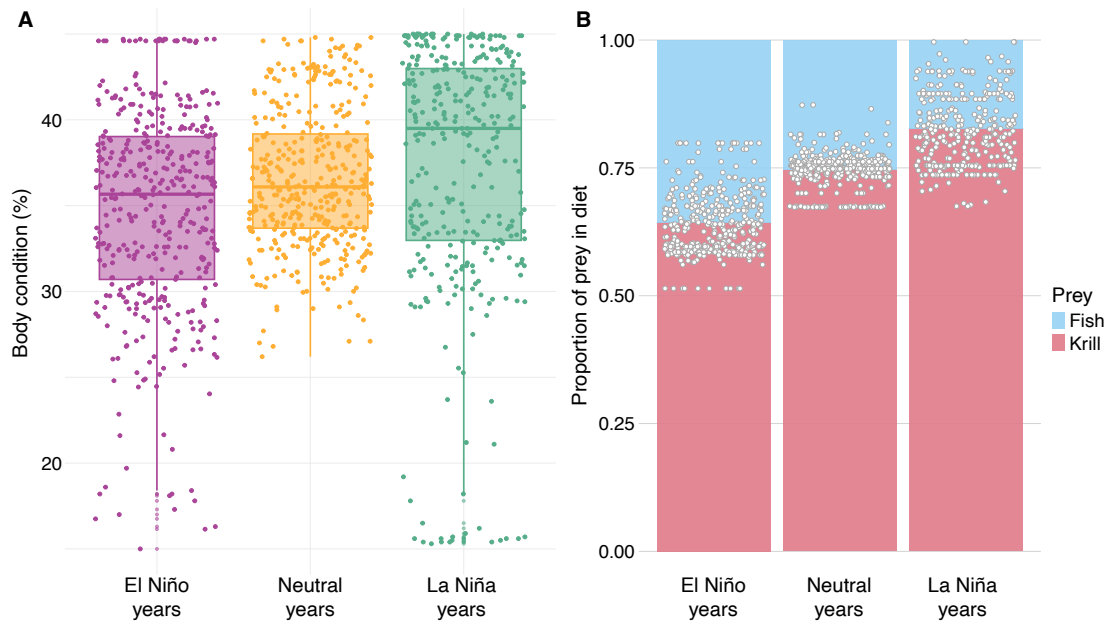


Figure 3.2. (A) Mean body condition of whales for one simulation near the end of the feeding season (ordinal day 319 or November 15) across El Niño, neutral, and La Niña years. (B) Proportion of prey in the diet of whales (for the same simulation in (A)) across El Niño, neutral, and La Niña years. The white points represent the proportion of krill in that individual's diet.

