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**A management-focused
population viability analysis for
North Atlantic right whales**

**US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole, Massachusetts
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A management-focused population viability analysis for North Atlantic right whales

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ABBREVIATIONS

CSIRO	Australian Commonwealth Scientific and Industrial Research Organisation
DDT	Dichlorodiphenyltrichloroethane, an insecticide used in agriculture
DFO	Department of Fisheries and Oceans Canada (Pêches et Océans Canada)
EMP	Expected minimum population size
ESA	U.S. Endangered Species Act of 1973, as amended (16 U.S.C. §1531 et seq.)
FR	Federal Register, the daily journal of the U.S. government, https://www.federalregister.gov/
GOM	Gulf of Maine
GSL	Gulf of St. Lawrence
HAB	Harmful algal bloom
IBM	Individual-based model
IUCN	International Union for the Conservation of Nature
MCMC	Markov chain Monte Carlo
MMPA	Marine Mammal Protection Act (16 U.S.C. § 1361 et seq.)
NARW	North Atlantic right whale (<i>Eubalaena glacialis</i>)
NMFS	NOAA National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
PBDEs	Polybrominated diphenyl esters, a class of compounds used as flame retardants
PBR	Potential Biological Removal
PCBs	Polychlorinated biphenyls, carcinogenic organic compounds formerly used in consumer and industrial products
PET	NARW Population Evaluation Tool
PQE	Probability of quasi-extinction
PVA	Population viability analysis
SARA	Canada's Species at Risk Act
USFWS	U.S. Fish and Wildlife Service

1. ABSTRACT

The North Atlantic right whale (*Eubalaena glacialis*) is among the most endangered whale species in the world and has been in decline since 2010. Considerable effort is directed toward its recovery by striving to remove threats. In this report, we describe the development of a population viability analysis for right whales that is designed to assess the current status, evaluate the contributions of various threats, and explore the management interventions needed to achieve recovery. The individual-based model that underlies this analysis accounts for age- and stage-specific survival and reproductive rates, the effects of severe injury from entanglement or vessel strike, and future changes in prey availability and accessibility. Several new or updated empirical analyses supplied parameter estimates, and parametric uncertainty was carefully incorporated into the model results.

We find that under the status quo conditions of 2019, prior to the enactment of new regulations by the U.S. and Canada after 2020, the North Atlantic right whale population would be expected to continue to fall, with a median decline of 75% in 100 years (95% projection interval, -98% to +9% change) and a probability of falling below 50 proven females of 0.934 in 100 years. If the recently enacted regulations reduce entanglement risk by 25%, however, the population would be expected to decrease by 42% over 100 years (95% projection interval -92% to +154% change), with a risk of falling below 50 proven females in 100 years of 0.705. If, instead, the recently enacted regulations reduce entanglement risk by 50%, the population would be expected to increase by 52% in 100 years (95% projection interval -83% to +497% change), with a probability of falling below 50 proven females of 0.349.

Of the 3 primary threats explored in this analysis, the risk of entanglement contributes the most to the long-term risk of quasi-extinction, followed closely by the risk of vessel strike, and much more distantly by a decrease in prey availability. In hypothetical scenarios that fully remove one threat at a time, removal of the entanglement threat alone reduces the probability of falling below 50 proven females in 100 years from 0.934 to 0.053; removal of the vessel strike threat alone reduces it to 0.343; and a return to higher prey conditions, but with both human-related threats still in place, reduces it to 0.875.

We explored a wide range of management intervention scenarios that changed the rate of entanglement risk (e.g., endline reductions, closures, implementation of ropeless/on-demand gear); the effect of entanglement (through use of weak rope technology); the rate of vessel traffic increase over time; and the severity of vessel strike risk through speed restrictions. We found, for example, that reducing entanglement risk alone by 25% reduces the risk of quasi-extinction from 0.934 to 0.705; reducing vessel strike risk alone by 25% reduces the risk of quasi-extinction from 0.934 to 0.846; but the combination of reducing both entanglement risk and vessel strike risk by 25% reduces the risk of quasi-extinction to 0.528.

This model and the results it produced are meant to represent an assessment of the current status of North Atlantic right whales using the best available scientific and commercial data and state-of-the-art analytical tools. Our knowledge of the future of the right whale population, however, has limitations. We have endeavored to fully incorporate uncertainty into this model, but there are many areas for continued improvement. We view this model as a living tool that can be improved, adapted, and extended as new data, new methods, and new questions arise.

2. PURPOSE AND SCOPE OF ANALYSIS

The North Atlantic right whale (NARW; *Eubalaena glacialis*) is among the most endangered whale species in the world (Caswell et al. 1999; Kraus et al. 2005; Cooke 2020). Prior to the whaling era, right whales may have numbered in the tens of thousands (NMFS 1991; Monsarrat et al. 2015), but intense whaling greatly reduced the population, with approximately 270 individuals accounted for in 1990 (Pace et al. 2017). The species is now protected under the Marine Mammal Protection Act (MMPA, 16 USC 1361 et seq.) and the Endangered Species Act of 1973 (ESA, 16 USC 1531 et seq.) in the U.S. and the Species at Risk Act (SARA, S.C. 2002, c. 29) and Marine Mammal Regulations of the Fisheries Act (SOR/2018-126) in Canada. Federal, state, and provincial management agencies, and their non-governmental and industry partners, are working to promote recovery of the species through actions that reduce the threats to right whales.

One of the scientific tools the management agencies have identified as a need is a population viability analysis (PVA) that can project the trajectory of the NARW population under a variety of scenarios. This report describes the development of such an evaluation tool, the structure of the underlying model, and preliminary results for a range of scenarios.

2.1 Background and Charge

The NARW Population Evaluation Tool (PET) Subgroup, which is constituted by the authors of this report, was established by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) in July 2018 under the North Atlantic Right Whale Recovery Plan U.S. Implementation Team. The charge of the Subgroup was to develop a PVA or other assessment tool that will allow the agency to characterize the NARW extinction risk—taking into account current and future threats—and will allow inquiry into how much improvement to present-day mortality and reproduction schedules is needed to improve population trajectories.

The U.S. recovery plan for the NARW was last revised in 2005 (NMFS 2005). The recovery plan indicates that NARWs may be considered for reclassification from “endangered” to “threatened” when all the following recovery criteria have been met:

1. “The population ecology (range, distribution, age structure, and gender ratios, etc.) and vital rates (age-specific survival, age-specific reproduction, and lifetime reproductive success) of NARWs are indicative of an increasing population;
2. The population has increased for a period of 35 years at an average rate of increase equal to or greater than 2% per year;
3. None of the known threats to NARWs (summarized in the five listing factors¹) are known to limit the population's growth rate; and
4. Given current and projected threats and environmental conditions, the NARW population has no more than a 1% chance of quasi-extinction in 100 years.”

¹ The Endangered Species Act of 1973 describes 5 factors by which the status of a species shall be determined: “(A) the present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence” (16 USC 1533(a)(1)).

The recovery plan recognized that not all the necessary tools were available to assess these criteria; 2 of the recovery actions addressed such gaps:

Action 2.0. “Develop demographically-based recovery criteria.” Recovery criterion 4 specifies a quasi-extinction probability that would indicate the risk is low enough for reclassification to threatened. To ensure the criterion meets the standards of “objective and measurable” specified in the Endangered Species Act (ESA), however, it is valuable to translate this guidance into demographic criteria, such as population size, structure, and trends.

Action 4.1. “Develop quantitative recovery criteria population models to determine extinction risk, and parameters to validate the model predictions.”

In its 2017 5-year review of the status of North Atlantic right whales (NMFS 2017), NMFS identified the following recommendation for future action: “NMFS should prioritize the development of a population viability analysis (PVA) or other assessment to determine the NARW extinction risk.” This recommendation arose from the NARW Recovery Plan Southeast U.S. Implementation Team and has the support of the NARW Recovery Plan Northeast U.S. Implementation Team.

Under Canada’s SARA, recovery is the cessation and reversal of the decline of an endangered, threatened, or extirpated species, and elimination or reduction of threats that limit species likelihood of persistence. A species is considered to be recovered “when its long-term persistence in the wild has been secured” (DFO 2014). Recognizing the long-term challenges faced by North Atlantic right whales, the SARA Recovery Strategy identifies an interim recovery goal “to achieve an increasing trend in population abundance over three generations,” where a generation is understood to be approximately 20 years (DFO 2014).

The need for a new assessment tool based on forward-looking projections has been affirmed by groups outside the government, as well as by the management agencies with jurisdiction. In a comprehensive review of information on NARWs, Moore et al. (2021) noted the importance of the effort described in this report for informing managers about NARW status and trends.

2.2 Objectives

Reflecting on the 2005 NMFS Recovery Plan, the 2014 SARA Recovery Strategy, the 2017 NMFS 5-year review, and its own charge, we, the NARW PET Subgroup, identified the following objectives for a PVA:

- *Estimate extinction risk under current and projected threats as we understand them at this time.* Such an estimate could be directly compared to recovery criteria 4. To develop an estimate of this risk, a PVA needs to incorporate the best available information about the current status of and threats to the population, forecast future threats and their demographic effects on NARWs, and fully integrate estimates of uncertainty.
- *Conduct a quantitative threats analysis.* Each regular 5-year review of the status of NARWs, and any reclassification, will need to undertake a 5-factor analysis to evaluate the threats acting on the species. A PVA can be used to enhance a 5-factor analysis by quantitatively estimating the effect of individual threats on the long-

term probability of extinction (Runge et al. 2017). For example, how much is the risk of extinction affected by the changing distribution of food sources, as mediated by climate change; entanglement in fishing gear; vessel strikes; or noise-induced stress?

- *Evaluate a series of relevant management alternatives.* A PVA can be used to evaluate the effect of potential management actions on the long-term extinction risk. For example, if it is possible to change the entanglement mortality rate or the vessel-strike mortality rate, how much might the risk of extinction change?
- *Conduct sensitivity analyses of the PVA model.* This objective has 2 elements: (1) understand the effect of mean values for demographic parameters on the output metrics of interest (e.g., how much is extinction risk affected by adult female survival?), and (2) understand the effect of uncertainty in the demographic parameters on the uncertainty in the output metrics. The first element is most useful for understanding where management action might be best directed; the second element is most useful for understanding where monitoring or research effort might best be directed.
- *Facilitate communication, outreach, and education with stakeholders and the public.* The tools developed by the NARW PET Subgroup could be used to communicate understanding about the demography of NARWs, the threats they face, and the potential effects of various interventions.

2.3 Model Structure

The charge to the PET Subgroup and the objectives developed for the PVA help to define the performance requirements and the underlying structure of the population model developed in this report.

2.3.1 Desired model outputs

The outputs of a population forecasting model provide information about the likelihood of outcomes that are desirable under statute or for other reasons. Identification of these desired outputs helps to shape the structure of the population model. We identified the following desired outputs from a NARW PVA:

- *Extinction (or quasi-extinction) risk over time.* The NARW recovery plan identifies the quasi-extinction risk over 100 years as a relevant metric, where “Quasi-extinction is defined (Ginzburg et al. 1982) as a small, critical population threshold whose lower boundary may be unacceptable for the continued survival of a species. This could be the population size at which factors such as demographics, inbreeding depression, or behavioral constraints prohibit survival” (NMFS 2005).
- *Minimum expected population size.* McCarthy and Thompson (2001) found that the expected minimum population (EMP) size is a robust and sensitive measure of threat. It is closely related to the probability of extinction but can sometimes provide a more sensitive measure. It is calculated from the replicates within a PVA by tabulating the minimum population size over a specific timeframe for each replicate, then averaging over replicates.

- *International Union for Conservation of Nature (IUCN) metrics.* The IUCN uses a variety of alternative metrics in its Red List criteria. Among them are the probability of a 30%, 50%, or 80% decline over 10 years or 3 generations, whichever is longer, up to 100 years. Such forecasts of decline can be calculated from the results of a PVA. Note that Taylor et al. (2007) estimated the generation time for NARW as 23.3 years (at the then-current population growth rate $r = 0.05$) or 35.7 years (at $r = 0$).
- *Population growth rate.* Some recovery plans include the population growth rate as a recovery criterion. This can only serve as an intermediate criterion because at some point, a healthy population recovers to its carrying capacity and stabilizes, but growth rate can be a good measure of progress toward that point. The 2014 SARA Recovery Strategy includes a positive growth rate over 3 generations as an interim recovery goal. The 2005 NMFS NARW Recovery Plan includes a criterion of 2% growth for 35 years, which would allow the population to double. A related metric is the probability of doubling over a 35-year period.
- *Other demographic metrics.* There are many other demographic metrics that contribute to the long-term probability of persistence and provide detail about some aspects of the population processes. Metrics like the annual calf counts, mean calving interval, overall mortality rates, and cause-specific mortality rates all provide measures of some aspect of the population demography. As in the polar bear (*Ursus maritimus*) recovery plan (USFWS 2016a), it is possible to derive values for these parameters that would suggest a population is approaching a desired long-term probability of persistence.

2.3.2 Threats represented

To forecast the risks facing the species into the future, and to investigate the role that different threats play in the status and management of NARWs, the model needs to incorporate mechanisms that link specific threats to demographic consequences. The following threats are incorporated into the structure of the model:

- Entanglement in fixed fishing gear, notably ropes used in the trap/pot and gillnet fisheries, and its effects on direct mortality of whales; indirect mortality through injury and energetic demands; and reduced reproduction through energetic demands.
- Vessel interactions, including lethal vessel strike, sublethal effects of vessel strike on survival, sublethal effects of vessel strike on reproduction, and nonlethal effects through behavioral disturbance and energetic exertion.
- Changes in availability of food resources—as driven both by multi-annual fluctuations and climate change—and their effects on reproduction through energetics.
- Anthropogenic noise in the marine environment and its effect on reproduction, with possible mechanisms of action through disruption of feeding behavior, masking of communication, and elevated stress.

2.3.3 Elements of the model structure

Some of the aspects of the model structure arise directly from the purposes of the model, while also taking into account the current knowledge about NARW demography. The overarching features of the model structure include:

- *Spatial and temporal structure.* The population model explicitly represents annual processes; sub-annual processes are only captured implicitly in annual transition rates. Likewise, the population model does not have explicit spatial structure—NARWs are represented as a single population.
- *Age- and stage-structure.* A combination of age- and stage-classes are used to represent right whale population dynamics: males and pre-breeding females are represented by age, and breeding females are represented by stages to reflect the physiological and energetic constraints of the breeding process.
- *Threats-based submodels.* The core dynamics in the model involve the transitions of animals among the age- and stage-classes, but this core model is supported by a series of submodels that govern the mechanisms by which the various threats affect the demographic rates.
- *Density dependence.* Density-dependent processes for NARWs are not well understood. Presumably, at some point, right whale density could reach a point where further population growth rate was limited by the availability of resources, but it is not clear whether the population could reach such a point within the time frame of our model projections (roughly 100 years).
- *Indirect links to management actions.* This model can be used by managers to understand how estimated risk reductions, possibly associated with specific management actions, might be anticipated to change the population trajectory. But note that the purposes of this model do not include direct links between specific management actions and long-term population dynamics. The inputs to the model are meant to be changes in demographic rates. The link between specific management actions and the induced change in demographic rates is the purview of other tools (like the Decision Support Tool used by NOAA in its Atlantic Large Whale Take Reduction Plan Rule, 86 Federal Register [FR] 51970).

2.4 Desired Simulations

The adjustable inputs to a population model are the settings that control different simulations; these settings define the types of questions that can be asked of the model. We have taken a “baseline and scenarios” approach (Runge et al. 2017; Williams et al. 2021). The baseline forecast incorporates the best estimates of current status and future threats to provide the current estimate for extinction risk. The scenarios are deviations from the baseline that reflect “what if” conditions of interest to managers and stakeholders. In addition to the baseline forecast, the types of scenarios considered include:

- *Threats-analysis scenarios.* This series of scenarios removes the threats from the baseline scenario one at a time and in some combinations to generate an

understanding of the relative contribution of the individual threats to the current risk of extinction and other measures of status.

- *Entanglement scenarios.* These scenarios investigate the effects on the future status of right whales of mitigation of entanglement including: (a) scenarios that change the incidence of entanglement (as might arise through fishery closures and a change in the amount of gear in the water); (b) scenarios that primarily reduce the effect of entanglement on adults and juveniles without a change in the incidence of entanglement (as might arise through a change in the breaking strength of ropes used in fishing); and (c) combinations between the incidence and effects of entanglement.
- *Vessel strike scenarios.* These scenarios investigate the effects of a change in interactions of vessels with NARWs that might emerge from: (a) changes in the interaction rates between vessels and whales (as might arise through routing measures, changes in the number of vessels, and development of active avoidance technology); (b) changes in the severity of an interaction (as might arise through changes in the sizes or distribution of vessels in NARW habitat); and (c) changes in both the incidence and severity of strikes (as might arise through speed restrictions).
- *Prey availability scenarios.* These scenarios investigate the effects of potential changes in distribution and availability of zooplankton prey (*Calanus sp.*), driven by changes in the climate.
- *Prey accessibility scenarios.* These scenarios simulate potential effects of environmental noise on prey accessibility by dialing up or down by various amounts the biomass of prey available to NARW.
- *Sensitivity analysis scenarios.* A number of scenarios were run to generate an understanding of how uncertainty in the parameters within the model affects the results of the projections.