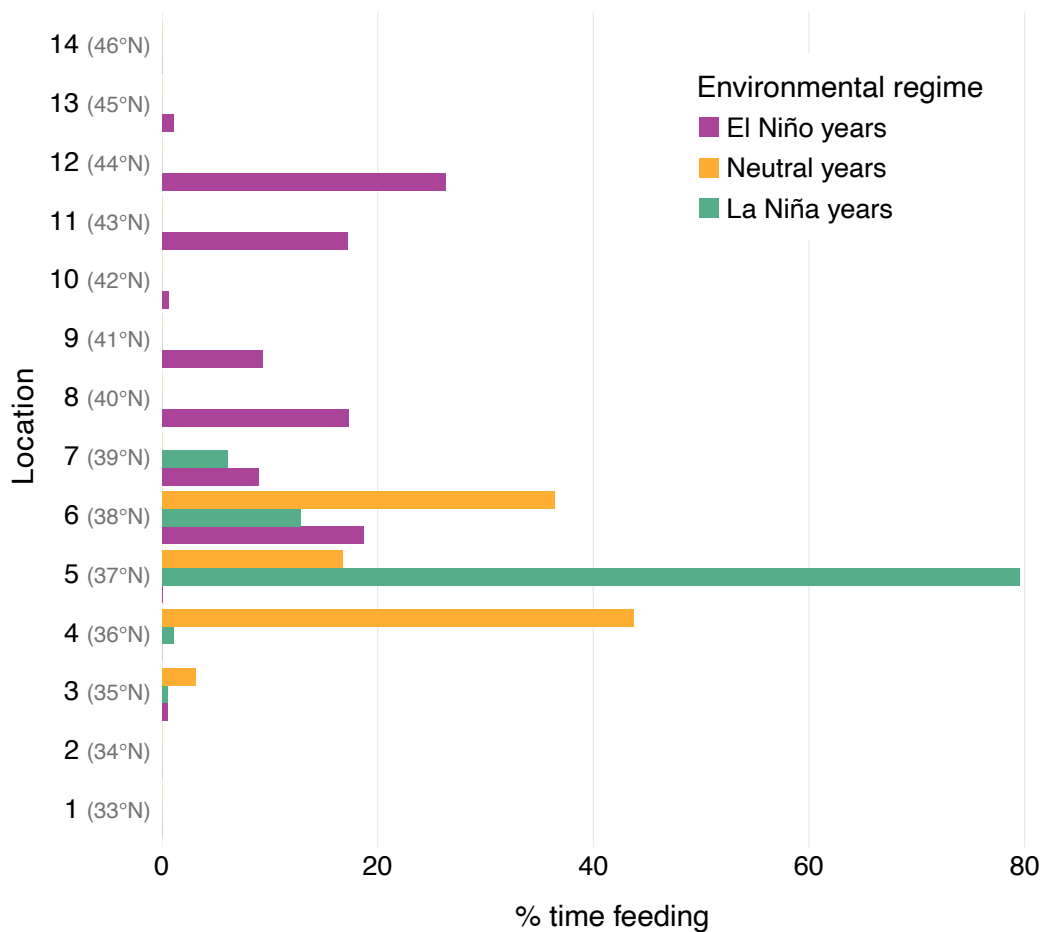


Figure 3.3. Percent time feeding across whales in each of the 14 foraging locations during El Niño, neutral, and La Niña years. A missing bar means that feeding did not occur in that location during the associated environmental regime. The approximate center latitude for each location is included next to the corresponding location.

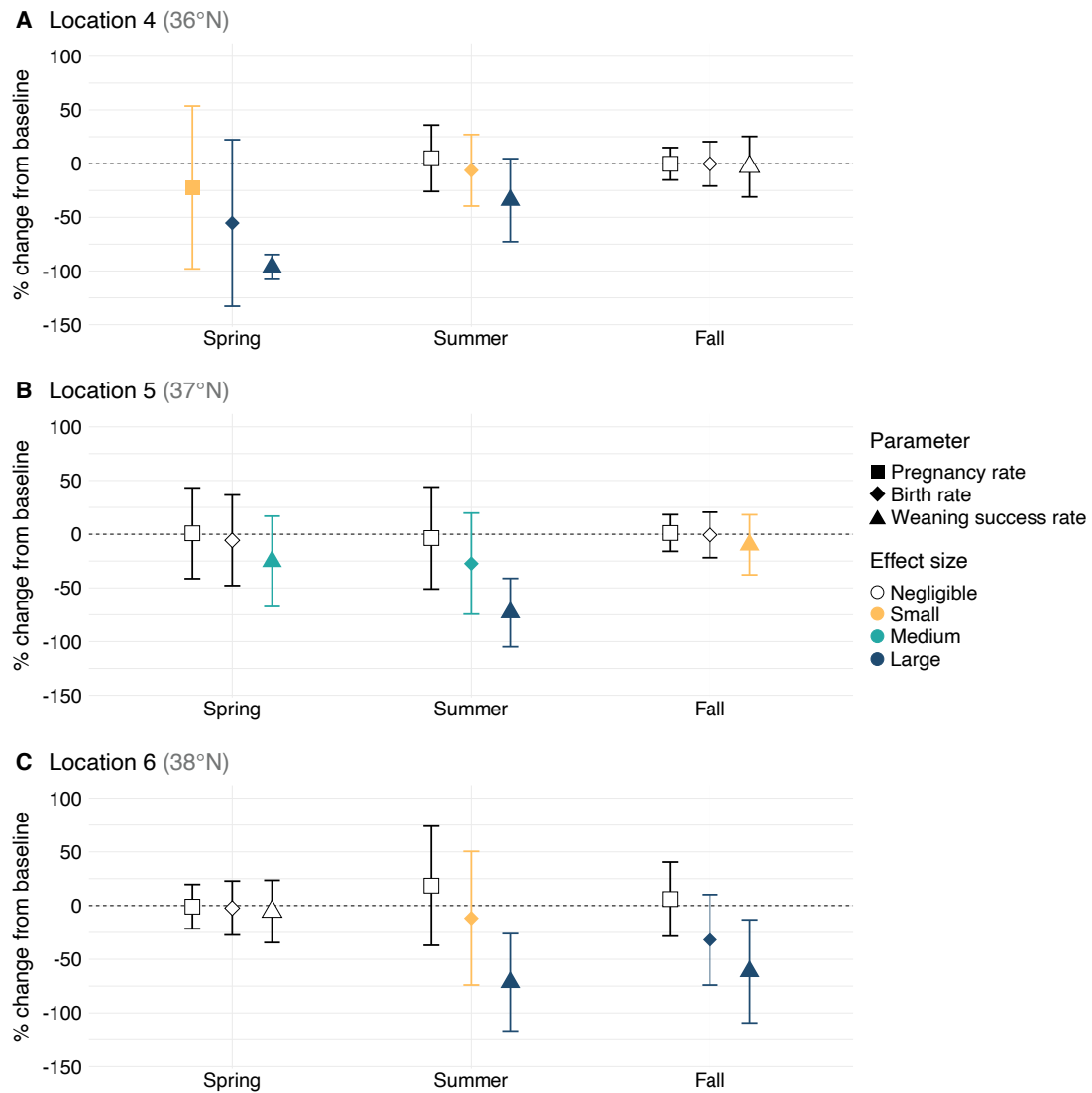


Figure 3.4. The influence of simulated general stressors on vital rates in (A) location 4 (B), location 5, and (C) location 6, with their approximate center latitudes included in parentheses. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor); error bars represent the standard deviation as percent change around the mean; shapes represent the measured vital rates (i.e., pregnancy rate, birth rate, and weaning success rate); and colors represent the effect size based on Cohen's *d*.