3. LITERATURE REVIEW

Because of their conservation status, proximity to human activities, and complicated economic interactions, right whales have been studied extensively, including through quantitative projection models. Here, we review the general use of PVAs, the use of quantitative projection models for NARWs, the current understanding of demography of NARWs, and the threats they face. This literature review serves as the background for the development of our model.

3.1 Population Viability Analysis: Concept and Uses

Population viability analysis is a set of methods for forecasting population dynamics into the future with particular attention to estimating the probability of extinction of the corresponding animal or plant. The development and use of a PVA is necessarily a forward-looking activity and requires careful consideration of how to use the available information to anticipate future risks and outcomes. The concept emerged in the 1980s, the term was coined in 1986 (Gilpin and Soulé 1986), and an important early review of applications was published in 1992 (Boyce 1992). There is widespread application of these methods for a number of purposes; in a recent review,

Chaudhary and Oli (2020) reviewed 160 PVAs of mammals and birds published between 1990 and 2017.

There are several potential uses of PVAs, including predicting the extinction risk of one or more populations of conservation concern (Morris and Doak 2002); predicting related metrics, such as the probabilities of dropping below given thresholds within a specified period of time (probability of quasi-extinction or PQE); evaluating the relative importance of various threats (Runge et al. 2017); comparing the effects of various management scenarios on predicted population outcomes (Ellner and Fieberg 2003; McCarthy et al. 2003); identifying management targets (Regehr et al. 2015); and identifying where more research is needed. The output metrics from PVAs vary depending on the context in which the analysis is used. They include probability of extinction; PQE; EMP size (McCarthy and Thompson 2001; Runge et al. 2017); and expected time until extinction or quasi-extinction (Morris and Doak 2002). Some important things to consider in most PVA projects are environmental stochasticity or temporal variation in vital rates (White 2000); parametric uncertainty (White 2000, McGowan et al. 2011); structural uncertainty (Bakker et al. 2009; Runge et al. 2017); demographic stochasticity; genetic dynamics (Boyce 1992); and the effects of various threats and management actions on vital rates (Runge et al. 2017). In addition, some PVAs have considered effects of disease, toxins, and other threats on health or energetics of individuals (sublethal effects; Munns 2006; Bradshaw et al. 2012; Forbes et al. 2016). Recently, some have begun to use PVAs to explore how populations may respond to immediate anthropogenic stressors, as well as the projected impacts of climate change (Williams et al. 2021).

3.2 The Use of Population Viability Analysis in Endangered Species Act Contexts

The plain language of the ESA (16 U.S.C. §1531 et seq.) suggests a concern with the probability of extinction. An endangered species is one “which is in danger of extinction throughout all or a significant portion of its range” (16 U.S.C. §1532(6)). Many of the decisions made under the ESA, such as listing, delisting, recovery planning, and permitting of incidental take, link in some way or another to the definition of endangered. If the definition of endangered invokes the need to estimate the probability of extinction, then PVA becomes a central tool for assessment under the ESA. Indeed, both the U.S. Fish and Wildlife Service (USFWS) and the NMFS—the 2 agencies charged with implementing the ESA—have used results from PVAs in a number of their management decisions (Runge 2021). Recently, USFWS developed guidance for species status assessment under the ESA, including how to incorporate PVAs (Smith et al. 2018; USFWS 2016b).

One of the ways in which PVA has been used the most under the ESA is in decisions regarding the classification of species (as “endangered,” “threatened,” or “not warranted” for listing), either in listing rules or in the recovery criteria in recovery plans. For example, the 2008 listing rule for polar bears (USFWS 2008b) and the 2017 reclassification rule for the West Indian manatee (*Trichechus manatus latirostris*; USFWS 2017) considered results from PVAs in making their determinations. There are many recovery plans that have stated recovery criteria in terms of the probability of extinction, with either explicit or implicit indication that a PVA will be needed to estimate that probability; examples include Louisiana black bears (*Ursus americanus luteolus*; USFWS 1995), Steller’s eiders (*Polysticta stelleri*; USFWS 2002), North Atlantic right whales (NMFS 2005), Florida panthers (*Puma concolor*; USFWS 2008a), and polar bears (USFWS 2016a), among others. USFWS and NMFS have also undertaken 3 joint exploratory efforts to establish policy thresholds for classifications when PVAs are used (Angliss et al. 2002; DeMaster

et al. 2004; Regan et al. 2009). Although these efforts have not resulted in the adoption of standard policy for interpreting PVAs in the context of listing decisions, they have been influential in encouraging the use of PVAs and guiding their development.

Another powerful way that PVAs could be used in an ESA context is in the development of recovery plans, particularly in the comparison of alternative strategies for recovery. For example, Runge et al. (2017) used a PVA to undertake a quantitative threats analysis for Florida manatees, identifying the strength of influence of individual threats on the future status of manatees, and thus allowing a comparison of potential recovery strategies.

3.3 North Atlantic Right Whale Projection Models

Several authors have developed projections for the NARW population, primarily based on estimation from mark-resight data. Both Caswell et al. (1999) and Fujiwara and Caswell (2001) used maximum likelihood-based, expanded Cormack-Jolly-Seber models to estimate right whale survival trends over time. The former used a stochastic simulation to project the female population, while the latter used a more complete stage-based matrix projection to examine future prospects for the species. Both papers concluded that a decrease in survival from 1980-1995 produced a decrease in the NARW growth rate. In an unpublished manuscript, Richard Pace (2015; unreferenced) developed an updated stochastic simulation based on resampling maximum-likelihood survival estimates and per capita calving rates from data collected from 1980-2005; his simulations produced no realizations that resulted in extinction, but the median projected growth rate under status quo conditions was lower than what had been observed over the data period. Meyer-Gutbrod and Greene (2018) used a matrix projection model similar to Fujiwara and Caswell (2001) but with fecundity influenced by an estimated relationship between prey abundance and calving rate. They then proceeded to look at the prospect of recovery under different changing ocean conditions and different mortality schedules for adult females. The most recent projection modeling effort to date was that of Corkeron et al. (2018) who used a matrix projection model together with comparisons of calf production among NARW and 3 populations of southern right whales (*Eubalaena australis*) to demonstrate that the NARW population's potential growth has been stifled by human-caused mortality.

Population projection models have also been used for retrospective analyses. Monsarrat et al. (2016) used spatially explicit historical catch information on relative densities of North Pacific right whales (*E. japonica*) to develop a habitat model that they projected onto the North Atlantic. Their model predicted a pre-exploitation abundance of 9,075-1,328 NARWs and additional potential feeding habitats rarely surveyed that may prove important in the future. The low end of their prediction interval captured the pre-exploitation estimate of 10,000 used by NMFS (1991) in the first NARW recovery plan. Kenney (2018) used an uncomplicated replacement strategy to posit the question, "What if there had been no entanglement mortality in the NARW population from 1990-2016?" He merely added back those animals documented as killed by entanglement to reveal that the population decline documented by Pace et al. (2017), using some seemingly reasonable assumptions, would likely not have occurred at all.

3.4 Demographic Analyses of North Atlantic Right Whales

Demographic studies of NARWs have benefited from an extensive survey effort and resulting catalog of individual sightings since 1979. Unique callosity patterns and other visually distinguishing characteristics have allowed researchers to track individuals across time (Kraus et al. 1986) and subsequently estimate NARW survival and causes of mortality (Kraus 1990; Caswell

et al. 1999). NARW survival analyses have identified the importance of human-caused mortality events (Knowlton and Kraus 2001; Schick et al. 2013; Corkeron et al. 2018), primarily vessel strikes (Vanderlaan et al. 2008; Conn et al. 2013; Mullen et al. 2013; van der Hoop et al. 2015; Crum et al. 2019) and fishing gear entanglement (Johnson et al. 2005; Pace et al. 2014; Robbins et al. 2015; van der Hoop et al. 2017). Evidence suggests that >88% of observed mortalities are caused by vessel strike and gear entanglements (Sharp et al. 2019) and, that in more recent years (i.e., 2010-2015), gear entanglements have surpassed vessel strikes as the most prevalent human-caused mortality source (Harcourt et al. 2019). The last comprehensive assessment of NARW survival (Pace et al. 2017) provided some evidence of higher annual adult survival for males (0.98) than females (0.97).

Surveys during the winter at the southeast U.S. NARW calving grounds (Figure 1) have historically allowed a high proportion of new calves to be observed each year, along with the identity of mothers, enabling comprehensive studies on reproduction in the population (Knowlton et al. 1994; Hamilton et al. 1998; Rolland et al. 2005; Miller et al. 2011). Annual fluctuations in calf production appear to be driven by prey resources (Meyer-Gutbrod et al. 2015) and the health of individual females (Rolland et al. 2016), although an assessment of female length versus reproductive output indicates smaller females are less successful (Stewart et al. 2022). This is coupled with the finding that NARWs are growing to shorter lengths in recent decades, likely as a result of entanglements and limited prey resources (Stewart et al. 2021).

North Atlantic right whale population estimation via mark-recapture served as a primary case study for the application of matrix population models (Fujiwara and Caswell 2001; Caswell and Fujiwara 2004), a framework that can be used to explore how demographic parameters contribute to population dynamics. This work indicated a decline in population growth rates from 1980-1995 due to decreasing adult female survival and increasing inter-birth intervals. Pace et al. (2017) provided the first statistical estimates of NARW population size over time (1990-2015) and indicated a decline in the population since 2010. While there was no apparent trend in adult female survival, low calf production was unable to compensate for mortalities (Pace et al. 2017), emphasizing concerns about how the population will fare into the future given threats from both climate change and anthropogenic activities (Meyer-Gutbrod and Greene 2018).

3.5 Threats to North Atlantic Right Whales

The North Atlantic right whale is among the most endangered whale species (Caswell et al. 1999; Kraus et al. 2005; Cooke 2020). Intense whaling (particularly in the 17th through 19th centuries) greatly reduced the population, which was estimated at approximately 270 individuals in 1990 (Pace et al. 2017), increasing to 483 in 2010 (Pace et al. 2017) with a recent decline to about 340 individuals (95% confidence range 333-347) in 2021 (Pettis et al. 2023; NEFSC 2023). The population decline over the past decade may be a result of low reproductive rates (Kraus et al. 2016; Stewart et al. 2022), low genetic diversity (Waldick et al. 2002; Frasier et al. 2022), change in prey dynamics and abundance (Meyer-Gutbrod et al. 2015; Plourde et al. 2019; Record et al. 2019), and human activities, such as vessel strikes (van der Hoop et al. 2015) and fishing gear entanglement (Knowlton et al. 2012; Knowlton et al. 2022; Robbins et al. 2015; van der Hoop et al. 2016; Kenney 2018). Quantifying the relative and absolute impacts of human stressors on NARW populations is hindered by the fact that observed carcasses accounted for only 36% of all estimated deaths from 1990-2017, and not all detected carcasses result in a cause-of-death determination (Pace et al. 2021).

3.5.1 Entanglement

North Atlantic right whales frequently get entangled in fixed fishing gear, including trap/pot and gillnet gear (Johnson et al. 2005; Knowlton et al. 2022). A population-wide assessment of documented entanglement events over a 30-year period (1980-2009), based on presence of gear or scars, indicated 83% of the population had evidence of 1 or more entanglements (Knowlton et al. 2012). Further, an annual assessment of entanglement rate showed that up to 26% of the sighted population was entangled annually and that the rate of serious events (either attached gear or severe injuries) had increased significantly over time (Knowlton et al. 2012). Entanglement rates since 2009 have not improved, and the annual level of serious entanglement remains consistently above 20% (Hamilton et al. 2022). These serious entanglements affect reproductive output, health, and survival (Robbins et al. 2015; van der Hoop et al. 2016; Pettis et al. 2017; Knowlton et al. 2022). This increase in serious events may have several causes, including lobster fishing efforts shifting further offshore, increase in lobster/crab fishing after groundfish closures, and increasing rope strengths with manufacturing changes (Knowlton et al. 2016). In addition, NARWs have been shifting both northward and into offshore waters (Record et al. 2019) where they continue to be exposed to heavy gear and strong ropes, a situation that is being addressed by fishery changes in both countries.

Two primary approaches exist to reduce entanglement threats from fixed fishing gear, including to (1) reduce the incidence of entanglements by implementing closures, reducing endlines, reducing the profile of groundline, and shifting to on-demand gear; and (2) reduce the risk of an entanglement being fatal or causing sublethal impacts through the use of reduced breaking strength ropes. A range of management actions have been implemented along the U.S. East Coast since 1997 (Borggaard et al. 2017; Pace et al. 2014) and along the Canadian East Coast since 2017 in an effort to reduce the mortality and serious injury of NARWs due to entanglements in fixed fishing gear.

There are several major trends in entanglement mitigation that can be expected to occur during the time frame of the PET model projection. NOAA Fisheries and the Atlantic Large Whale Take Reduction Team met in April 2019 to talk about modifications to the Atlantic Large Whale Take Reduction Plan (i.e., measures in addition to large seasonal closures, broad-based sinking groundline, and others already in place) to reduce take below the level mandated by the MMPA (i.e., Potential Biological Removal [PBR]; estimated to require a 60-80% reduction in risk in trap/pot and gillnet). During that meeting, near consensus was reached on additional measures to reduce vertical line risk by at least 60% for American lobster (*Homarus americanus*) and Jonah crab (*Cancer borealis*) fisheries in the Gulf of Maine and Southern New England. The U.S. federal rulemaking process, which included new and extended closures, broad-based weak rope requirements, and measures to reduce vertical line (estimated at the time to reach this 60% risk reduction) was published in September 2021 and implemented in October 2021 (Lobster Management Area 1 closure) and May 2022 (NMFS 2021). Note that updates to inputs to the model used to estimate risk reduction later estimated that only a 48% risk reduction would be possible relative to all fisheries covered under the plan. During meetings in late 2022, NOAA Fisheries informed the Take Reduction Team that additional risk reduction would be needed to reduce mortality and serious injury of right whales in U.S. fisheries to a level below the PBR level (Wade 1998). Risk reduction is being implemented in Canada through mandatory fisheries closure protocols for all non-tended fixed gear fisheries in habitat important to NARW and by expanded use of on-demand fishing gear and reduced breaking strength ropes, especially for the Gulf of St. Lawrence snow crab (*Chionoecetes opilio*) and American lobster fisheries. Measures for weak

ropes in Canada are required by the end of 2024 (SCFO 2023). Finally, Canada has implemented efforts to address the threat of ghost gear through retrieval efforts and lost gear reporting requirements. Looking forward, entanglement risk assessment models can be used to integrate anticipated changes in the reductions in the chance of encounter (e.g., ropeless/on-demand fishing, sinking groundline) or of a lethal entanglement (e.g., reduced breaking strength ropes) into the baseline projection and the scenarios explored within the PET model.

3.5.2 *Vessel strike*

Vessel strikes are a source of mortality for all large whale species in the western North Atlantic (van der Hoop et al. 2012). NARWs are more vulnerable to vessel strikes than other large whale species on a per capita basis (Vanderlaan and Taggart 2007) and experience vessel collisions throughout their range (Knowlton and Brown 2007; Laist et al. 2014; van der Hoop et al. 2015). Vessel strikes are one of the leading causes of death for NARWs and were responsible for 16 of 38 (42.1%) observed human-induced mortalities from 2003-2018 (Sharp et al. 2019).

Reducing vessel speed and separating whales and vessels via routing measures remain the most effective options available to reduce vessel collisions with right whales (Conn and Silber 2013; Laist et al. 2001; Vanderlaan et al. 2008). A range of management actions have been implemented along the U.S. East Coast since 2008 and along the Canadian East Coast since 2003, including vessel re-rerouting and speed restrictions, in an effort to reduce the mortality of NARWs due to vessel collisions.

Studies are currently being initiated by NOAA, DFO, Dalhousie University, the New England Aquarium, and other partners to update information on vessel traffic and NARW distributions to better quantify risks and mortality rates under current conditions (e.g., Garrison et al. 2022). The data from these studies could be integrated into models that combine data on vessel and whale spatial distribution, vessel speed and size, and whale behavior to quantify vessel strike related mortality (e.g., Rockwood et al. 2017; Crum et al. 2019).