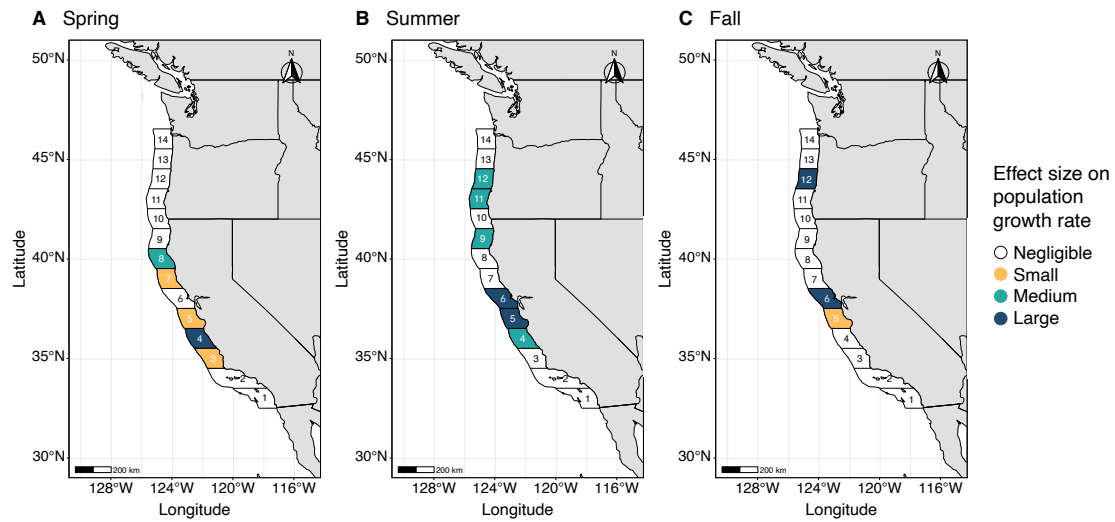


Figure 3.5. The influence of simulated general stressors on population growth rate in (A) spring, (B) summer, and (C) fall. The colors of each location represent the effect size based on Cohen's *d*.

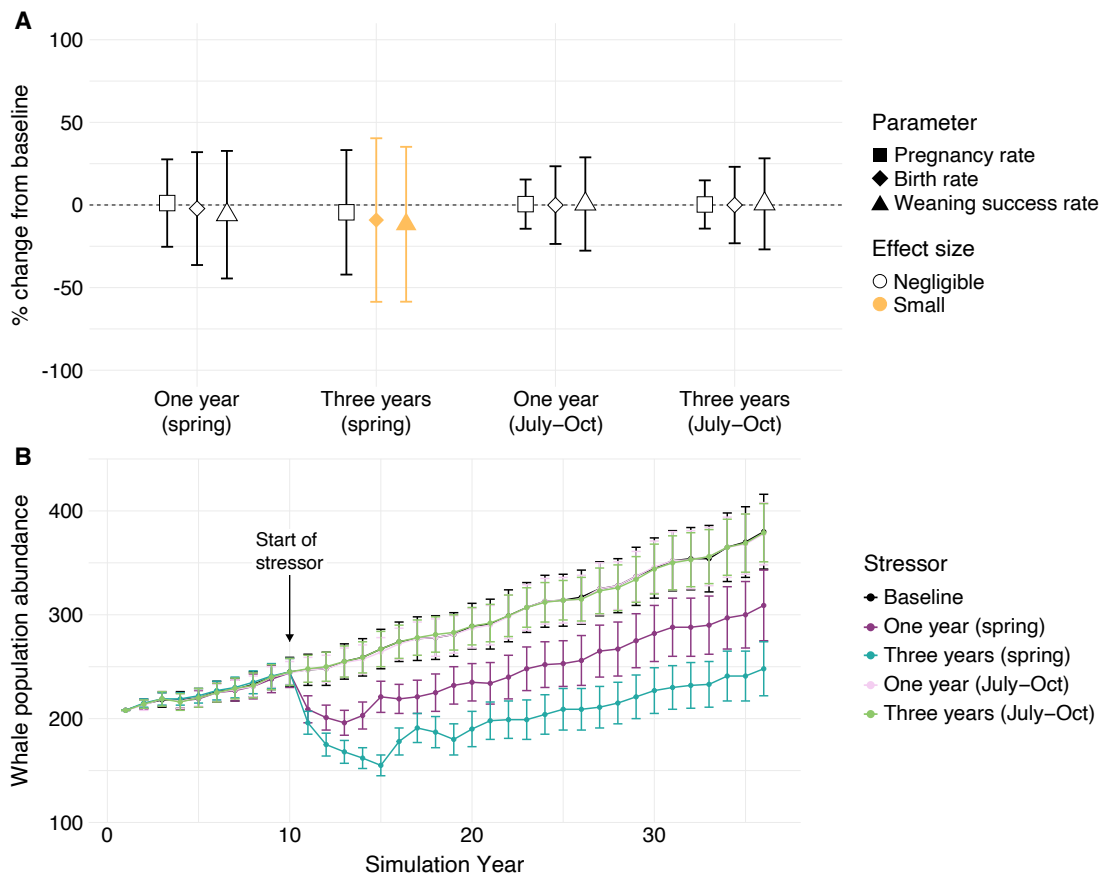


Figure 3.6. (A) The influence of simulated construction stressors on vital rates. In the plot, points represent the mean percent change from baseline simulations (i.e., no stressor); error bars represent the standard deviation as percent change around the mean; shapes represent the measured vital rates (i.e., pregnancy rate, birth rate, and weaning success rate); and colors represent the effect size based on Cohen's *d*. The x-axis represents the simulated construction stressor scenarios. (B) Population trajectories for baseline conditions and four construction scenarios; error bars represent the standard deviation.