There are several major trends that can be anticipated in the characteristics of vessel traffic during the time frame of the PET model projection. Over the past 2 decades, commercial vessel traffic, primarily cargo vessels, increased along the North American East Coast in response to both economic growth and increasing imports from overseas ports in Asia. Data provided by the American Association of Port Authorities (AAPA) show an average annual increase in cargo amounts (expressed as Twenty-Foot Container Equivalent Units [TEUs]) of 3.5% per year for Atlantic ports of Canada and the U.S. since 2010; AAPA 2018). Similar annual trends in TEUs averaging a 3.5% annual increase for the U.S. and 4.0% for Canada since 2020 are reported overall for each country (including Pacific ports) in data provided by the World Bank (World Bank Group 2022). However, in recent years, this increase in total cargo was accompanied by increased total capacity of cargo vessels along the North American East Coast. The widening of the Panama Canal in 2016 and subsequent changes in port infrastructure allowed increased port calls of vessels in the 10,000-15,000 TEU range compared to a historical typical vessel capacity of 5,000-6,000 TEUs (Mongelluzzo 2020). Thus, while the amount of cargo entering North American ports will likely continue to increase, the actual number of vessel calls, and thus transits of large cargo vessels through NARW habitat, may decrease as vessel capacity also rises. Recent proposals to expand offshore wind energy development along the U.S. East Coast between North Carolina and the Gulf of Maine will also likely result in increases in vessel traffic due to construction and maintenance trips to offshore energy sites (Barkaszi et al. 2021). However, routing measures may be implemented to reduce the potential conflict between developed wind farms and along-coast vessel traffic (Coast Guard 2020). Finally, the recent proposed rule to implement mandatory vessel speed

reductions (NMFS 2022) may eventually be implemented along the U.S. East Coast and additional mitigation efforts may be deployed along the Canadian East Coast. Looking forward, vessel strike risk assessment models could be used to integrate anticipated changes in the volume and spatial distribution of vessel traffic into the baseline projection and the scenarios explored within the PET model.

3.5.3 Health and bioenergetic effects on demography

A variety of studies have been carried out related to assessing health in NARWs (Fauquier et al. 2020; Moore et al. 2021). The main tool that has been used is a Visual Health Assessment approach (Pettis et al. 2004). Using an ordinal system, 4 parameters are evaluated for each grouping of sightings that occur within the same season and year including body condition, skin condition, presence/absence of rake marks, and cyamids in the blowholes. Using a hierarchical Bayesian approach, these visual health assessment scores have been integrated with sightings and prior distributions to create a health curve over time for each individual ranging from 0 to 100 (Schick et al. 2013; Rolland et al. 2016). Using these tools, comparisons of health between different demographic groups have shown that reproductive females are the most vulnerable to health fluctuations in relation to their reproductive status (Pettis et al. 2004; Rolland et al. 2016). Pregnancy has not been observed in females with health scores below 65. Population-wide changes in health scores were seen over time, with the 1980's showing higher scores (mean score 79.8), the 1990's showing lower scores (mean 75.2)—including poor calving years at the end of the decade—and the early 2000's showing still lower scores (mean 72.5; Rolland et al. 2016). Food limitation and disease events may be partly responsible for these fluctuating health scores.

Further work has been done to evaluate the impacts of entanglements on health. Results show that health of reproductive (“proven”) females that experience entanglement is more negatively affected than other demographic groups that experience entanglements (Knowlton et al. 2022). A population-wide assessment of health over time indicates that entanglement may be the main factor affecting the health fluctuations seen over decades (Rolland et al. 2016; Knowlton et al. 2022).

Pace et al. (2017) showed a declining population starting in 2010 with a steeper decline noted in females. This decline in females may be the result of the negative impacts that they experience from entanglements (Pettis et al. 2017). These impacts are affecting reproductive output and survival (Knowlton et al. 2022; Stewart et al. 2022).

3.5.4 Prey availability and prey limitation effects

North Atlantic right whales feed primarily on later life stages (C4 or older) of *Calanus finmarchicus* in their traditional feeding areas (reviewed in Baumgartner et al. 2007). Bottom-up processes—such as copepod abundance, the North Atlantic Oscillation, sea surface temperature, and primary production—may influence NARW demography, bioenergetics, and distribution (Hlista et al. 2009; Pendleton et al. 2009; Davies et al. 2015; Meyer-Gutbrod et al. 2015; Ganley et al. 2022). An index of *C. finmarchicus* abundance derived from Continuous Plankton Recorder data has been demographically linked to NARW annual calf production for the period of 1980-2010, indicating negative anomalies in the 1990s and positive anomalies in the 1980s and 2000s (Greene et al. 2013; Meyer-Gutbrod et al. 2015). Long-term copepod monitoring programs have confirmed trends in *C. finmarchicus* abundance over this period and have highlighted a pronounced decline in their abundance since 2010 in all the traditional feeding areas of NARW (Sorochan et al. 2019). Prey abundance reductions since 2010 coincided with a decline in NARW

use of their traditional feeding areas (Pettis et al. 2016, 2017; Davis et al. 2017; Davies et al. 2019) and in their annual calving rate (Pettis et al. 2022).

In recent years, Cape Cod Bay and the Gulf of St. Lawrence (GSL) have gained in importance as respectively spring and summer feeding areas for NARW, with a documented 30-40% of the population using these areas seasonally (Simard et al. 2019; Ganley et al. 2019; Crowe et al. 2021). The biomass of copepods in the GSL is dominated by a larger species of *Calanus* (*C. hyperboreus*; Sorochan et al. 2019), the importance of which in the diet of NARW feeding in this area is currently unknown. Bioenergetics modeling indicates that the energy that NARWs may gain by feeding on *C. finmarchicus* or *C. hyperboreus* in the GSL declined between 2011 and 2017 compared to 2006-2010 (Lehoux et al. 2020) and was likely insufficient to meet energy requirements of pregnant and lactating females in most years of this period (Gavrilchuk et al. 2021). Sexually mature females that have been seen in the GSL in very recent years (2016-2021) appear to have been more successful at reproducing than females not seen in the GSL over this 5-year period (Bishop et al. 2022). However, the continued low calving rates documented in recent years (Pettis et al. 2022) in spite of a large number of NARWs using the area to feed suggests that the GSL may remain a suboptimal foraging habitat for many of the NARWs.

3.5.5 Noise effects on health and demography

In order to model population consequences of noise in NARWs, evidence is needed that noise disrupts a vital life process (e.g., feeding, reproduction) directly or indirectly (e.g., via impacts of noise on prey species). Several pathways of effects are possible. Noise impact studies often distinguish between short-term responses to acute noise sources (e.g., seismic surveys or sonar) and impacts of chronic, low-amplitude noise (e.g., shipping), but the boundary between these 2 kinds of noise can be fuzzy. The distinction can be useful to retain because overt behavioral responses to noise may be detectable, but one should not expect to see a behavioral response to acoustic masking. The term “masking” is used to discuss both the process and extent to which the ability of one animal to hear a signal is decreased by the presence of anthropogenic noise (Erbe et al. 2016).

Large knowledge gaps on effects of shipping noise on NARW behavior (e.g., feeding, reproduction) hinder efforts to model population consequences of noise directly. There are many indirect lines of evidence to support the conclusion that anthropogenic noise should affect NARW ecology. In other words, a relationship between ocean noise and NARW demography would not be surprising, but empirical data may be lacking to parameterize the relationship.

3.5.5.1 Acute effects: behavioral responses

Tagged whales showed behavioral responses to novel sounds but not to ship noise (Nowacek et al. 2004). Nowacek et al. (2004) hypothesize that NARWs may have habituated to ship noise. Ship noise has been found to disrupt foraging behavior of other large baleen whales (e.g., Blair et al. 2016), but no comparable studies have been published on NARW foraging behavior and ship noise.

3.5.5.2 Chronic effects: masking and stress

Chronic ocean noise causes large decreases in communication space of NARWs relative to quiet conditions, particularly for low-amplitude contact calls (Clark et al. 2009). Right whales have some ability to compensate for this masking effect by increasing the source level of their calls (Parks et al. 2011), but there is little information on the energetic consequences of this compensation or the biological limits of compensatory mechanisms. Chronic ocean noise results in elevated stress levels in NARWs (Rolland et al. 2012).

The extent to which lost communication space (i.e., masking) can be translated to demographic consequences hinges on the function of sound in NARW ecology. Previous studies on other cetaceans (whales, dolphins, and porpoises) have modeled population consequences of noise via disruption of foraging activities (e.g., Williams et al. 2016), but the role of sound in foraging ecology in NARWs is poorly understood (Parks and Tyack 2005). Noise could cause population-level impacts in NARWs through pathways of effects other than reducing foraging efficiency, but noise impacts on foraging may be the most tractable pathway to study. Noise could affect reproductive rate by masking acoustic cues used in mate selection or disrupting mating behavior. Noise could affect calf survival by masking acoustic cues used to maintain contact between mothers and calves (e.g., Vergara et al. 2021). Acoustic studies have associated particular calls with a given age-sex class of NARW (e.g., scream calls made by females, gunshot sounds made by males, warbles made by calves or mother-calf pairs; Parks and Tyack 2005). Calls with higher source levels (e.g., gunshot calls) will be less susceptible to acoustic masking than those with lower source levels (e.g., warbles). Low-amplitude calls made by mother-calf pairs may be particularly susceptible to acoustic masking (Parks et al. 2019). Masking calls used for contact between mother and calf could result in increased risk of vessel strike or entanglement in NARW calves.

3.5.5.3 Indirect effects

Indirect effects of vessel noise (or more likely vessel-generated turbulence) on copepod mortality have been observed (Bickel et al. 2011). This has been found with phytoplankton, as well (Das Sarkar et al. 2019). For the same reason, one would expect underwater turbines from offshore renewable energy facilities to increase non-consumptive mortality of copepods (Schlezinger et al. 2013).

There is mixed evidence on the effects of seismic airgun blasts (used to detect subsea resources and map seabed geology), which are much higher in amplitude than vessel noise, on zooplankton mortality. McCauley et al. (2017) reported mortality in a diverse community of zooplankton species up to a range of 1.2 km from the source array, whereas Fields et al. (2019) found no mortality of *Calanus finmarchicus* at even higher received levels only 25 m from the airgun array. Fields et al. (2019) speculated that the differences between the 2 studies may be due to a higher tolerance of *C. finmarchicus* to noise than the zooplankton species in the study by McCauley et al. (2017), or that the McCauley results were confounded by the effects of the research vessel's own propeller cavitation on zooplankton mortality. A study by the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) tested some of the predictions by McCauley et al. (2017) at various spatial and temporal scales (Richardson et al. 2017). The authors found that zooplankton abundance in the survey region declined during seismic surveys by a point estimate of 22% and that time to recovery to 95% of pre-survey abundance took 26 days. Although the authors interpreted these results as indicating a localized effect with a quick recovery time, there may be scenarios in which a 22% reduction in localized copepod abundance for a month could be detrimental to survival and recovery of an endangered copepod specialist like NARWs. This detrimental reduction of copepod abundance may be particularly true in a species like the NARW, in which individuals have only a few months to replenish energy stores after pregnancy or store the energy needed for a lengthy period of fasting and reproduction. Localized depletion in copepod density may have a nonlinear effect on NARW foraging success. Previous studies have found that as prey density declines below some threshold, so too does the probability that NARWs will initiate foraging activity (Mayo et al. 1990).

3.5.6 Contaminants

In order to model population consequences of contaminants in NARWs, a dose-response relationship is needed to model demographic consequences (“response”) of a given rate of uptake (“dose”) of a given pollutant, either directly (e.g., through effects on adult mortality, pregnancy rate, early calf survival) or indirectly (e.g., immunosuppression; Hall et al. 2006). Dose-response relationships are common in the pharmaceutical and toxicological literature (e.g., Ritz 2010), but for logistical and ethical reasons, they will never be derived experimentally for NARWs. Several pathways of effects are possible.

Several constraints hinder efforts to model population consequences of contaminants in cetaceans in terms of the contaminant measurements, the cetacean vital rates, and statistical efforts to find relationships between the two. First, lab studies on homologous species measure intake of a single contaminant of concern, whereas field studies of wild cetaceans measure the tissue concentration of the suite of contaminants to which an individual is exposed over its lifetime. The tissue concentration most feasible to measure in free-ranging cetaceans (e.g., blubber concentrations) may not provide an accurate reflection of the dose to which the animal responds (e.g., liver concentrations for certain chemicals; Aguilar and Borrell 1994; Aguilar et al. 1999). Contaminant composition and levels may change dramatically over the decades of study needed to measure demographic rates of long-lived cetaceans (e.g., Ross et al. 2000; Hickie et al. 2007). As jurisdictions ban chemicals and new chemicals enter the market, whales are exposed to an ever-changing mixture of pollutants. Although trends vary widely geographically and across various trophic levels, many marine mammal species have experienced a decrease since the 1970s in dichlorodiphenyltrichloroethane (DDT), a plateau in levels of polychlorinated biphenyls (PCBs), and an increase in emerging flame retardants, such as polybrominated diphenyl esters (PBDEs; reviewed in Law et al. 2012). Second, vital rates are difficult to study in long-lived cetaceans, and some of the most plausible pathways of effects (e.g., contaminants reducing pregnancy rates) may be harder to measure than pathways less likely to be affected (e.g., effects on adult survival), which means that many studies in ecotoxicology use endpoints (e.g., histopathology, immune assays) that stop short of demography (Desforges et al. 2016). Third, even for well-studied species for which good contaminant data and demographic rates are available, it may be impossible to draw a causal link between the two (O’Shea and Brownell 1994).

In the absence of good correlative studies between complex contaminant exposure histories and the complex population dynamics of long-lived cetaceans, it will be necessary to extrapolate from a vastly simplified model of the relationship between one stressor and a likely population-level response. With that aim, and the above-mentioned caveats in mind, one approach is available to model effects of PCBs on NARW demography. Hall et al. (2018) developed an individual-based model (IBM), parameterized largely from lab studies of mink (*Neogale vison*) and field studies of bottlenose dolphins (*Tursiops truncatus*), to explore plausible relationships between PCB tissue concentration and cetacean population growth rates in bottlenose dolphins, killer whales (*Orcinus orca*), and humpback whales (*Megaptera novaeangliae*). Data and code from the Hall et al. (2018) IBM are available as an open-source package. Hall’s model allows one to compare various scenarios of PCB uptake or accumulation rates to empirical measurements of blubber PCB concentration in animals of a given age or sex. The most recent study of contaminant composition and levels in NARWs suggests that legacy organochlorine pesticides (e.g., DDT), PCBs, and first-generation brominated flame retardants persist in NARWs (Montie et al. 2010), but concentrations are lower in low-trophic-level NARWs than has been observed in higher-trophic-level odontocetes. Some point estimates of PCBs in NARW samples were above the 17 mg/kg lipid

weight threshold value proposed for PCB toxicity in the blubber of marine mammals (Kannan et al. 2000). In contrast, a study by Weisbrod et al. (2009) reported total PCB tissue concentrations averaging ~5.4 mg/kg in 1994 and 1996. Mean age of known whales was ~5 years, which translates very roughly to an annual accumulation of 1-2 mg/kg/year. Hall et al. (2018) predicted that annual accumulation rates <5 mg/kg/yr were not expected to carry any demographic consequences unless one models a confounding effect of immunosuppression and disease. Legacy contaminants like PCBs have declined in some species, but not in others, in the decades since efforts have been made to control their widespread use (Law et al. 2014). Given the lack of recent tissue concentration measurements of PCBs in NARWs, or a model to predict population-level consequences of those contaminants in NARWs, we declined to include PCBs or other contaminants in the current version of this model.

Montie et al. (2010) shared data on a suite of contaminant levels measured in 5 NARWs in a supporting information file. These could be converted into annual accumulation rates and explored using the IBM framework published by Hall et al. (2018). Several complications remain. The best measurements of tissue concentration of contaminants come from carcasses rather than from blubber biopsies of living animals. Hall’s model may be best used to model only the partial contribution of PCB exposure to reproduction via increased calf mortality. But if NARW calf survival is already being measured in the population, it will be important not to “double count” this pathway of effects—the partial contribution of PCB levels to NARW reproduction may already be subsumed within empirical estimates of NARW calf survival. Hall’s model does allow one to explore the impacts of PCBs on non-calf survival via immunosuppression. It may be useful for management purposes to know how much of the effects of health and disease could be explained by PCBs. If data are available on the entire suite of contaminants to which NARWs are exposed, it may require an expert elicitation process to generate scenarios on the relative toxicity of contaminants other than PCBs. In addition, cadmium and chromate exposure have been identified as contaminants of concern for NARWs (Browning et al. 2017; Ierardi et al. 2021), but we are unaware of any quantitative relationship to link these contaminants to demographic consequences. We discuss possible ways forward in section 9.3.

3.5.7 Disease and harmful algal blooms

The role of disease and harmful algal blooms (HABs) in affecting NARW reproduction and survival is not well understood (see Moore et al. 2021 for a synthesis of studies on this topic). Although an analysis of fecal samples has documented exposure to 2 classes of HABs—paralytic shellfish poisoning and domoic acid—the effects on NARWs are not clear. Two parasites, giardia and cryptosporidium, have also been documented in fecal samples. There is some indication that there is a decline in body condition when there is a co-infection with these parasites, but these findings are preliminary. Thus, the role of biotoxin and parasite exposure on NARW health remains unclear and is not included at this time in the PET framework.

4. MODEL DESCRIPTION

The PET PVA consists of a core stage-structured model and several submodels for NARWs: mortality, reproduction, entanglement, vessel strike, prey availability, and prey accessibility. How this model handles density dependence, stochasticity, and uncertainty are important, as in any PVA (Chaudhary and Oli 2020). We finish this section by describing the various outputs of the model.

We programmed the PVA in R version 4.2.1 (R Core Team 2022). Our code is available at a NEFSC Github repository (https://github.com/NEFSC/PSD-NARW_PET_PVA). Running all scenarios took approximately 40 hours of computer time using parallel processing with 7 cores on a 1.80 GHz processor with 32GB of RAM.

4.1 Core Stage-structured Model

The PET model is an IBM (Grimm and Railsback 2005) built around the life history of NARWs (Figure 2), with an annual transition and a census date of approximately July 1. An individual animal is described by one stage class at any point in time and proceeds through a series of stage classes based on transitions due to age and reproductive events. Males are described by 6 classes based on age. Females are described by 13 classes based on age for pre-reproductive individuals and on reproductive state for breeding individuals.

4.1.1 Stage descriptions

4.1.1.1 First-year male and female NARW calves (0.5 years old)

Calves (stages F_1 and M_1) first appear in the model at approximately 6 months of age because the census date is July 1 and most calves are born in December or January. Neonatal survival is incorporated into the early calf-loss rate (κ), and the first survival rate that is applied to calves is the survival from age 0.5 to age 1.5 (s_1). For clarity of presentation, calves appear for the first time in Figure 2 as yearlings (1.5 years old); in the year prior to that, they are shown as part of a mother-calf pair. However, because calf survival does not depend on survival of its mother in either the IBM or the figure, these representations are equivalent mathematically. That is, we assume that calves greater than 0.5 years old, while still in attendance with their mothers, are gaining independence and can survive if their mother dies. Note that for neonates (calves less than 0.5 years old), the model assumes that death of the mother results in death of the neonate; indeed, in the model, it would be as if the calf had never been born.

4.1.1.2 Subadult males (1.5 to 4.5 years old)

Subadult NARW males are tracked in the model by age until they reach reproductive maturity. The stages M_2 , M_3 , M_4 , and M_5 represent males of approximately 1.5, 2.5, 3.5, and 4.5 years of age, respectively.

4.1.1.3 Adult males (≥ 5.5 years old)

After NARWs reach reproductive maturity, defined in this model as age 5.5, males are no longer tracked by age. Thus, the stage M_A includes all males 5.5 years old and older. Because the IBM keeps track of individual animals, the age of older males can be determined, but none of the parameters in the model are governed by that age, so the representation in Figure 2 is appropriate.

4.1.1.4 Subadult females (1.5 to 3.5 years old)

Like males, NARW subadult females are tracked in the model by age until they reach reproductive maturity. The stages F_2 , F_3 , and F_4 represent females of approximately 1.5, 2.5, and 3.5 years of age, respectively.

4.1.1.5 Pre-breeding females (4.5 to ≥ 9.5 years old)

Pre-breeding NARW females are tracked in the model by age until their first successful pregnancy. Thus, the numbered stages (F_5 through F_9) represent nulliparous (pre-breeding) individuals (of ages 4.5 through 8.5, respectively); the last numbered stage (F_{10}) includes nulliparous females aged 9.5 or older.

4.1.1.6 Breeding females

Once NARW females have had their first successful pregnancy, they are no longer tracked by age but by reproductive class. The stage F_C represents an adult female with an attendant first-year calf (0.5 years old). The stage F_R represents a “resting female,” the year after she has given birth to a calf. The stage F_W represents a “waiting female,” who is capable of breeding and could appear with a first-year calf a year later. It’s worth noting that the stage F_W is a mixture of pregnant and non-pregnant females, which are not distinguished in the model. The transition structure among the 3 breeding stages reflects the physiological constraints imposed by the life-history of large whales.

4.1.2 Transitions

The life history of NARWs can be expressed as a series of transitions between stages (Figure 2). These transitions are represented by survival and reproductive probabilities. Survival probability s_X is the probability of a whale starting a year (July 1st) in stage X surviving to the next year. Breeding probability B or B_X is the probability of a waiting adult female or a nulliparous female of age X calving within the next year. Because calves are born in winter, the calf-loss probability κ is the probability that a calf dies before its first July 1st. Mothers that lose their calf in this period cannot calve again the next year, and so make a transition to the resting stage (F_R) instead of to the waiting stage (F_W).

4.1.3 Difference equations

Although the PET model for NARWs is an IBM, the life history diagram (Figure 2) can also be expressed in a series of difference equations that govern the transitions among states. The survival of subadult males and females is age-specific, thus,

$$N_{X+1,t+1}^M = s_X N_{X,t}^M, \text{ for } X = 1 \dots 4, \text{ and} \quad (1)$$

$$N_{X+1,t+1}^F = s_X N_{X,t}^F, \text{ for } X = 1 \dots 4 \quad (2)$$

where s_X represents the survival rate for age-class X . For older males, survival is governed by an adult survival rate, s_M ,

$$N_{A,t+1}^M = s_M (N_{5,t}^M + N_{A,t}^M). \quad (3)$$

For older nulliparous females, survival is governed by an adult survival rate, s_F , and age-dependent first-breeding probabilities, B_X ,

$$N_{X+1,t+1}^F = s_F (1 - B_X) N_{X,t}^F, \text{ for } X = 5 \dots 8, \text{ and} \quad (4)$$

$$N_{10,t+1}^F = s_F [(1 - B_9) N_{9,t}^F + (1 - B_{10}) N_{10,t}^F]. \quad (5)$$

The difference equations for breeding females capture both the survival and reproductive processes. The number of females with calves in a given year (F_C) arises from nulliparous or waiting females who survive, successfully breed, and retain the calf for the first 6 months,

$$N_{C,t+1}^F = s_F (1 - \kappa) (\sum_{X=5 \dots 10} B_X N_{X,t}^F + B N_{W,t}^F). \quad (6)$$

Females enter the resting state either by surviving after being with a first-year calf the previous year or by successfully breeding but losing the calf before it was 6 months old in the previous year,

$$N_{R,t+1}^F = s_C N_{C,t}^F + s_F \kappa \left(\sum_{X=5 \dots 10} B_X N_{X,t}^F + B N_{W,t}^F \right). \quad (7)$$

Females enter the waiting state either by surviving a year after the resting state or by surviving and failing to breed from the waiting state,

$$N_{W,t+1}^F = s_R N_{R,t}^F + s_F (1 - B) N_{W,t}^F. \quad (8)$$

Finally, for completeness, note that first-year calves are not explicitly shown in Figure 2, but they are calculated from the number of adult females with calves,

$$N_{1,t}^M = \frac{N_{C,t}^F}{2}, \text{ and} \quad (9)$$

$$N_{1,t}^F = \frac{N_{C,t}^F}{2}. \quad (10)$$

4.2 Submodels

We can divide the PET NARW IBM into submodels (Figure 3). The first of these is the mortality submodel (Section 4.2.1), which ties cause-specific hazard rates with survival probabilities (Section 4.1.3). The second is the reproduction submodel (Section 4.2.2), which produces probabilities of reproduction for female right whales (Section 4.1.3). The third is the entanglement submodel (Section 4.2.3), which explains how NARWs obtain and heal from severe entanglement wounds. These wounds can have both immediate and delayed lethal effects (affecting the mortality submodel), as well as sublethal effects (affecting the reproduction submodel). The fourth is the vessel strike submodel (Section 4.2.4), which explains how NARWs obtain and heal from severe vessel strike wounds. These wounds can have immediate and delayed lethal effects (affecting the mortality submodel). The fifth submodel is prey availability (Section 4.2.5), which has sublethal effects on the reproduction submodel. The sixth and final submodel is prey accessibility (as affected by noise; Section 4.2.6). The submodels that specifically affect individuals each time step are applied in the IBM in this order: injury (entanglement and vessel strikes), then mortality, and then reproduction.

4.2.1 Mortality submodel

We model the probabilities of NARW mortality due to entanglement, vessel strike, and natural causes in terms of hazard rates, a measure of the intensity of events an individual is exposed to (Ergon et al. 2018). The mortality hazard rates can be tied into survival probabilities (Section 4.1.3), conditional on the severe injury status of the whale:

$$\log(s_{i,t}) = -(h_{i,t}^{\text{mN}} + h_{i,t}^{\text{mE}} + h_{i,t}^{\text{mV}}) \quad (11)$$

$$h_{i,t}^{\text{mN}} = 0 \quad (12)$$

$$h_{i,t}^{\text{mE}} = \begin{cases} \exp(\alpha_0^{\text{mE}} + \alpha_a^{\text{mE}}(5 - a_{i,t}^\dagger) + \alpha_{FC}^{\text{mE}} I_{i,t}^{FC} + \alpha_{FR}^{\text{mE}} I_{i,t}^{FR}) & \text{if } W_{i,t} = 1 \\ 0 & \text{otherwise} \end{cases} \quad (13)$$

$$h_{i,t}^{\text{mV}} = \begin{cases} \exp(\alpha_0^{\text{mV}} + \alpha_a^{\text{mV}}(5 - a_{i,t}^\dagger) + \alpha_{FC}^{\text{mV}} I_{i,t}^{FC} + \alpha_{FR}^{\text{mV}} I_{i,t}^{FR}) & \text{if } W_{i,t} = 2 \\ 0 & \text{otherwise} \end{cases} \quad (14)$$

where $s_{i,t}$ is the survival probability of whale i in year t ; $h_{i,t}^{\text{mN}}$ is the hazard rate for natural mortality, conditional on whale i not being severely injured in year t ($W_{i,t} = 0$); $h_{i,t}^{\text{mE}}$ is the hazard rate for entanglement mortality, conditional on whale i being severely injured due to entanglement in year t ($W_{i,t} = 1$); $h_{i,t}^{\text{mV}}$ is the hazard rate for vessel strike mortality, conditional on whale i being severely injured due to vessel strike in year t ($W_{i,t} = 2$); α_0^{mE} is the log-scale baseline hazard rate for entanglement mortality; α_a^{mE} is the coefficient for effect of age on entanglement mortality hazard; α_{FC}^{mE} is the coefficient for the effect of being a female with a calf; $I_{i,t}^{FC}$ is an indicator variable that is 1 if individual i is a female with a calf in year t and 0 otherwise; α_{FR}^{mE} is the coefficient for the effect of being a resting female; $I_{i,t}^{FR}$ is an indicator variable that is 1 if individual i is a resting female in year t and 0 otherwise; $a_{i,t}^\dagger$ is the age of the whale if that age is less than 5 and 5 otherwise; and α_0^{mV} is the log-scale baseline hazard rate for vessel strike mortality. Because we modeled each source of mortality as only occurring if the whale has a severe wound from that cause (except natural mortality, which only occurs if the whale has no severe wound), these equations can also be expressed as:

$$s_{i,t} = \begin{cases} 1 & \text{if } W_{i,t} = 0 \\ \exp(-h_{i,t}^{\text{mE}}) & \text{if } W_{i,t} = 1. \\ \exp(-h_{i,t}^{\text{mV}}) & \text{if } W_{i,t} = 2 \end{cases} \quad (15)$$

We modeled mortality hazards as being affected by age, stage, injury status, and year, but not prey availability, contaminants, or noise (directly or indirectly). We hypothesized prey availability was more likely to affect reproductive capacity than survival (Meyer-Gutbrod et al. 2015), while the issues of contaminants and noise had insufficient empirical data to support hypothesized relationships with mortality rate. We considered having the cumulative stress of multiple wounds over the years affect mortality. In the end, while we could imagine how to accomplish this with the IBM structure, we could not find empirical evidence to support a more complicated structure linking past history of injury to demographic rates, and so did not include such effects in the model.

4.2.2 Reproduction submodel

The probability of reproduction, given that a NARW is either a pre-breeding female or a waiting female, is given by:

$$\text{logit}(B_{i,t} | a_{i,t} \in \{F_{5+}, F_W\}) = \boldsymbol{\beta}'_a \mathbf{a}_{i,t} + \beta_w I_{i,t}^1 + \beta_{p,1} P_{t,1} + \beta_{p,2} P_{t,2} + \epsilon_t^r \quad (16)$$

where $\boldsymbol{\beta}'_a$ is a row matrix of the effects of stage on probability of reproduction, β_w is the effect of a severe wound on probability of reproduction, $I_{i,t}^1$ is an indicator variable for individual i having

a severe wound in year t ($W_{i,t} > 0$), $\beta_{p,l}$ is the effect of prey in location l on probability of reproduction, $P_{t,l}$ is the prey rolling average abundance for year t in location l (see prey availability submodel, Section 4.2.5), and ε_t^r is the (random normal) effect of year t on reproduction (see environmental stochasticity, Section 4.4.1), with

$$\beta_a = \begin{bmatrix} - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ \beta_5 \\ \beta_6 \\ \beta_7 \\ \beta_8 \\ \beta_9 \\ \beta_{10} \\ - \\ - \\ \beta_w \end{bmatrix} \quad (17)$$

where the dashes (–) indicate stages where the coefficient isn't defined, as those stages can't reproduce.

Thus, reproductive probability is affected by age, stage, severe injury status (owing to entanglement or vessel strike), and prey availability, but not by contaminants, or noise directly (it could affect reproduction indirectly through prey accessibility). This was because we found no empirical evidence to indicate an influence of these latter factors on reproduction.

The probability of calf loss (κ) is the probability that a calf dies between birth and reaching its first July 1st. Mothers that lose their calf in this period cannot calve again the following year, and so transition to the resting stage instead of back to the waiting stage. The probability of calf loss does not depend on the age or breeding stage of the mother.

4.2.3 Entanglement submodel

We used a matrix formulation to keep track of the probabilities of transitioning between wound states ($W_{i,t+1} = 0, 1, \text{ or } 2$):

$$\Psi_{i,t} = \begin{matrix} W_{i,t} = 0 \\ W_{i,t} = 1 \\ W_{i,t} = 2 \end{matrix} \begin{bmatrix} 1 - \psi_{i,t}^{i0,i} & \psi_{i,t}^{i0,iE} & \psi_{i,t}^{i0,iV} \\ \psi_{i,t}^{iE,i0} & 1 - \psi_{i,t}^{iE,i0} & 0 \\ \psi_{i,t}^{iV,i0} & 0 & 1 - \psi_{i,t}^{iV,i0} \end{bmatrix} \quad (18)$$

where $\psi_{i,t}^{i0,i}$ is the probability of whale i obtaining a severe injury (of some type) in year t ; $\psi_{i,t}^{i0,iE}$ is the probability of obtaining a severe entanglement injury; $\psi_{i,t}^{i0,iV}$ is the probability of obtaining a severe vessel strike injury; $\psi_{i,t}^{iE,i0}$ is the probability of healing from a severe entanglement wound obtained in a previous year; and $\psi_{i,t}^{iV,i0}$ is the probability of healing from a severe vessel strike wound obtained in a previous year.

Like the mortality model, we modeled the probabilities of obtaining severe injuries due to entanglement (and vessel strikes) in terms of hazard rates (Ergon et al. 2018). The hazard rates for obtaining severe injuries can be used to calculate the corresponding annual probabilities:

$$\psi_{i,t}^{i0,i} = 1 - e^{-(h_{i,t}^{iE} + h_{i,t}^{iV})} \quad (19)$$

$$\psi_{i,t}^{i0,iE} = \psi_{i,t}^{i0,i} \frac{h_{i,t}^{iE}}{h_{i,t}^{iE} + h_{i,t}^{iV}} \quad (20)$$

where $h_{i,t}^{iE}$ is the hazard rate for severe entanglement injuries and $h_{i,t}^{iV}$ is the hazard rate for severe vessel strike injuries (Section 4.2.4). The hazard rate for whale i obtaining a severe entanglement injury in year t is a function of the whale's stage and the year:

$$h_{i,t}^{iE} = \exp(\alpha_0^{iE} + \alpha_a^{iE}(5 - a_{i,t}^+) + \alpha_{FC}^{iE} I_{i,t}^{FC} + \alpha_{FR}^{iE} I_{i,t}^{FR} + \varepsilon_t^{iE}) \Delta_t^{iE} \quad (21)$$

where α_0^{iE} is the log baseline hazard rate for entanglement injury; α_a^{iE} is the coefficient for the effect of age on probability of severe entanglement injury; α_{FC}^{iE} is the coefficient for the effect of being a female with a calf; α_{FR}^{iE} is the coefficient for the effect of being a resting female; ε_t^{iE} is a random normal effect of year t ; and Δ_t^{iE} is an entanglement injury change factor (Section 6.3.1).

We did not model the probability of healing from a severe entanglement wound obtained in a previous year ($\psi_{i,t}^{iE,i0}$) in terms of hazard rates. Instead, we estimated it directly on the probability scale (Section 5.3).