3.9 Supplementary material

3.9.1 Appendix A: Energy gained from feeding

Energy gained from feeding (E_{gained}). On the feeding grounds, a whale could gain energy by feeding on krill or fish, and the amount of energy gained depended on the whale's physiology, location, time, and the environmental regime.

The total energy gained on a given day (kJ/day) was calculated as:

$$E_{gained} = pe_j \times me_j \quad (1)$$

where pe_j is the proportion of energy encountered for prey type j and me_j is the maximum energy that a whale can gain of prey type j on a given day. The maximum daily energy that could be gained was calculated as:

$$me_j = f_{capacity} \times n_{filled} \times M \times ed_j \quad (2)$$

where $f_{capacity}$ is the whale's forestomach capacity in kg, $n_{filled} = 8$ is the number of times the forestomach can be filled, $M = 0.85$ is the metabolic efficiency, and ed_j is the energy density of prey type j in kJ/kg. The number of times the forestomach could be filled depended on the time available to feed (24 hours) and the time it takes to clear the forestomach (3 hours (1)). Metabolic efficiency was estimated from existing values of fecal efficiency (93%) from minke whales (*Balaenoptera acutorostrata*) (2) and predicted values of urinary efficiency (92%) reported in the literature (3-5). The energy density of krill was 3,628 kJ/kg (which assumes a diet comprised of 80% *T. spinifera* and 20% *E. pacifica* (6)) and the energy density of fish was 6,000 kJ/kg (6).

A whale's forestomach capacity (kg) was calculated as (1, 7):

$$f_{capacity} = 0.47 \times L(t)^{2.78} \quad (3)$$

where $L(t)$ is the body length of the whale at time t in meters.

Body length on a given day, $L(t)$, was determined using a combination of age-length growth functions for fetuses, calves, juveniles, and adults obtained from the literature and reported below (8-10). For the calf/juvenile age-length function, a *scalar* = 0.276 was used to align the endpoint of the calf/juvenile length function and start point of the adult length function.

Fetus	$L(t) = (3.5684 \times month^2 - 3.2984) \times 0.01$	(4)
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Calf/juvenile	$L(t) = (11.448 + scalar) \times (1 - e^{-0.977 \times (year + 0.459)})$	(5)
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Adult	$L(t) = (45.21 \times 1 - e^{-0.205 \times (year + 4.936)}) \times 0.3048$	(6)
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3.9.2 Appendix B: Sensitivity analysis

Table B1 provides a list of model parameters tested in the sensitivity analysis. Table B2 provides a list of key vital rates (i.e., pregnancy, birth, weaning success, and population growth rates) and their values from the original model. Details of how each model parameter affected model results under baseline conditions are reported below with summary tables (Tables B3 through B7). Each summary table lists the four key vital rates, their value using the adjusted model parameter, and the Cohen's d value to assess the effect of the adjustment on the associated vital rate. Positive values indicate an adverse effect while negative values indicate a positive effect on vital rates, with values of ± 0.2 , ± 0.5 , and ± 0.8 indicating small, medium, and large effects, respectively. The values for the vital rates in the summary tables are presented as mean (SD).

Table B1. List of model parameters tested in the sensitivity analysis.

Model parameter/description	Original value	Sensitivity combinations
Maximum threshold for female body condition	45%	40%, 50%
Age threshold for mother/calf to leave breeding grounds	50 days	$\pm 50\%$
Multiplier for prey environment	1.36	1.6, 2.0
Shape parameter of the fitness function	8	$\pm 25\%$
Scale parameter of the fitness function	0.28	$\pm 25\%$

Table B2. List of key vital rates and their values from the original model.

Life-history parameter	Mean	SD
Pregnancy rate (%) ¹	32.98	5.06
Birth rate (%)	26.83	5.75
Weaning success rate (%)	57.02	16.21
Population growth rate (%)	1.73	2.1

Notes: ¹ Calculated on ordinal day 16 (January 16) and includes only sexually mature whales (≥ 5 years old).

Maximum threshold for female body condition. Reducing the maximum body condition threshold had a positive, medium effect on pregnancy rate and adverse, large effects on weaning success and population growth rates. With a smaller reserve to store energy, fewer females were successfully weaned and added to the population, which subsequently led to a decrease in the population growth rate. An increase in pregnancy rate was likely mediated by females choosing to wean and abandon their calves early and becoming pregnant in the following year. In contrast, increasing the maximum body condition threshold only had positive, medium effects on pregnancy, weaning success, and population growth rates. With a larger energy reserve, more females became pregnant and successfully weaned their calves, which led to a higher population growth rate.

Table B3. Summary table for the sensitivity analysis for the maximum threshold for female body condition.