4.2.4 Vessel strike submodel

Similar to severe entanglement wounds (Section 4.2.4), we modeled the probability of a NARW obtaining a severe vessel strike wound ($\psi_{i,t}^{i0,iV}$) in terms of hazard rates:

$$\psi_{i,t}^{i0,iV} = \psi_{i,t}^{i0,i} \frac{h_{i,t}^{iV}}{h_{i,t}^{iE} + h_{i,t}^{iV}}. \quad (22)$$

The equation for the hazard rate for obtaining severe vessel strike wounds was similar to that for entanglement wounds:

$$h_{i,t}^{iV} = \exp(\alpha_0^{iV} + \alpha_a^{iV}(5 - a_{i,t}^+) + \alpha_{FC}^{iV} I_{i,t}^{FC} + \alpha_{FR}^{iV} I_{i,t}^{FR} + \varepsilon_t^{iV}) \Delta_t^{iV} \quad (23)$$

where α_0^{iV} is the log baseline hazard rate for vessel strike injury; α_a^{iV} is the coefficient for the effect of age on probability of severe vessel strike injury; α_{FC}^{iV} is the coefficient for the effect of being a

female with a calf; α_{FR}^{iV} is the coefficient for the effect of being a resting female; ε_t^{iV} is a random normal effect of year t ; and Δ_t^{iV} is a vessel strike injury change factor (Section 6.3.2).

As our wound observation history (Section 5.1.1) did not include any whales that showed severe vessel strike wounds in subsequent years, we assumed that all whales that survived severe vessel strike wounds moved back into the uninjured state by the next year ($\psi_{i,t}^{iV,i0} = 1$).

4.2.5 Prey availability submodel

Prey for NARWs in a given year has at least 3 components: biomass, distribution, and accessibility (for more on the latter, see Section 4.2.6). We represent the 3-year rolling average prey biomass in location l ending in year t as $P_{t,l}$. Locations for historical prey data are 1) GSL and 2) GOM. For prediction, we assume the historical relationship between prey and reproduction will hold but that the locations where whales go for that prey may change,

$$\mathbf{c}_t \sim \text{sample}(\mathbf{c}_{y \in Y}^h) \quad (24)$$

$$C_{t,l} = c_{t,l} + \log(\Delta^{\text{noise}}) \quad (25)$$

$$\text{prey}_{t,l} = \frac{C_{t-2,l} + C_{t-1,l} + C_{t,l}}{3} \quad (26)$$

$$P_{t,l} = \frac{\text{prey}_{t,l} - \overline{\text{prey}}_l^h}{\text{SD}(\text{prey}_l^h)} \quad (27)$$

where \mathbf{c}_t is the log-scale *Calanus* prey availability in the 2 locations ($c_{t,1}$ and $c_{t,2}$), generated by selecting from the log-scale prey historical data (\mathbf{c}_y^h ; section 5.1.4) from the 2 historical locations for the same year y , selected from reference year set Y ; $C_{t,l}$ is the log-scale prey accessibility in year t and location l , adjusted by noise factor Δ^N (Sections 4.2.6 and 6.3.4); and $\text{prey}_{t,l}$ is the non-normalized 3-year unweighted rolling average log prey biomass in location l ending in year t . We normalized $P_{t,l}$ by subtracting the historical mean rolling average prey biomass, $\overline{\text{prey}}_l^h$, and dividing by its standard deviation, $\text{SD}(\text{prey}_l^h)$, to match the reproduction submodel (Section 4.2.2) with how prey was treated in the reproductive estimation model (Section 5.3).

4.2.6 Prey accessibility submodel

To provide a way to simulate some of the potential effects of environmental noise on NARWs, we included a control parameter in the prey availability submodel that could dial the prey availability down or up by a specified percentage. We recognize this is a coarse way to represent a reduction in prey accessibility caused by environmental noise limiting the ability of whales to locate and acquire food, but it allows us to investigate the potential impact of such a mechanism. We note that this is not the only way that noise could affect whale demography, nor is noise the only mechanism by which prey accessibility could be diminished.

4.3 Density Dependence

We implemented ceiling density dependence, in which vital rates and population dynamics were unaffected by density dependence until the NARW population size reaches the carrying capacity or ceiling, which the population will not grow beyond (Akçakaya et al. 1999). We set the

carrying capacity at 10,000 total NARWs. In each year of each simulation, if the population size went above 10,000, first-year calves were removed until the population was at 10,000.

We chose this functional form of density dependence and limit for several reasons. We needed to have some form of population limitation included, both for biological realism and computational tractability (in an IBM, speed is highly dependent on the population size). However, we had little information about the level or type of density dependence in this population and insufficient data with which to estimate density-dependent parameters. Therefore, we went with the simplest form of density dependence available (no parameters other than carrying capacity). We targeted newborn calves in implementing the ceiling because when density-dependent vital rates can be estimated, typically it targets survival of the youngest age classes or fecundity, especially in long-lived organisms (Lande et al. 2002; van de Kerk et al. 2019). We chose a limit of 10,000 based on estimates of pre-exploitation abundance (NMFS 1991; Monsarrat et al. 2015), but acknowledge current and future carrying capacity could be lower or higher than that.

4.4 Stochasticity and Uncertainty

One of the important modeling philosophies we embraced was the intention to represent uncertainty as fully as possible, so that the outputs of the model can be viewed as probabilistic statements about the future, conditional on the state of knowledge at the time the model is run. Thus, the NARW PET model includes stochasticity (to represent the aleatory uncertainty that is out of our control) and parametric uncertainty (to represent the epistemic uncertainty that could potentially be reduced over time through research and monitoring).

In the PET model, there are 2 forms of stochasticity: environmental and demographic. Environmental stochasticity can be defined as how annual changes in the environment, modeled as random variation around a mean effect, affect population vital rates, either directly or indirectly. Demographic stochasticity can be defined as how chance events happening to individuals affect the population trajectory. All of the parameters in the PET model are estimated with uncertainty (Section 5), and we carry that uncertainty into the simulations by sampling from the joint posterior distribution for all the parameters for each replicate.

In the simulation structure, parametric uncertainty, scenario control, and environmental and demographic stochasticity are nested processes (Figure 4; McGowan et al. 2011). By sampling from parametric uncertainty in the outermost loop of the simulations, we generate parallel replicates across scenarios; thus, the 52nd replicate in one scenario corresponds to the 52nd replicate in any other scenario. This structure allows the simulations to more powerfully capture the differences across scenarios.

4.4.1 Environmental stochasticity

The NARW PET model includes both direct and indirect environmental stochasticity. The direct environmental stochasticity is included as random annual variation in the reproduction equation (ε_t^r ; Section 4.2.2). There is indirect environmental stochasticity affecting reproduction through the prey availability submodel (Section 4.2.5). We also incorporated indirect environmental stochasticity affecting both mortality and reproduction through random annual variation in obtaining severe entanglement wounds (ε_t^{iE} ; Section 4.2.3) and severe vessel strike wounds (ε_t^{iV} ; Section 4.2.4). All of the ε terms were normally distributed with mean 0 and variance estimated in the injury/mortality analysis (Section 5.2) or the reproduction analysis (Section 5.3):

$$\varepsilon_t^r \sim \text{Normal}(0, (\sigma^r)^2)$$

$$\begin{aligned}\varepsilon_t^{iE} &\sim \text{Normal}\left(0, (\sigma^{iE})^2\right) \\ \varepsilon_t^{iV} &\sim \text{Normal}\left(0, (\sigma^{iV})^2\right).\end{aligned}\tag{28}$$

In general, we applied environmental stochasticity in common across scenarios. For example, if year 10 of bootstrap run 20 was a low (good) year for entanglement mortality hazard (given a severe entanglement wound) in one scenario, then year 10 of bootstrap run 20 was also a low year for that in the other scenarios. One exception is that the random prey selection was done separately for the 2 prey availability scenarios (Section 6.3.3).

4.4.2 Demographic stochasticity

As an individual-based model, the NARW PET model includes demographic stochasticity naturally. There are binomial (Bernoulli) random draws for every individual wounding, survival, and reproductive transition, as well as for the sex of the newborn calves. Due to its functioning on individuals, it is impossible to apply demographic stochasticity in common across scenarios.

4.4.3 Parametric uncertainty

Parametric uncertainty from the estimation steps is stored as n_{boot} (1000) samples from the posterior of each parameter (Supplemental Table S1). In the n th iteration of the parametric bootstrap loop (Figure 4), the PET model selects the n th value from each posterior (preserving any correlation between parameters estimated together). Note that the scenario loop is (functionally) inside the parametric bootstrap loop, so that the n th iteration of the bootstrap loop has the same parameter values for every scenario, except as the scenario may specifically change them (Ellner and Fieberg 2003). For example, the *100% entanglement reduction* scenario has all the same values as the *Base* scenario for all iterations, except for parameter Δ_t^{iE} (which is 0 in the absence of entanglement under 100% reduction).

4.5 Output Metrics

Drawing from its purposes, the PET model was designed to produce specific output variables. These output variables represent a range of ways of examining the long-term status of the population and the potential effects of management actions.

4.5.1 Abundance

The most straight-forward measure of population status is the total population size in any given year ($N_t = \mathbf{1}'\mathbf{n}_t$, the sum of the individuals in all the stage classes at approximately July 1). Other subsets of stages can also be tracked over time; we focus specifically on the number of proven females at time t ($N_t^P = N_{C,t}^F + N_{R,t}^F + N_{W,t}^F$) (i.e., the number of females alive that have successfully produced a first-year calf).

4.5.2 Probability of quasi-extinction

As a measure of long-term risk of extinction, we calculate the probability of quasi-extinction (i.e., the probability that the population has dropped below a given threshold before or at time τ),

$$p\left(\min_{t=0 \text{ to } \tau} N_t < Q\right).\tag{29}$$

Mechanically, this is calculated as the fraction of bootstrap replicates for which the quasi-extinction criterion is met by or at time τ . As with abundance, the probability of quasi-extinction can be calculated for subsets of stages; we again focus on the probability that the number of proven females drops below a given threshold before or at time τ . We contrast a number of different quasi-extinction thresholds (Q), including 1 (outright extinction), 10, 50, and 100.

4.5.3 Expected minimum population size

In some cases, the probability of quasi-extinction can mask important differences among scenarios. As a more sensitive measure of threat of extinction, we calculated the EMP size (McCarthy and Thompson 2001),

$$\frac{1}{n_{boot}} \sum_{j=1}^{n_{boot}} \min_{t=0 \text{ to } \tau} N_{t,j} \quad (30)$$

where $N_{t,j}$ is the total population size at time t in bootstrap replicate j .

4.5.4 Probability of population decline (IUCN metrics)

The IUCN uses the probability of population decline as one of its criteria for classification. For whales, the relevant time scale is 3 generations or 100 years, whichever is less. We assumed that the generation time for NARWs under stable conditions is at least 33.3 years (Taylor et al. 2007 provided an estimate of 35.3 yr), so that 3 generations is at least 100 years. We calculate the probability of population decline from the bootstrap replicates within a scenario as

$$p \left(\frac{N_0 - \left(\min_{t=0 \text{ to } 100} N_t \right)}{N_0} > C \right) = \frac{1}{n_{boot}} \sum_{j=1}^{n_{boot}} I \left(\frac{N_{0,j} - \left(\min_{t=0 \text{ to } 100} N_{t,j} \right)}{N_{0,j}} > C \right) \quad (31)$$

where C is the critical threshold of 0.3, 0.5, or 0.8 (at least a 30%, 50%, or 80% decline), and I is an indicator function that takes the value 1 if the condition in parenthesis is met and 0 otherwise. That is, for each bootstrap replicate j , the minimum abundance within 100 years is found, and the greatest decline over that period is calculated. Then, the fraction of bootstrap replicates that exceed the critical threshold is found. Note that the decline is calculated based on the lowest population size over the 100-year period, not just the final population size.

4.5.5 Probability of population increase over one to three generations

The U.S. NARW Recovery Plan (NMFS 2005) includes a criterion of 2% growth over 35 years, which would allow the population to double. To assess the likelihood of achieving this criterion, we calculate the probability of the population doubling over 35 years as

$$p \left(\frac{N_{35}}{N_0} \geq 2 \right) \quad (32)$$

by calculating the fraction of replicates within each scenario that show at least a doubling in population size between year 0 and year 35.

Canada will be revisiting the abundance recovery target for NARWs in 2024 as part of a new Recovery Potential Assessment (RPA) on the basis of currently developing guidelines. Conservation status of species in Canada is determined (along with other criteria) by the number of mature individuals, which must exceed 250 or 1,000 for a species such as the NARW to be a candidate for delisting to Threatened or Species of Special Concern, respectively

(<https://www.canada.ca/en/environment-climate-change/services/species-risk-act-accord-funding/listing-process/quantitative-criteria-guidelines-status-table-2.html>). The number of mature animals (where mature individuals include the M_A , F_C , F_R , and F_W classes) already exceeds 250 (Section 5.4; mean estimate 282; 95% credible interval: 267-294). Using the current population size and age structure (Section 5.4) as a starting point, we estimated the proportion of replicates that surpassed the threshold of 1,000 mature individuals and the median time to surpass the threshold (based on realized growth rates). For those replicates that surpassed the threshold, we calculated the median population size at the time the threshold was crossed.

5. PARAMETER ESTIMATION

We developed estimates for the parameters in the model, primarily with new or updated analyses that matched the structure of the population model precisely. In most cases, estimates for the parameters in the model could be developed from empirical analyses of historical data. We were deliberate about the estimation and inclusion of epistemic uncertainty in the parameter estimates, so that the results of the projections ultimately encompass that uncertainty.

The mortality and reproduction analyses both used multistate capture-recapture models (Lebreton et al. 2009) but took different approaches to defining the observed states and estimating transition probabilities. The mortality analysis estimated transition probabilities for injury and mortality states while treating reproductive states as individual attributes. Conversely, the reproduction analysis estimated transition probabilities for reproductive states while treating injury/wounding states as individual attributes. Ideally, some type of integrated population model (e.g., Plard et al. 2019) could be constructed to jointly estimate all relevant parameters in a single framework; for computational purposes here, we took separate approaches.

In the sections that follow, we describe the estimates for the NARW mortality rates, reproductive rates, initial population size, and threat-related parameters. More complete descriptions of the parameter estimation methods and results, including tests for goodness-of-fit, can be found in Linden et al. (2023a, 2023b).

5.1 Common Data Sets

Several data sets were used for multiple analyses. We describe those data sets first, then refer to them in the description of the individual analyses.

5.1.1 Sightings data

To develop parameter estimates that characterized the variability and uncertainty among demographic parameters that were used in our projection models, we relied heavily on the sightings database of cataloged NARWs contributed by members of the North Atlantic Right Whale Consortium and curated by the New England Aquarium (Hamilton et al. 2007). Depending on the location of each sighting and the suite of photos taken during the event, these sightings provided evidence for proof of life, proof of calving, and documentation of wounding status. To appropriately estimate wounding rates, one needs information about whether or not a sighting was adequate to detect a wound, and that judgment was not available to us. However, NARWs are frequently sighted multiple times within a year, thus reducing the probability of missing severe wounds.

The data were extracted on 23 December 2021 and included 691 whales >0.5 years old known to be alive sometime during 1 April 1990-30 September 2019 (NARWC 2021). The data

were supplemented by the New England Aquarium (A. Knowlton, unpublished data; unreferenced) with detected wounding events from inspection of images associated with all sightings of identified individuals when the suite of images was adequate for evaluation. Although we initially considered evidence for all levels of wound classification (Knowlton et al. 2016), our final retrospective analyses included only severe wounds as possibly affecting survival or reproduction. In addition to severe wounds detected on free-swimming whales, we classified a wound as severe when necropsy evidence (Section 5.1.2) determined the cause of death of a recovered whale to be due to vessel strike or entanglement.

5.1.2 Carcass recoveries

Data on recovered carcasses of all large whales are gathered and maintained by multiple stranding networks situated along the Atlantic coasts of U.S. and Canada (<https://www.fisheries.noaa.gov/report>). We relied on a detailed list of documented NARW mortalities aggregated from those networks at the NMFS Northeast Fisheries Science Center (example documented in Henry et al. 2020) and also summarized by Moore et al. (2004) and Sharp et al. (2019). Our retrospective reproduction and cause of death models only incorporated those carcasses for which the catalog identity of the individual could be determined and where the death occurred from 1 April 1990-30 September 2019.

5.1.3 Sightings histories

We constructed sightings histories by individual and year with a defined capture period of 1 April-30 September (i.e., “summer” surveys), between which transitions of individual states (e.g., live/dead, healthy/injured) could be observed. State definitions differed in specificity between the reproduction analysis and the mortality analysis but were logically consistent. Age class and sex were known for 85% and 94% of individuals, respectively. We assumed an individual’s injury state was unknown during those capture periods that lacked a sighting within 6 months of the anniversary date of the capture period (1 July). Known deaths were recorded as an observed death state the following capture period.

We used sightings collected in the southern U.S. Atlantic coast during the calving season (generally 1 Dec–30 Mar; “winter” surveys) to provide evidence of reproductive state and supplement individual attributes in the sightings histories from the summer capture period. The winter surveys are believed to provide a near-complete census of calf production, though we allowed for missed calves in the reproduction analysis (Section 5.3). Importantly, we used sightings from the summer surveys directly following winter surveys to provide evidence of early loss of calves. Because the early loss of a calf may allow a female to calve again in 2 years due to reduced loss of body stores, this was an important consideration for the probability of calving and the production of 0.5-year-old calves entering the population.

5.1.4 Prey data (*Calanus indices*)

An annual index for prey availability for NARWs in the western Atlantic (east coast waters of the U.S. and Canada) was obtained for the period of 1986-2019 (Figure 5) using yearly anomalies in total *Calanus* spp. biomass reported for the eastern Gulf of Maine (eGOM), western Gulf of Maine (wGOM), Georges Bank, and the southwest Gulf of St. Lawrence (swGSL; see also fig. 6 in Sorochan et al. 2019). The authors Sorochan et al. (2019) graciously augmented the published time series with data from 2017-2019 and provided estimates of biomass expressed as log annual mean estimates (in mg dry weight per m²) with standard error and 95% confidence interval (K. Sorochan of DFO, 2022, unpublished data; unreferenced). As in Sorochan et al. (2019), these annual estimates represented average predictions from general linear models using

data from all available years (i.e., 1977-2019 for the GOM, and 1982-2019 for the GSL), and either year and station as factors for the swGSL, or year, quarter, and strata as factors for the GOM. Quarters (periods of 3 months) replaced months from the original study as a more adequate measure of seasonality (2022 memo from K. Sorochan of DFO to author D. Linden).

We initially explored several relationships between the various indices and per capita number of calves produced using generalized linear models to help guide potential covariates for probability of reproduction. We found useful correlations between calving rate and the *Calanus* indices from the eGOM and the swGSL when the latter were calculated as the geometric mean of a 3-year moving window (Figure 5). The window included the focal year (t) and 2 previous years ($t-1$, $t-2$) and roughly coincided with a typical 3-4-year calving interval for NARWs (Taylor et al. 2007). We hypothesized that the *Calanus* indices represented a multiyear feature of prey conditions that helped determine whether individual females would have the energy stores to reproduce.

5.2 Mortality Analysis

5.2.1 Methods

The multistate capture-recapture model for cause of NARW mortality (Linden et al. 2023a) estimated individual transitions between states of health, injury, and death. We restricted injuries to those that were deemed severe. We allowed rates of mortality and injury to vary by the 2 causes (entanglement and vessel strike), by individual attributes, and—for injury rates—by year. Individual variation in rates was according to age and reproductive state (not with calf, with calf, recently with calf, or “resting”). Structural temporal variation was represented by a regime shift to accommodate potential changes in risk associated with the GOM ecosystem and the subsequent distribution shift by whales (circa 2013). Both injury rates also accommodated for random temporal variation; early model exploration suggested little support for temporal variation in mortality rates.

We defined the following 6 true states for each year starting with an individual’s first capture: 1) alive; 2) injured by entanglement; 3) recent death by entanglement; 4) injured by vessel strike; 5) recent death by vessel strike; and 6) dead. Individuals with an unknown initial age or sex were assigned values according to probability distributions. Imputed initial ages were randomly drawn to be between 1.5 and 4.5 with a Dirichlet distribution weighted toward younger ages, while imputed sex was a function of the overall observed sex ratio.

This was a hidden Markov model, and observed states included: 1) seen alive; 2) seen injured by entanglement; 3) recovered dead by entanglement; 4) seen injured by vessel strike; 5) recovered dead by vessel strike; 6) seen injured by unknown cause; 7) recovered dead by unknown cause; and 8) not seen. Sighting probability was allowed to vary by sex and randomly across both time and individuals. Detection of an injury during live sightings and successful cause determination for carcasses were constant across time and causes. The recovery rate of a carcass varied by cause and randomly across time. Parameters were estimated within a Bayesian framework using Markov chain Monte Carlo (MCMC). We used a model selection technique (variable selection by reversible jump MCMC) that estimated probabilities of covariate inclusion for rates of injury and mortality (Linden et al. 2023a). This resulted in some covariate effects being set to 0 if evidence for the effect was weak.

5.2.2 Results

Parameter estimates for the full posterior distributions (not conditional on inclusion) are presented in Supplemental Table S1. The hazard rate of severe injury due to entanglement for the average NARW individual (0.028; 95% credible interval: 0.019, 0.038) was twice the hazard rate of vessel strike (0.012; 95% credible interval: 0.005, 0.023). The reverse was true for mortality rate, conditional on injury, as the entanglement mortality hazard rate (0.875; 95% credible interval: 0.607, 1.113) was less than half the mortality hazard rate for vessel strike (2.571; 95% credible interval: 1.673, 3.683). The mortality hazards translated into survival probabilities of 0.42 and 0.08 for individuals with severe injuries due to entanglement and vessel strike, respectively. Given the covariate effects, including the increased rate of entanglement injury for females with calves (1.118; 95% credible interval: 0.000, 1.750) and years after 2013 (0.603; 95% credible interval: 0.400, 0.820), and the increased rate of vessel strike injury for resting females (0.795; 95% credible interval: 0.000, 1.988) and years after 2013 (0.290; 95% credible interval: -0.191, 0.664), the full picture is more nuanced than indicated by the average rates (Figure 6).

5.3 Reproduction Analysis

5.3.1 Methods

Our multistate capture-recapture model to estimate reproduction probability (Linden et al. 2023b) was guided by the same stage structure we used in our projection model (Figure 2). We allowed survival rates and reproduction probabilities to vary with age and wounding state, with a shared effect for severe wounds regardless of cause. We allowed for random variation of stage-specific survival rates among years. We also included 2 food indices as potential influences on reproduction (Section 5.1.3), and, similar to the mortality model, estimated a temporal regime shift for years after 2013 that interacted with proven breeding status (i.e., unique effects for proven vs. unproven females).

We defined the following true states for each year starting with an individual's first capture: 1) male; 2) nulliparous female; 3) female with calf; 4) female in resting state; 5) female in waiting state; and 6) dead. Yearly transitions from 3 to 4 to 5 were fixed (given survival) except for females with an early loss of calf (losing the calf prior to the capture period), who would skip state 3.

Individuals with an unknown age, sex, or wounding state were assigned values according to probability distributions. Imputed ages were randomly drawn to be between 1.5 and 9.5 with a Dirichlet distribution weighted toward younger ages, while imputed sex was a function of the overall sex ratio. Imputed wounds were estimated from year-specific probabilities for entanglement and a single probability for vessel strike.

Observed states included: 1) seen with no calf; 2) seen with a calf; and 3) not seen. Sighting probability was allowed to vary by sex and randomly across both time and individuals. The probability of a missed calf, leading to an incorrect observation, was estimated.

Parameters were estimated within a Bayesian framework using MCMC. We used a model selection technique (variable selection by reversible jump MCMC) that estimated probabilities of covariate inclusion for 4 coefficients in the linear model for probability of reproduction: (1) the swGSL prey index; (2) the eGOM prey index; (3) the regime shift for proven females; and (4) the 2013 regime shift for unproven females. This resulted in some covariate effects being set to 0 if evidence for the effect was weak. We restricted the prior distribution for the effect of a severe injury on reproduction to be negative after initial model fitting suggested weak evidence for this effect (despite strong prior expectations).

5.3.2 Results

Although the retrospective reproduction model produced estimates of survival and reproduction probabilities that could be used in our projection model, we selected only the reproduction probabilities from the results (see the mortality analysis above in Section 5.2.2 for the survival rates that were included in the projections). We found that the probability of calving increased with age among nulliparous females and was highest overall among proven females in the waiting state (Figure 7). We also estimated an early calf loss rate (κ) of 5.4% (95% credible interval, 3.9-7.1%). Mean calving probabilities were positively associated with the swGSL index but not the eGOM index (Figure 8), indicating the latter was no longer explanatory (relative to the raw calving rates) once individual reproductive cycles and other model structure (e.g., yearly random effects) were taken into account. Temporal variability in expected calving probabilities across the retrospective time series was therefore a function of the swGSL prey index and unexplained annual deviances (Figure 9). Additionally, the presence of a severe injury decreased the probability of reproduction for proven females from 0.27 (95% credible interval: 0.21, 0.34) to 0.09 (95% credible interval: 0.00, 0.27), although we note the large uncertainty.

5.4 Initial Population Size and Structure

To estimate the initial population size for starting the simulations, we used the posterior distribution of alive states from the last occasion included in the reproduction model (Section 5.3), which produced a starting sex, age, stage, and wound-status structure. Each replicate of the simulation used a different sample from this joint posterior distribution. We used this model instead of the state-space abundance model used in stock assessments (Pace et al. 2017; Pace 2021) for 2 reasons. First, despite more recent sightings data being available (and abundance estimates generated), we were limited to 2019 for data available on prey indices and wounding status. Second, we required the 18 stage classes as defined by the reproduction model; these are not available from the Pace et al. (2017) state-space model. As noted elsewhere, an integrated population model could facilitate joint estimation of all relevant population parameters and should be a priority for further development.

The median estimated population size in 2019 was 362 (95% credible interval, 345-378). The estimated number of mature proven females in the posterior distribution for the initial population size was 69 (95% credible interval, 62-75).

5.5 Threat-related Parameters

Several parameters in the model were related to how the threats were represented in the scenarios and required judgments beyond what empirical evidence could offer. The rationale for those judgments is described below.

5.5.1 Entanglement and vessel strike parameters

The mortality analysis provided estimates of severe injury rates due to entanglement and vessel strike that we assumed represented the general threat of these phenomena. Removal (or mitigation) of a threat would involve scaling the hazard rate. We assumed that relative differences by age/stage of whales remained the same, as did the hazard rates for mortality conditional on injury. We used 2019 as the reference year from the mortality analysis to calculate the expected rates of injury and mortality for the population projections; this meant that the effect sizes representing increased rates after 2013 were embedded. We did not include the latent random temporal effects that were estimated for 2019, but we did use the corresponding variance estimates

to simulate environmental stochasticity in the expected rates (as explained in Section 4.4.1). In this sense, the threat of injury and mortality reflected the expected rates from 2014-2019.

5.5.2 Prey limitation

We assumed the large-scale ecosystem changes that have been observed in the western Atlantic since 2010 (Section 3.5.4) would continue into the future. The prey indices that were used in the reproduction analysis indicated generally lower availability after 2010 (Figure 5) and correspondingly lower expected probabilities of calving (Figure 9). Therefore, we considered the threat of prey limitation to represent a new normal for NARWs compared to historical patterns of fluctuating availability with periods of high abundance (2000s) and low abundance (1990s).

6. SCENARIO DESIGN

The simulations run with the population projection model were constructed using a “baseline and scenarios” philosophy (Runge et al. 2017; Williams et al. 2021), in which one scenario serves as a baseline and the other scenarios are modifications that focus on specific “what-if” questions. The baseline simulation is meant to represent the best understanding of the future status of the population under current threats and regulatory conditions; thus, it can serve for the purposes of status assessment. The modified scenarios explore such topics as the contributions of the individual threats to the current status and the potential for future management actions to mitigate the threats.

6.1 Baseline Scenarios

The baseline scenario uses the reproductive rates, injury rates, and mortality rates from the recent past (2010-2019 for prey-influenced reproduction; 2014-2019 for injury/mortality), as well as the relationships between demographic rates and predictor variables derived from the analyses described above, to represent the conditions under which the NARW will respond over time. The baseline scenario assumes that current vessel speed regulations will remain constant, as will the overall vessel traffic, thus the vessel strike injury rate will remain constant over the period of projection (as a proportion of the NARW population size). The baseline scenario assumes that the lower prey availability observed from 2010-2019 will continue indefinitely.

It was difficult to know how to form the baseline, however, with respect to entanglement injury rate because the effects of recently enacted regulations have not yet been observed. As noted above, the U.S. enacted new regulations in May 2022 (NMFS 2021), which are intended to reduce entanglement risk; Canada has also continued to revise and implement new measures, especially in the GSL, to reduce such risk (SCFO 2023). Under the baseline philosophy described above, because these measures have been promulgated by the respective authorities, they should be considered part of the baseline, but we do not yet know how effective the measures will be. As a result, we constructed 3 alternative baselines that differ based on the assumed efficacy of these entanglement reduction measures. Baseline 1 (which we also refer to as the “status quo”) ignores the new entanglement reduction measures and assumes that the rates of injury and mortality from entanglement will continue at the rates seen since 2013. Baseline 2 assumes that entanglement injury rates are reduced by 25% compared to the status quo; this represents full achievement of the efficacy estimated in the U.S. Atlantic Large Whale Take Reduction Plan Rule (NMFS 2021), in east coast waters of either the U.S. or Canada, which we assume represents about half the entanglement risk area for NARWs. Baseline 3 assumes that both countries’ regulations are as

effective as estimated, and the future entanglement injury rate is reduced by 50% compared to the status quo.

6.2 Threats Analysis Scenarios

In the threats analysis scenarios, we wanted to examine how much each threat is contributing to the risk of quasi-extinction of NARWs under the baseline. We used baseline 1 (status quo) as the comparison point, then fully removed each threat one at a time, then in all combinations. Thus, one of the scenarios has the baseline vessel strike and prey threats but fully removes the threat due to entanglement; another has the baseline entanglement and prey threats but fully removes the threat due to vessel strike; and so on. If we represent the degree of each threat on a scale of 0 (none) to 1 (current), the scenarios can be represented with a triplet (x, y, z) for the entanglement, vessel strike, and prey threats, respectively. The baseline (status quo) is represented as (1, 1, 1). The remainder of the threats analysis scenarios are: (0, 1, 1), (1, 0, 1), (1, 1, 0), (0, 0, 1), (0, 1, 0), (1, 0, 0), and (0, 0, 0).

6.3 Management Scenarios

In the management scenarios, we examined how changes in NARW demographic rates, brought about by potential management interventions, could change the population trajectory. The intention was not to make an inference about how a specific management action would change the long-term growth rate of the population, but rather how the demographic changes induced by management actions would change the growth rate. We examined scenarios associated with entanglement risk, vessel strike risk, prey availability, and prey accessibility.

6.3.1 Entanglement scenarios

To evaluate the benefits of entanglement risk reduction on NARWs, 2 sets of scenarios were explored. The first set of scenarios explored the reduction of entanglement risk for all animals at 10% increments from 0-100%. This risk reduction could be accomplished by closures (which would present 100% risk reduction for the given area) or implementation of ropeless/on-demand gear (which presents a partial but not complete reduction of risk if floating groundlines or gillnets were still present). The second set of scenarios explored changes in the severity of entanglement through implementation of weak ropes in the entire endline, which is expected to effectively reduce entanglement risk for adults but provide only partial reduction of risk for juveniles because they don't have as much strength to break the ropes (Knowlton et al. 2016). The risk reduction under full implementation was estimated at 90% for adults and 60% for juveniles. The weak-rope scenario was also implemented at 50% (that is, 45% risk reduction for adults and 30% for juveniles) and compared to the corresponding implementation of full entanglement reduction.

6.3.2 Vessel strike scenarios

The risk of vessel strike mortality is a function of the number and types of vessels transiting the NARW habitat, vessel speed, the spatial distribution of whales, and the resulting likelihood of close interactions between vessels and whales as influenced by whale behavior, including behavioral reactions to approaching vessels (e.g., Rockwood et al. 2017; Crum et al. 2019; Garrison et al. 2022). To develop scenarios for future trends in vessel strike mortality, we examined available information on trends in commercial vessel traffic along the North American east coast and considered the impact of possible management efforts to reduce vessel strike risk by implementing broad scale mandatory vessel speed restrictions. As discussed in Section 3.5.2, the average increase in cargo container volume has been 3.5% annually for Atlantic ports in the U.S.

and Canada since 2010 (AAPA 2018). Assuming this correlates directly to increased vessel transits (i.e., kilometers of vessel tracks through the right whale habitat), we applied a vessel strike mortality risk model (Garrison et al. 2022) to simulate the resulting annual increase in right whale mortality due to large vessel strikes. The estimated annual increase in mortality averaged +0.7%, and this was used as an upper bound in our projected scenario. To approximate the effect of increasing vessel capacity on cargo vessel traffic, we assumed a doubling of average cargo vessel capacity over the next 20 years and estimated the resulting change in the number of vessel calls. This resulted in an annual decrease in cargo vessel calls to Atlantic ports of approximately 1% per year and an annual decrease of 0.3% in vessel strike mortality from the mortality risk model. The long-term trends in vessel capacity and vessel calls to ports along the Atlantic coast of the U.S. and Canada are uncertain and are unlikely to be linear as both port capacity and vessel types change over time. Given the uncertainties in long-term trends in vessel traffic patterns noted above, we considered 3 projected scenarios for future trends in vessel strike mortality associated with changes in total vessel traffic: -0.3% annual decrease, status quo (no change), and a +0.7% annual increase.