Life-history parameter	Max = 40%	Cohen's <i>d</i>	Max = 50%	Cohen's <i>d</i>
Pregnancy rate (%)	39.81 (16.02)	-0.57	37.06 (14.53)	-0.38
Birth rate (%)	27.43 (18.19)	-0.04	28.07 (10.80)	-0.14
Weaning success rate (%)	18.06 (23.81)	1.91	66.70 (26.82)	-0.44
Population growth rate (%)	-2.17 (3.04)	1.49	2.43 (3.14)	-0.26

Age threshold for mother/calf to leave breeding grounds. Shifting the age threshold to day 25 meant mothers and calves could leave the breeding grounds earlier, whereas shifting it to day 75 meant they left later. While this did not have a significant effect on pregnancy and birth rates, it did affect weaning success and population growth rates. When mothers and calves could leave the breeding grounds earlier, mothers did not have to rely on their energy reserves for an extended period, allowing more mothers to nurse and maintain their calves. This led to a medium, positive effect on weaning success rate and a small, positive effect on population growth rate. Shifting the age threshold to day 75 meant mothers had to rely on their energy reserves for an extended period. As a result, more mothers abandoned their calves which subsequently led to lower weaning success and population growth rates.

Table B4. Summary table for the sensitivity analysis for the age threshold (for the calf, in days) for a mother/calf to leave the breeding grounds.

Life-history parameter	Day = 25	Cohen's <i>d</i>	Day = 75	Cohen's <i>d</i>
Pregnancy rate (%)	33.95 (8.02)	-0.14	33.19 (6.35)	-0.04
Birth rate (%)	27.64 (7.93)	-0.12	26.29 (6.45)	0.09
Weaning success rate (%)	66.20 (17.80)	-0.54	34.77 (18.96)	1.26
Population growth rate (%)	2.50 (2.34)	-0.35	-0.35 (2.62)	0.88

Multiplier for the prey environment. Increasing the prey multiplier had significant, positive effects on the four key vital rates, leading to increased pregnancy, birth, and weaning rates, which subsequently led to higher population growth rates.

Without a prey multiplier, simulated populations crashed before the end of the simulation.

Table B5. Summary table for the sensitivity analysis for the multiplier for the prey environment.

Life-history parameter	Multiplier = 1.6	Cohen's <i>d</i>	Multiplier = 2.0	Cohen's <i>d</i>
Pregnancy rate (%)	42.69 (5.70)	-1.80	54.41 (9.31)	-2.86
Birth rate (%)	35.65 (7.84)	-1.28	45.70 (11.42)	-2.09
Weaning success rate (%)	77.32 (12.52)	-1.40	80.22 (8.56)	-1.79
Population growth rate (%)	4.94 (2.01)	-1.56	6.83 (2.85)	-2.04

Shape parameter of the fitness function. The shape parameter influenced the steepness of the fitness function. Varying this parameter by $\pm 25\%$ from the original value had negligible effects on the four key vital rates.

Table B6. Summary table for the sensitivity analysis for the shape parameter of the fitness function.

Life-history parameter	Shape = 6	Cohen's <i>d</i>	Shape = 10	Cohen's <i>d</i>
Pregnancy rate (%)	33.28 (4.62)	-0.06	33.14 (5.35)	-0.03
Birth rate (%)	26.50 (5.76)	0.06	26.62 (6.34)	0.03
Weaning success rate (%)	54.69 (16.20)	0.14	57.38 (16.13)	-0.02
Population growth rate (%)	1.50 (2.20)	0.11	1.68 (2.11)	0.02

Scale parameter of the fitness function. The scale parameter is the proportion of blubber mass at which the calf has a 50% chance of surviving to 10.5 months old, when it can be added to the population. Therefore, a value of 0.35, which is higher than what was used in the original model, meant that the calf had to be in better body

condition at 10.5 months old and vice versa when this value was 0.21, which is lower than what was used in the original model. Therefore, when this value was higher, there was a large, adverse effect on weaning success rate and, subsequently, a medium, adverse effect on population growth rate. When this value was lower, weaning success and population growth rates were higher.

Table B7. Summary table for the sensitivity analysis for the scale parameter of the fitness function.

Life-history parameter	Scale = 0.21	Cohen's <i>d</i>	Scale = 0.35	Cohen's <i>d</i>
Pregnancy rate (%)	33.96 (7.41)	-0.15	33.09 (4.67)	-0.02
Birth rate (%)	27.39 (7.54)	-0.08	26.48 (5.46)	0.06
Weaning success rate (%)	64.99 (17.47)	-0.47	41.82 (16.37)	0.93
Population growth rate (%)	2.38 (2.28)	-0.30	0.44 (2.29)	0.59

3.9.3 Appendix C: Tables of life-history parameters and Cohen's *d* values

Table C1. Calculated life-history parameters under baseline conditions (no stressors).

Parameter	Mean	SD
Age at first birth (years)	6.13	0.38
Weaning day for successfully weaned calves (ordinal day)	291	16
Interbirth interval (years)	3.94	0.51
Pregnancy rate (%) ¹	32.98	5.06
Birth rate (%)	26.83	5.75
Weaning success rate (%)	57.02	16.21
First year survival rate (%)	95.74	5.30
Recruitment rate (%) ²	80.83	11.42
Death rate (%)	3.58	1.13
Population growth rate (%)	1.73	2.1

Note: ¹ Calculated on ordinal day 16 (January 16, the day after a whale can implant) and includes only sexually mature whales (≥ 5 years old); ² percentage of calves in a given cohort (i.e., calves born in the same year) who reach sexual maturity and successfully give birth.