Vessel speed restrictions have been a key approach to mitigating the potential effects of vessel strikes on large whale populations. For NARWs, both the lethality of vessel strikes and the likelihood of interactions occurring were reduced by limiting large vessel speeds to less than 10 knots (Conn and Silber 2013). Recently, NMFS published a proposed rule which includes expanding the spatial and temporal scope of speed restrictions in U.S. waters (NMFS 2022). While the boundaries and overall effectiveness of this rule are yet to be determined, we considered a scenario where a broad-scale speed restriction for all vessels would result in a 25% reduction of the risk of NARW mortality due to vessel strikes.

Vessel strike scenarios examined the NARW population consequences of reduced risk from a reasonably achievable speed restriction (e.g., 25%) and also the possibility of annual changes in traffic (both increases and decreases). Including the status quo of the baseline 1 scenario, this resulted in 6 different scenarios for all combinations of speed restriction implementation and annual traffic changes.

6.3.3 Prey availability scenarios

The prey availability scenarios rely on the relationships between relative *Calanus* abundance and NARW calf production (Figure 8) to explore future conditions that take some form of previously observed conditions. Two scenarios were considered for future prey availability. The “steady” scenario mimics a situation where prey availability is not limited due to climate change and prey distributional changes do not affect the NARW population. Specifically, this scenario considered the possibility that future fluctuations in prey availability will mirror the observed fluctuations between 1990 and 2009, such that periods of high and low availability are represented as they have been observed (this was implemented as a random draw from the empirical distribution; Figure 10). The “decline” scenario considers the possibility that the lower prey availability observed since 2010 will continue into the future. Values for future relative prey are then drawn randomly from those observed between 2010 and 2019 (Figure 10). The “decline” scenario is included in the baseline.

We considered the “decline” scenario to be a representative baseline for expected future conditions based on the following observations. First, current predictions of *Calanus* biomass and occurrence suggest that traditional feeding areas of NARWs in the GOM-Georges Bank area (southwest of Nova Scotia), on the Scotian Shelf (southeast of Nova Scotia), and in the Bay of Fundy (Figure 1) will remain of low quality for foraging NARWs over the coming decades and that NARWs will continue to be forced to seek new foraging habitats (Reygondeau and Beaugrand

2011; Grieve et al. 2017; Sorochan et al. 2019; Ross et al. 2021). Second, modeling results for the GSL regarding habitat suitability for NARWs, as well as predictions of *C. finmarchicus* and *C. hyperboreus* biomass, indicate that suitability is and has been marginal in this area, especially for pregnant and lactating females (Gavrilchuk et al. 2021; Lehoux et al. 2020) and is likely to decline over the medium term (2021 presentation from S. Ploudre of DFO to authors). Third, while habitat suitability in Newfoundland and Labrador shelf waters (Figure 1) or East Greenland might increase over time, there is currently no indication that these habitats are exploited by any significant numbers of NARWs (Delarue et al. 2022; Mattmüller et al. 2022). Fourth, the missing half or two-thirds of the NARW population during the foraging period might be exploiting offshore waters of the Labrador Sea (north of Newfoundland and Labrador) and the mid- or eastern Atlantic where the probability of occurrence of *C. finmarchicus* is high and is likely to remain high with climate change (Reygondeau and Beaugrand 2011; Monsarrat 2015). However, the low calving rate observed since 2010 indicates that densities in these areas, if they are currently exploited by NARWs, remain insufficient for a large number of them to build energy reserves adequate to ensure reproductive success (Bishop et al. 2022).

6.3.4 Prey accessibility (noise and disturbance) scenarios

We explored the effects of varying prey accessibility, where abundance of *Calanus* alone does not explain NARW population responses due to masking from noise pollution and other disturbances. The scenarios involved scalar changes in projected prey, both positive and negative, with the baseline 1 scenario serving as the reference (i.e., prey accessibility = 100%) and prey accessibility ranging from 70% to 130% in 10% increments. These scenarios represented potential changes due to, for example, increased shipping, seismic noise, or windfarm construction noise that could result in such levels of disruption, or due to mitigation efforts that reduce levels of noise below those experienced between 2010 and 2019.

6.4 Sensitivity Analysis

To examine which parameters were having the strongest effects on the output of the model, we looked at the sensitivity of the EMP size (Section 4.5.3) to the individual parameter values. To do this, we used the results from the baseline 1 (status quo) scenario. For each bootstrap replicate, we calculated the EMP. Then, for one parameter at a time, we plotted the EMP against the parameter value, across replicates. We limited the parameters to include only those from the mortality analysis that were model-selected >50% of the time and those from the reproduction analysis that related to the probability of reproduction (i.e., the betas) and the calf-loss rate (κ). To calculate a measure that could be compared across parameters, we fit a linear regression through the trend in EMP for each parameter, then calculated the expected difference in EMP at the 2.5% and 97.5% quantiles of the parameter value. For the purposes of comparison, we flagged regression coefficients that had a p-value of ≤ 0.05 .

7. RESULTS

The results of the projections from the NARW population model show the outcomes expected from each scenario. We begin with the results from the baseline scenarios, using a variety of metrics, to establish the expected future dynamics under our current understanding of the threats. Then, we present the results from the threats analysis and management scenarios, with a

focus on the PQE and how it differs across scenarios. Finally, we present the results of the sensitivity analysis to understand the role that uncertainty in the parameters is playing in the results.

7.1 Baseline Scenarios

The baseline scenarios project the trajectory of the NARW population while accounting for uncertainty. In our judgement, they incorporate the best available scientific and commercial information about NARWs and the primary threats they face. As noted above, there are 3 baseline scenarios that represent different assumptions about the efficacy of recently enacted regulations designed to reduce entanglement risk. In the sections that follow, several metrics are displayed for the baseline scenarios, including population projections, quasi-extinction rates, the EMP size, and metrics concerning rates of increase or decline.

7.1.1 Baseline population projections

Under the baseline 1 scenario (the “status quo” scenario), the total NARW population size is expected to decline steadily over the next 100 years, with a median decline of about 75% (Figure 11A). The 95% projection interval, however, is wide and includes trajectories that show a 98% decline as well as a 9% increase.

The baseline 2 scenario (25% entanglement reduction) indicated a steady decreasing population on average, with a median population that is 42% smaller after 100 years (Figure 11B). Again, there was considerable uncertainty, with the 95% projection interval including a 92% decline and a 154% increase. Finally, baseline 3 scenario (50% entanglement reduction) resulted in an increasing population for most projections, with a median increase of 52% (Figure 11C). The highest projection in the 95% interval indicated a 497% increase while the lowest indicated an 83% decrease.

As in any population, the long-term population growth rate for NARWs is a function of the per capita birth and death rates, with a stable population (growth rate $\lambda = 1$) occurring when the birth and death rates are equal (Figure 12). By plotting the realized birth and death rates for the baseline scenarios on this same graph, the transition from negative to positive average growth is apparent (Figure 12). In addition to the expected differences among baseline scenarios in death rate due to reduced entanglement, there are also differences in birth rate due to marginally higher probabilities of reproduction when entanglement rates are reduced.

7.1.2 Probability of quasi-extinction

To understand the risks posed by the threats to NARWs, we calculated the PQE, specifically the probability that the number of proven females would fall below thresholds of 10, 50, or 100 animals by any point in time (Figure 13). A quasi-extinction threshold of 100 proven females was not informative because the population was already below this value at the start. A quasi-extinction threshold of 10 mature females was also not very informative because the probability was uniformly low for all scenarios and time points. At a threshold of 50 proven females, the PQE for the baseline 1 scenario increased quickly to 0.874 at 50 years and 0.934 at 100 years (Figure 13A). The other baseline scenarios had lower PQEs; baseline 2 increased to 0.601 at 50 years and 0.705 at 100 years (Figure 13B), while baseline 3 increased to 0.298 at 50 years and 0.349 at 100 years (Figure 13C). Across baselines, the reduction of entanglement risk by 25% reduced the PQE at 100 years from 0.934 to 0.705 and the reduction of entanglement risk by 50% reduced the same probability of extinction to 0.349.

7.1.3 Expected minimum population size

The EMP size provides another measure of the risk of decline by calculating the minimum population size in each replicate up to a given point in time, then taking the average across replicates. This metric roughly answers the following question: on average, how low do we think the population size could get at any point before a specific time? This metric necessarily decreases (or at least does not increase) over time. The EMP size is fairly sensitive to the differences in the 3 baseline scenarios, with values of 107, 203, and 302 individuals, respectively, at 100 years (Figure 14).

7.1.4 Probability of population decline or increase

The probabilities of population change in NARWs, whether measures of decline (IUCN metrics) or increase (recovery criteria), reflected the same patterns across the 3 baselines as growth rate, PQE, and EMP (Table 1). The baseline 1 (status quo) scenario had higher probabilities of decline and lower probabilities of increase compared to the other baselines. The median time to surpass 1,000 mature individuals was >100 years for all 3 baselines. For the baseline 2 and baseline 3 scenarios, when the population reached 1,000 mature individuals, the total population size was $N = 1,533$ on average.

7.2 Threats Analysis

For the remainder of the results, we focus on the PQE for proven females, a metric that is both based in the intent of the federal conservation laws and has a sufficient ability to discern differences among scenarios. To examine the contributions of the 3 primary threats (entanglement, vessel strike, and prey loss) to long-term risk for NARWs, we compare the probability that the number of proven females falls below 50 individuals in 100 years under various removals of threats (Table 2). The presence of all threats (e.g., entanglement and vessel strike risk, post-2010 prey availability) is the baseline 1 scenario (note the value of 0.934 matches that in Figure 13A). If prey availability were to follow the historic patterns (1990-2009) compared to the post-2010 conditions, the PQE reduces slightly to 0.875. The full removal of the vessel strike risk alone reduces the PQE to 0.343, and the full removal of the entanglement risk alone reduces it to 0.053. Thus, while all threats contribute to the overall risk of quasi-extinction, the entanglement and vessel strike threats have a much stronger effect than the risk of prey reduction.

7.3 Management Scenarios

7.3.1 Entanglement

The influence of entanglement severe injury and mortality on population trajectories is apparent in Figure 15, where incremental reductions correspond to reduced PQEs for proven females. With 0% entanglement reduction (equivalent to baseline 1 scenario), the probability of falling below 50 proven females at 100 years was 0.934. The PQE decreased by almost half at 40% entanglement reduction (PQE = 0.479). Weak rope implementation was less effective than full entanglement risk reduction, as expected (Figure 16). The PQEs were still significant at a 50% implementation, with entanglement reduction at 0.349 and weak rope at 0.621.

7.3.2 Vessel strike

The scenarios exploring changes in vessel strike risk to NARWs (via rates of severe injury and mortality) indicated that speed restrictions that reduce the collision risk can lower the PQEs, although long-term trends in vessel traffic would modulate the effectiveness of such mitigation

(Figure 17). In the absence of a speed restriction, the probabilities of falling below 50 proven females in 100 years were 0.901, 0.934, and 0.982 for long-term changes in vessel traffic at annual rates of -0.3, 0, and 0.7%, respectively. With a speed restriction resulting in a 25% reduction in vessel strike risk, those probabilities decreased to 0.803, 0.846, and 0.929 for annual rates of -0.3, 0, and 0.7%, respectively.

Considering vessel strike and entanglement risk reduction in combination, the probabilities of falling below 50 proven females in 100 years were 0.639, 0.705, and 0.861 for long-term changes in vessel traffic at annual rates of -0.3, 0, and 0.7%, respectively, when the entanglement risk is reduced by 25% (Figure 18). A speed restriction that reduces vessel strike risk by 25% combined with entanglement risk reduction of 25% results in a PQE of 0.528 (when the annual rate of vessel traffic remains constant).

7.3.3 Prey availability

Under a scenario where vessel strike and entanglement risks to NARWs are maintained as in the baseline 1 scenario, but where prey distribution and abundance follow historical patterns (the “steady” scenario), the PQE (at N=50 proven females) is expected to increase to 0.875 over the next 100 years (Figure 19). Under post-2010 prey conditions (baseline 1 scenario), the PQE increases more steeply to 0.934 in 100 years (Figure 19).

7.3.4 Prey accessibility

Changes in prey accessibility with reference to the baseline 1 scenario had a moderate influence on the probabilities of NARW quasi-extinction (Figure 20). At 70% accessibility compared to the current levels of prey accessibility (100%), the probability of falling below 50 proven females was 0.983 after 50 years; for a threshold of 10 proven females, the probability was 0.721 after 100 years. Increasing prey accessibility to 110% of current levels was akin to the “steady” scenario representing historical prey dynamics (Figure 19).

7.4 Sensitivity Analysis

There were several parameters for which the EMP size exhibited sensitivity (Figures 21 and 22). For parameters governing mortality, the average injury rates due to entanglement (α_0^{iE}) and vessel strike (α_0^{iV}) both (a) had regression coefficients with notable relationships (as measured by a p-value of ≤ 0.05) and (b) showed relatively large differences in EMP size between extreme values. Other mortality rate parameters had notable relationships that were all negative, but differences in expected minimum population size were relatively small. All parameters associated with age-specific reproduction (i.e., the “beta” parameters) also had notable relationships and large differences in EMP size. The counterintuitive result for waiting proven females (β_W) was due to a negative correlation with the regime effect for unproven females (Section 5.3.2).

8. DISCUSSION

The PVA described in this report was designed to provide insights about the current status of NARWs, to allow inference about the contribution of different threats to the long-term status of the species, and to examine the potential for several classes of management intervention to improve the prognosis for conservation. As with any modeling endeavor, there are limitations to the nature of inference about future outcomes, which are discussed below.

8.1 Status

Without the management interventions enacted in 2022 and anticipated in 2023—that is, under the demographic conditions and regulatory setting circa 2019—the model forecasts a continued decline in the NARW population, with an expected decline of 75% over the next 100 years (Figure 11A). There is considerable uncertainty in this forecast, with more severe declines as well as potential stability compatible with the available evidence. Taking account of these trends and their uncertainty, the risk of quasi-extinction (dropping below 50 proven females) is very high: 87% within 50 years, and 93% within 100 years (Figure 13A). The probability of the population declining by at least 50% in 100 years is 0.829, the probability of it doubling in 35 years is <0.001 , and the probability of it growing to more than 1000 mature animals in 100 years is also <0.001 (Table 1).

The steep decline (~22%) of the population from 2015-2019, however, was not forecasted to continue as sharply under the status quo scenario. The steep decline was largely driven by high mortality in 2017 and 2019 combined with no observed births in 2018. The demographic rates used for projections drew from expected reproduction as related to prey dynamics observed after 2010 (when the western Atlantic ecosystem changed) and expected mortality rates as observed after 2013 (when NARW distribution changed). Thus, while the realized rate of population change from 2015-2019 was strongly negative due to a confluence of poor outcomes, the expected rate of population change going forward is less severe.

The analysis herein does not constitute a status assessment under any of the relevant classification systems; rather, these metrics were designed to inform such assessments. Although NMFS and USFWS have not established generic thresholds that associate quasi-extinction rates with listing categories under the ESA, the rate of quasi-extinction under the baseline 1 (status quo) scenario is compatible with other species that are listed as endangered (Runge 2021). The U.S. recovery plan for NARWs seeks to reduce the chance of quasi-extinction in 100 years below 1% to allow reclassification to threatened (NMFS 2005). Under the SARA NARW Recovery Plan Strategy, Canada identified an interim recovery goal to achieve an increasing population over 3 generations, the probability of which is approximately 0 for the status quo scenario. Thus, the model results under the status quo scenario are consistent with the current classification of NARWs as endangered in the U.S. and Canada. With regard to IUCN criteria, the model predicts that a 50% decline over 100 years (a criterion related to an “Endangered” classification) has a probability of 0.829 under the status quo scenario and that an 80% decline over 100 years (a criterion related to a “Critically Endangered” classification) has a probability of 0.435.

The baseline 1 (status quo) scenario may not, however, be the best representation of the current status of NARWs because new management interventions have been and are being implemented in the U.S. and Canada between 2022 and 2023. The baseline 2 scenario was designed to reflect the potential efficacy of new regulations designed to reduce entanglement risk in the U.S. With a 25% reduction in entanglement risk rangewide (representing 50% reduction in half the range), the median projection is stable to slightly decreasing (Figure 11B). The uncertainty in this projection is still wide, with a range that encompasses both continued decline and strong increase. The risk of quasi-extinction (dropping below 50 proven females in 100 years) is cut to 0.705 by this reduction in entanglement risk (Figure 13B), and the various risks of decline are also reduced (Table 1). Thus, if the recently enacted U.S. regulations have the effect of reducing rangewide entanglement risk by 25%, the model predicts the population will continue to decline, although the risk of quasi-extinction will have been partially reduced.

Looking at interventions taken in both the U.S. and Canada, if they collectively have the effect of reducing entanglement risk by 50% rangewide (baseline 3 scenario), then the median results of the model forecast a steady growth in the population size over the next 100 years (Figure 11C). Under this scenario, the probability of dropping below 50 proven females in 100 years decreases to 0.349 (from 0.934 in the status quo scenario; Figure 13C). The probability of declining by 50% decreases to a low level (0.141), and the probability of growing to greater than 1000 mature adults is possible (0.098; Table 1). Another useful metric to compare the 3 baseline scenarios is the EMP size: over the next 100 years, the model forecasts an average (across replicates) minimum population size of 107, 203, and 302 individuals for the baseline 1, baseline 2, and baseline 3 scenarios (Figure 14), showing how much the reduction in entanglement risk buffers the NARW population from the risk of falling to low levels.