Table C2. Selected life-history parameters under the general stressor scenarios in spring (March to May).

Parameter	Mean	SD	Cohen's <i>d</i>
Location 1			
Pregnancy rate (%)	32.89	5.07	0.02
Birth rate (%)	26.78	5.77	0.01
Weaning success rate (%)	56.73	16.09	0.02
Population growth rate (%)	1.70	2.10	0.01
Location 2			
Pregnancy rate (%)	32.92	5.02	0.01
Birth rate (%)	26.82	5.78	0.00
Weaning success rate (%)	57.4	16.35	-0.03
Population growth rate (%)	1.76	2.17	-0.01
Location 3			
Pregnancy rate (%)	34.82	6.25	-0.32
Birth rate (%)	26.68	7.06	0.02
Weaning success rate (%)	50.65	19.86	0.35
Population growth rate (%)	1.10	2.33	0.28
Location 4			
Pregnancy rate (%)	25.66	25.00	0.41
Birth rate (%)	11.99	20.80	0.97

Weaning success rate (%)	2.16	6.59	4.43
Population growth rate (%)	-4.16	2.17	2.76
Location 5			
Pregnancy rate (%)	33.27	13.95	-0.03
Birth rate (%)	25.31	11.32	0.17
Weaning success rate (%)	42.63	23.99	0.70
Population growth rate (%)	0.29	3.88	0.46
Location 6			
Pregnancy rate (%)	32.65	6.78	0.06
Birth rate (%)	26.21	6.72	0.10
Weaning success rate (%)	53.88	16.51	0.19
Population growth rate (%)	1.38	2.19	0.16
Location 7			
Pregnancy rate (%)	32.37	6.89	0.10
Birth rate (%)	26.25	6.63	0.09
Weaning success rate (%)	51.37	18.82	0.32
Population growth rate (%)	1.08	2.27	0.30
Location 8			
Pregnancy rate (%)	32.52	9.14	0.06
Birth rate (%)	25.71	8.19	0.16
Weaning success rate (%)	46.41	23.58	0.52
Population growth rate (%)	0.29	2.43	0.63
Location 9			
Pregnancy rate (%)	33.07	5.07	-0.02
Birth rate (%)	26.75	5.76	0.01
Weaning success rate (%)	58.25	16.73	-0.07
Population growth rate (%)	1.73	2.16	0.00
Location 10			
Pregnancy rate (%)	33.04	5.02	-0.01
Birth rate (%)	26.76	5.69	0.01
Weaning success rate (%)	57.63	16.56	-0.04
Population growth rate (%)	1.77	2.22	-0.02
Location 11			
Pregnancy rate (%)	32.92	5.07	0.01
Birth rate (%)	26.79	5.73	0.01
Weaning success rate (%)	58.03	16.40	-0.06
Population growth rate (%)	1.77	2.04	-0.02
Location 12			
Pregnancy rate (%)	32.89	5.13	0.02
Birth rate (%)	26.83	5.86	0.00
Weaning success rate (%)	57.47	16.92	-0.03
Population growth rate (%)	1.75	2.08	-0.01

Location 13			
Pregnancy rate (%)	32.98	4.99	0.00
Birth rate (%)	26.76	5.66	0.01
Weaning success rate (%)	57.27	16.65	-0.02
Population growth rate (%)	1.69	2.17	0.02
Location 14			
Pregnancy rate (%)	32.91	5.12	0.01
Birth rate (%)	26.83	5.81	0.00
Weaning success rate (%)	57.37	16.89	-0.02
Population growth rate (%)	1.74	2.19	0.00

Table C3. Selected life-history parameters under the general stressor scenarios in summer (June to August).

Parameter	Mean	SD	Cohen's <i>d</i>
Location 1			
Pregnancy rate (%)	33.01	503	-0.01
Birth rate (%)	26.75	5.82	0.01
Weaning success rate (%)	57.88	16.00	-0.05
Population growth rate (%)	1.79	2.12	-0.03
Location 2			
Pregnancy rate (%)	33.03	5.03	-0.01
Birth rate (%)	26.75	5.82	0.01
Weaning success rate (%)	57.48	16.86	-0.03
Population growth rate (%)	1.76	2.17	-0.01
Location 3			
Pregnancy rate (%)	32.90	4.94	0.02
Birth rate (%)	26.77	5.58	0.01
Weaning success rate (%)	57.58	16.10	-0.03
Population growth rate (%)	1.79	2.12	-0.03
Location 4			
Pregnancy rate (%)	34.62	10.19	-0.20
Birth rate (%)	25.15	8.93	0.22
Weaning success rate (%)	37.62	22.04	1.00
Population growth rate (%)	-0.07	2.96	0.70
Location 5			
Pregnancy rate (%)	31.81	15.66	0.10
Birth rate (%)	19.49	12.63	0.75
Weaning success rate (%)	15.40	18.15	2.42
Population growth rate (%)	-3.88	4.95	1.48
Location 6			
Pregnancy rate (%)	39.07	18.30	-0.45
Birth rate (%)	23.67	16.69	0.25

Weaning success rate (%)	16.28	25.84	1.89
Population growth rate (%)	-2.67	2.46	1.92
Location 7			
Pregnancy rate (%)	32.96	5.04	0.00
Birth rate (%)	26.85	5.84	0.00
Weaning success rate (%)	57.66	16.82	-0.04
Population growth rate (%)	1.75	2.25	-0.01
Location 8			
Pregnancy rate (%)	32.89	5.05	0.02
Birth rate (%)	26.77	5.79	0.01
Weaning success rate (%)	57.32	15.60	-0.02
Population growth rate (%)	1.74	2.09	0.00
Location 9			
Pregnancy rate (%)	32.49	9.46	0.06
Birth rate (%)	25.53	8.43	0.18
Weaning success rate (%)	48.48	23.84	0.42
Population growth rate (%)	0.47	2.48	0.55
Location 10			
Pregnancy rate (%)	33.03	5.03	-0.01
Birth rate (%)	26.80	5.83	0.01
Weaning success rate (%)	58.31	17.02	-0.08
Population growth rate (%)	1.84	2.10	-0.05
Location 11			
Pregnancy rate (%)	32.52	8.84	0.06
Birth rate (%)	25.62	8.08	0.17
Weaning success rate (%)	48.35	22.70	0.44
Population growth rate (%)	0.57	2.37	0.52
Location 12			
Pregnancy rate (%)	32.39	10.15	0.07
Birth rate (%)	25.25	8.75	0.21
Weaning success rate (%)	47.39	24.27	0.47
Population growth rate (%)	0.40	2.52	0.57
Location 13			
Pregnancy rate (%)	32.97	4.94	0.00
Birth rate (%)	26.81	5.63	0.00
Weaning success rate (%)	57.88	16.69	-0.05
Population growth rate (%)	1.72	2.23	0.00
Location 14			
Pregnancy rate (%)	33.00	5.07	0.00
Birth rate (%)	26.73	5.71	0.02
Weaning success rate (%)	57.49	16.83	-0.03
Population growth rate (%)	1.72	2.10	0.00

Table C4. Selected life-history parameters under the general stressor scenarios in fall (September to November).

Parameter	Mean	SD	Cohen's <i>d</i>
Location 1			
Pregnancy rate (%)	32.97	4.97	0.00
Birth rate (%)	26.74	5.70	0.02
Weaning success rate (%)	57.40	16.66	-0.02
Population growth rate (%)	1.71	2.13	0.01
Location 2			
Pregnancy rate (%)	32.97	5.03	0.00
Birth rate (%)	26.81	5.76	0.00
Weaning success rate (%)	57.69	16.65	-0.04
Population growth rate (%)	1.76	2.15	-0.01
Location 3			
Pregnancy rate (%)	33.04	5.13	-0.01
Birth rate (%)	26.76	5.94	0.01
Weaning success rate (%)	57.56	16.83	-0.03
Population growth rate (%)	1.77	2.17	-0.02
Location 4			
Pregnancy rate (%)	32.93	4.97	0.01
Birth rate (%)	26.77	5.94	0.01
Weaning success rate (%)	55.40	16.06	0.10
Population growth rate (%)	1.56	2.10	0.08
Location 5			
Pregnancy rate (%)	33.36	5.64	-0.07
Birth rate (%)	26.65	5.68	0.03
Weaning success rate (%)	51.40	15.97	0.35
Population growth rate (%)	1.29	2.27	0.20
Location 6			
Pregnancy rate (%)	34.96	11.37	-0.22
Birth rate (%)	18.26	11.29	0.96
Weaning success rate (%)	22.09	27.39	1.55
Population growth rate (%)	-2.08	3.68	1.27
Location 7			
Pregnancy rate (%)	33.28	6.00	-0.05
Birth rate (%)	26.58	6.26	0.04
Weaning success rate (%)	52.82	17.55	0.25
Population growth rate (%)	1.32	2.41	0.18
Location 8			
Pregnancy rate (%)	32.76	5.54	0.04
Birth rate (%)	26.64	6.03	0.03
Weaning success rate (%)	57.09	15.97	0.00

Population growth rate (%)	1.62	2.18	0.05
Location 9			
Pregnancy rate (%)	33.04	5.02	-0.01
Birth rate (%)	26.76	5.69	0.01
Weaning success rate (%)	57.63	16.56	-0.04
Population growth rate (%)	1.77	2.22	-0.02
Location 10			
Pregnancy rate (%)	32.94	5.08	0.01
Birth rate (%)	26.73	5.73	0.02
Weaning success rate (%)	57.72	15.96	-0.04
Population growth rate (%)	1.77	2.15	-0.02
Location 11			
Pregnancy rate (%)	33.00	5.35	0.00
Birth rate (%)	26.61	5.86	0.04
Weaning success rate (%)	55.97	17.06	0.06
Population growth rate (%)	1.62	2.16	0.05
Location 12			
Pregnancy rate (%)	33.42	11.71	-0.05
Birth rate (%)	25.11	11.25	0.19
Weaning success rate (%)	45.42	25.01	0.55
Population growth rate (%)	-1.27	3.85	0.97
Location 13			
Pregnancy rate (%)	32.62	7.86	0.05
Birth rate (%)	26.29	7.76	0.08
Weaning success rate (%)	59.53	16.87	-0.15
Population growth rate (%)	1.72	2.20	0.00
Location 14			
Pregnancy rate (%)	33.06	5.10	-0.02
Birth rate (%)	26.76	5.81	0.01
Weaning success rate (%)	57.80	16.48	-0.05
Population growth rate (%)	1.71	2.18	0.01

Table C5. Selected life-history parameters under the construction stressor scenarios in location 4.

Parameter	Mean	SD	Cohen's <i>d</i>
1 year (year 10), spring (March to May)			
Pregnancy rate (%)	33.26	8.70	-0.05
Birth rate (%)	26.09	9.11	0.07
Weaning success rate (%)	53.97	22.13	0.17
Population growth rate (%)	1.20	3.90	0.18
3 years (years 10 to 12), spring (March to May)			
Pregnancy rate (%)	31.42	12.39	0.16

Birth rate (%)	24.24	13.20	0.24
Weaning success rate (%)	50.65	26.87	0.30
Population growth rate (%)	0.66	5.73	0.25
1 year (year 10), most likely construction window (July to October)			
Pregnancy rate (%)	33.05	4.90	-0.03
Birth rate (%)	26.65	6.27	0.00
Weaning success rate (%)	57.68	16.19	-0.02
Population growth rate (%)	1.74	2.08	0.00
3 years (years 10 to 12), most likely construction window (July to October)			
Pregnancy rate (%)	32.98	4.80	-0.02
Birth rate (%)	26.66	6.17	0.00
Weaning success rate (%)	57.73	15.80	-0.02
Population growth rate (%)	1.74	2.00	0.00

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Synthesis

My dissertation provides a qualitative and quantitative basis for assessing the effects of natural and anthropogenic stressors on population dynamics and comparing different stressor scenarios associated with our expanding offshore footprint.

In Chapter 1, I synthesized existing Population Consequences of Disturbance (PCoD) models developed for marine mammals to provide insights into what contextual factors influence a population's likelihood and duration of exposure and sensitivity to disturbance. By taking a holistic view of model results, I identified essential life-history traits (e.g., movement, reproduction), stressor characteristics (e.g., spatial and temporal overlap), and environmental conditions (e.g., seasonal changes, climatic oscillations) to consider when assessing risk. I also described how they can be evaluated when determining a population's vulnerability to disturbance. This information is valuable for identifying which species are at high risk of population-level effects, thus allowing wildlife managers and practitioners to prioritize their efforts and focus subsequent analyses on those most vulnerable.

Then, in Chapter 2, I added to the existing suite of PCoD models available for marine mammals by developing the first stochastic dynamic programming (SDP) model for humpback whales. With this model, I examined the temporal sensitivities of humpback whales (*Megaptera novaeangliae*) to simulated reductions in krill availability, mediated by climate change and krill fishing (i.e., stressors), on their western Antarctic Peninsula feeding grounds. The effect of simulated stressors on vital rates (e.g., pregnancy, birth, weaning success, and population growth rates) varied

depending on the severity of the krill reduction and whether both stressors were present. Across simulations, the effects were greatest during years when krill availability was poor due to their natural, interannual fluctuations. However, when stressors did not occur during poor krill years, impacts on the population were reduced. Finally, when climate change and krill fishing stressors occurred concurrently, the combined effects were greater than climate change in isolation, with some populations crashing before the end of the 25-year simulation. This information highlights the importance of considering the environmental context in which human activities operate when developing strategies to mitigate negative consequences on populations.

Finally, in Chapter 3, I extended the SDP model from the previous chapter to examine the spatial and temporal sensitivities of an endangered humpback whale population to stressors on their feeding grounds in the California Current Ecosystem. Simulated scenarios demonstrated that seasonal and interannual variability influenced whales' diets, spatial use of their feeding grounds, and the effects of stressors on vital rates. Stressors offshore the central and north central coasts of California and southern and central Oregon had the greatest impact on vital rates. Specifically, the most sensitive locations and times were offshore the Big Sur coast in spring, the greater Monterey Bay area in summer, and offshore San Francisco and the Greater Farallones region in fall. When a stressor did occur in important foraging locations during energetically vulnerable times, adjusting the temporal features of the stressor reduced impacts on vital rates. These results emphasize the need to carefully plan human

activities to avoid critical foraging locations and times, and how adjusting a stressor's features can reduce impacts when avoidance is not possible.

The SDP model presented in Chapters 2 and 3 provides a general framework to explore the ecology of humpback whales and quantify the effects of human activities and anthropogenic climate change on population dynamics. As a result, this model can help identify sensitive feeding times and areas for vulnerable populations, as well as predict the impact of multiple stressors on a population's vital rates. While the effects of anthropogenic climate change cannot be directly managed, potential effects may be alleviated by adaptively managing human activities.

Collectively, the chapters of my dissertation provide actionable tools that help identify vulnerable species through qualitative analyses and can assess the level of impact using quantitative methods. These approaches can help guide the streamlined assessment and responsible planning of human activities that minimize impacts on vulnerable populations.