In designing the baseline scenarios, we made an effort to represent our best scientific assessment of the existing primary threats while accounting for the current regulatory setting. The baselines account for actions and interventions that have been committed to; they do not include new mitigations that could be put into place but are not yet proposed or enacted. At this time, however, we do not know which of the 3 baseline scenarios is the best representation of current status. Regulations have been enacted and other interventions have been put into place to reduce entanglement risk, but those are so recent that there are no data yet to evaluate compliance and efficacy, and indeed, there is litigation in the U.S. over some of the measures.

8.2 Threats Comparison

The 3 primary threats investigated in this PVA were entanglement risk, vessel strike risk, and the long-term reduction in prey resources for NARWs. To understand the contribution of these threats to the overall status, we examined the hypothetical scenarios of fully removing each threat one at a time. The strongest contributor to long-term extinction risk was entanglement: fully removing entanglement mortality reduced the PQE (to 50 proven females in 100 years) from 0.934 (in the baseline 1 scenario) to 0.053 (Table 2); that is, removing this one threat alone could reduce the risk of extinction to low levels. Similarly, fully removing vessel strike mortality could also substantially reduce the PQE to 0.343. Compared to the other threats, the risk of prey decline is not as large a contributor to the risk of quasi-extinction, as removing that threat reduces the PQE slightly (to 0.875; Table 2).

8.3 Potential for Management to Affect Recovery

The results from the model suggest that management interventions, if effective enough, could, indeed, promote recovery of NARWs. Focusing first on entanglement risk, progressive reduction of the entanglement risk decreased the PQE (to 50 proven females in 100 years) from 0.934 (status quo) to 0.705 (at 25% reduction) to 0.349 (at 50% reduction) to 0.053 (at 100% reduction; Figure 15, right panel). The use of “weak rope” technology is not as effective as use of closures or ropeless/on-demand gear but still has a positive benefit (Figure 16); for instance, implementation of weak rope technology over 50% of the range would be about equivalent to closures or ropeless/on-demand gear over 30% of the range (PQEs 0.621 and 0.639, respectively).

One of the concerns about vessel strike risk is the potential increase in vessel encounters with whales if the number of transits increases over time with an increase in global trade volume. If vessel encounters increase by 0.7% per year over time, the PQE is predicted to increase to 0.982 (compared to 0.934 if vessel encounters stay constant); a decrease in vessel encounters by 0.3% per year over time would lower the quasi-extinction risk to 0.901 (Figure 17). Introduction of speed

restrictions that reduced the vessel strike risk by 25% would lower the risk of quasi-extinction to 0.846 (with constant encounter rate and no reduction of entanglement; Figure 17).

The population viability model can also be used to understand the combined effect of multiple mitigations. Reducing entanglement risk alone by 25% reduces the risk of quasi-extinction from 0.934 to 0.705 (Figure 15). Reducing vessel strike risk alone by 25% (with constant encounter rates) reduces the risk of quasi-extinction from 0.934 to 0.846 (Figure 17). The combination of reducing both entanglement risk and vessel strike risk by 25% reduces the risk of quasi-extinction to 0.528 (Figure 18). Thus, there might be potential to investigate what combinations of management interventions would achieve recovery quickly and efficiently.

Note that these results are not meant to predict the effects of any specific regulation or intervention. Rather, the PVA is designed to take as input a particular threat risk reduction (e.g., 25% reduction in entanglement risk) and project its effect on the long-term status of NARWs. Predicting the degrees of risk reduction that any specific regulations would achieve is the purpose of other tools (e.g., the Decision Support Tool used by NOAA in its 2021 rulemaking). We can imagine how these types of tools could be coupled together, but that work has not yet been undertaken.

8.4 Caveats

The model we have developed represents our understanding of the best available scientific and commercial data about NARWs, accounts for the major threats as we understand them, and explicitly integrates our uncertainty about the host of parameters in the model. There are many assumptions and scientific judgments we had to make to build this model, however, and transparency about these assumptions is important for conveying the status of the science and the strength of the inferences we can make. It can also help guide where additional information could help support continued development of the PVA. In the following subsections, we discuss caveats related to data limitations, model structure, representation of entanglement risk, representation of vessel strike risk, and the distribution of whales and their prey.

8.4.1 Data limitations

The nature of the data sets regarding NARWs produces several data limitations.

- First, there are lags between when data are collected, when they become available for analysis, when inferences begin to be robust, and when the results of a population model can be produced. The data used for this model extend through 2019, so the starting point for the model projections is 2019, 4 years earlier than the intended release of the model results. The consequence (as discussed in Section 8.1) is that it is difficult to incorporate the effects of very recent changes in demography, threats, or regulations.
- Second, there are a number of gaps in the datasets that affect inference: not all whales are seen every year; not all carcasses are recovered; not all causes of death can be determined; and others. The mark-recapture methods we use produce unbiased estimates of overall mortality rates, but the effect of “cryptic mortality” (carcasses that are not recovered) introduces uncertainty in the proportion of mortality due to entanglement, vessel strike, or other factors.
- Third, the model relies on an estimate of how severe injury (via entanglement or vessel strike) affects survival and reproduction, but the injury state cannot always be observed. For example, blunt force trauma (from vessel strike) is typically not

detected during observations of live animals but only when a carcass is recovered and flensed.

- Fourth, because not all carcasses are recovered, we make inference about the causes of mortality from the carcasses that are recovered and can be necropsied (Pace et al. 2021 estimate that only about one-third of the carcasses of whales that die are recovered) and from individuals known to be severely injured before disappearing. It is difficult to estimate, however, whether carcasses are recovered with equal probability across causes of death; Linden et al. (2023a) suggest lower carcass recovery rates for entanglement deaths compared to those for vessel strike but estimation uncertainty is much larger for the latter.
- Fifth, both the mortality analysis (Linden et al. 2023a) and the reproduction analysis (Linden et al. 2023b) include post-2013 regime effects that attempt to explain changes in demographic rates across the time series without fully understanding the mechanisms; additional knowledge regarding the persistence of the estimated changes into the future would better inform the projections.

To the extent possible, we have embedded all of these data limitations in our estimates of uncertainty, which contributes to the overall uncertainty in the model results.

8.4.2 Model structure

We built the structure of the population model based on our understanding of the demography and reproductive physiology of NARWs, but we did not investigate the sensitivity of the results to structural uncertainties in the model. Several aspects of the structure warrant some comment.

- First, we did not include a sophisticated treatment of density-dependent dynamics. Instead, we imposed a ceiling form of density dependence. This is surely not the actual mechanism by which the NARW population would approach and stabilize around its carrying capacity, but we're assuming those dynamics do not matter over the next 3-10 decades.
- Second, the reproductive stages we have chosen for adult females (F_C , F_R , F_W) are based on the physiological constraints that a long pregnancy and long lactation period impose on a large mammal, but the transitions individual animals undergo are presumably more complex and nuanced than we have represented.
- Third, for nulliparous females, we have assumed that age is the best predictor of the probability of moving into the breeding class and that once females begin breeding, age is no longer a relevant predictor of their success. While there is empirical evidence that supports these assumptions, again, the real world is surely more nuanced than we have described in the model.
- Fourth, there is an important potential predictor of survival and reproduction in whales that we have not included in the structure of the model—some measure of the health of an individual. As discussed in Section 3.5.3, there is a growing body of work that links health and bioenergetic state to demography in whales and other large mammals, but we have not yet been able to successfully develop empirical estimation models that allowed us to incorporate such dynamics.
- Fifth, we have not included Allee effects (reduced population growth rates at small population sizes) or inbreeding depression (reduction in survival or reproductive rates owing to loss of genetic variability in small populations) dynamics in the

model. There is not compelling empirical evidence for either of these dynamics in the NARW population, and there is even some evidence for a mechanism that would reduce the risk of inbreeding depression (Frasier et al. 2013).

- Sixth, although an individual-based model like this one can capture the effects of complex social dynamics (like social structure, mating dynamics, and sex-ratio effects on reproduction) on population dynamics, we have not yet included these types of mechanisms in the model. In part, our focus was on the role of anthropogenic threats in affecting the future of NARWs and there is not yet empirical evidence for these kinds of effects, but nevertheless, it is possible these dynamics could affect right whale viability.

These and other questions about model structure provide potential avenues for future research.

8.4.3 Entanglement scenarios

The process by which whales interact with gear, at times resulting in severe injury from entanglement, is complex. The temporal and spatial overlap between whales and gear that poses an entanglement risk affects the outcomes, as does the type of gear. We have designed scenarios that attempt to address at least 2 aspects of this threat (the frequency of encounter and the severity of encounter), but we know there are more subtle aspects that are of interest to management, industry, and the public. We did not include in our scenarios any future changes in fishing pressure or regulations; instead, we assumed that absent new regulations, the risk of entanglement would remain constant. We also did not include the possibility of increased risk of entanglement through new industries (e.g., kelp or mussel aquaculture). These omissions were deliberate, as we wanted to represent the threats as we understand them currently, and we assumed that significant expansions of industries that pose a potential entanglement risk to whales would have to consult with the appropriate regulatory agencies. Finally, as noted in Section 8.1, we had some difficulty representing the consequences of recent mitigation that have not yet been observed (e.g., recent regulations meant to reduce entanglement risk).

8.4.4 Vessel strike scenarios

Understanding the long-term future trends in the risk of mortality due to vessel strikes is complicated by a number of factors. First, the risk of vessel strikes is influenced by the spatiotemporal overlap between whales and vessel traffic. It is unknown whether or not the current movement and residency patterns of NARWs will persist into the future. Second, the future trends in commercial vessel traffic are driven by a variety of long-term economic factors, and as noted in Section 3.5.2, it is unclear whether or not the ongoing trends toward larger commercial vessels will result in net increases or decreases in the number of ships transiting through NARW habitats. As ports expand their capability to handle these larger vessels, traffic may also be redistributed along the North American East Coast, again influencing the overall risk of vessel strikes. Third, in addition to changes in vessel traffic and distribution, vessel speed also plays a role in the risk and severity of injury experienced by whales. Future changes in the spatiotemporal patterns of vessel speeds are uncertain. Finally, the development of offshore wind energy along the U.S. coast between North Carolina and the GOM may result in local or regional increases in smaller vessel traffic. The magnitude of these changes, transit paths, and the types of vessels involved are not yet known. Similarly, the eventual development of wind farms will necessitate the re-routing of vessel traffic into designated fairways, which again will influence the overall risk of vessel strikes. The NARW PET model is not designed to capture these complex spatial and temporal dynamics, but it is rather intended to evaluate the net or cumulative effects of changes in vessel strike mortality

rate on the NARW population. Encounter risk models (e.g., Garrison et al. 2022, Rockwood et al. 2017) can be used to develop simulations that evaluate the net impacts of changes in vessel traffic or the effects of mitigation strategies, and the outputs of these models can be used as inputs to the PET model to evaluate long-term impacts on population trajectory and risk of quasi-extinction.

One future consideration for the NARW PET model is to evaluate the potential effects of sublethal vessel strikes that may cause injury to individual animals. This consideration may be more important in the future if the number of transits of smaller vessels, as opposed to large cargo vessels, changes substantially within NARW habitats. As with entanglement injuries, it is likely that incurring a sublethal injury due to a vessel strike and the subsequent healing of that injury imposes an energetic cost that can influence survival and reproduction. However, this process is not currently captured in the PET model nor in the encounter-risk models used to evaluate the risk of vessel strikes to date. Understanding the rate of sublethal vessel strikes in the population and their impacts on lifetime survival and reproduction would be a valuable addition to the current PET modeling framework.

8.4.5 Shifts in the distributions of NARWs and their prey

There is uncertainty surrounding the future distribution and abundance of NARW prey. Depth, surface, bottom-water temperature, and surface and bottom-water salinity have been identified as significant predictors of *C. finmarchicus* mean densities or probability of occurrence in a number of models (Reygondeau and Beaugrand 2011; Chust et al. 2014; Albouy-Boyer et al. 2016; Grieve et al. 2017; Sorochan et al. 2019). The distribution and ecological niche of *C. finmarchicus* in the North Atlantic Ocean have shifted north as a result of sea warming (Reygondeau and Beaugrand 2011; Chust et al. 2014). Forecasts of future warming predict a continued decline in *C. finmarchicus* occurrence and abundance at the southern edge of the species suitable habitat, with a potential increase in abundance at its northern edge, particularly in the Barents Sea (Reygondeau and Beaugrand 2011; Grieve et al. 2017). At the southern end of *C. finmarchicus* range, changes in copepod community composition are expected in response to ocean warming, with small and lipid-poor species typical of temperate latitudes gradually replacing lipid-rich copepods that currently constitute NARW prey through range expansion of these southern species. This gradual change toward a more temperate community is already observed on the Scotian Shelf and to a lesser extent in the GSL (Blais et al. 2019; Johnson et al. 2018; DFO 2019). In the GSL, densities of *C. finmarchicus* and *C. hyperboreus* are expected to decline as bottom-water temperature continues to rise (Galbraith et al. 2021) and exceed thermal optima for these 2 species (Reygondeau and Beaugrand 2011; Schultz et al. 2020). The shelf waters off Newfoundland and Labrador are less likely to change drastically in temperature with climate change compared to other areas (Loder and Wang 2015; Saba et al. 2016). Densities of *C. finmarchicus* in these waters are currently comparable or higher than those reported for the GOM and GSL (Sorochan et al. 2019), and the probability of the species occurrence in these and in offshore waters is likely to remain relatively stable or to increase over the next decades (Reygondeau and Beaugrand 2011).

The capacity and rapidity for NARWs to adapt to a change in prey abundance and distribution is uncertain. The decline in NARW summer occurrence in the Bay of Fundy coincided in time (2010) with the documented decline in prey availability in the area (Sorochan et al. 2019; Davies et al. 2019), suggesting NARWs rapidly react to inadequate food resources. Passive acoustic monitoring in the GSL since 2011, however, indicates that it took NARWs a full 5 years (Simard et al. 2019) before their use of this area increased to appreciable levels (30-40% of the population; Crowe et al. 2021). In addition, most of the population during the summer months

currently remains unaccounted for, with only small numbers of NARWs detected in southern New England waters, the Bay of Fundy, and Massachusetts Bay since 2010 (Davis et al. 2017; Charif et al. 2020; Quintana-Rizzo et al. 2021; O'Brien et al. 2022).

Historically, NARWs ranged across the North Atlantic, possibly forming 2 populations (Frasier et al. 2022). Only a few individuals have been detected elsewhere in the North Atlantic over the past 2 decades, mainly to the south and east of Newfoundland (Canada) and to the southeast of Greenland (Monsarrat et al. 2015). Whether this is due to a lack of survey effort or a range reduction following whaling is unclear. Acoustic and visual survey efforts have intensified in Newfoundland and Labrador Shelf waters in recent years but have failed so far to detect any significant numbers of NARWs (Delarue et al. 2022). Similarly, passive acoustic monitoring in Davis Strait and East Greenland failed to detect NARWs in the mid-2000s (Davis et al. 2017), and recent recording stations in East Greenland have been too inshore (Mattmüller et al. 2022) to rule out a possible recent increase in NARW use of the region. However, a year-long acoustic study on the Cape Farewell Ground, a historical whaling ground, from 2007-2008 documented numerous calls primarily from July-November suggesting some NARWs are using these historical offshore areas, but they are rarely surveyed (Mellinger et al. 2011). However, the continued low calving rates reported for NARWs (Pettis et al. 2023) suggest that a large proportion of adult females has failed to find suitable feeding habitats since 2010. Taken together, uncertainty about changes in future prey distribution, the ability of whales to detect and adapt to a change in prey, and the full range over which NARWs may be able to disperse raises questions about the future distribution and reproductive success of right whales. The prey scenarios we ran attempted to capture some very broad features of these questions but certainly do not capture any of the nuances.

8.5 Insights from the Sensitivity Analysis

We designed the sensitivity analysis to investigate how much uncertainty about each of the parameters was contributing to uncertainty in the expected minimum population (EMP) size of NARWs in the status quo scenario. This type of question can help identify where additional research might be fruitful for reducing uncertainty in the population projections. Two parameters related to survival showed both a notable relationship with EMP and explained differences in EMP greater than 10 (Figure 22): α_0^{IE} and α_0^{IV} . Both parameters come from the entanglement and vessel-strike submodels and are governing the average injury rates for both causes. Reducing uncertainty in these parameters may require either better data sets or better models for estimating the injury rates. The data sets that indicate injury status and the data sets that are used to ascertain cause of death contain a lot of missing values; creative new field and analytical methods would be needed to improve them. The other parameters for which the projections exhibited sensitivity were the age-specific probabilities of first reproduction and the probability of reproduction for waiting females (Figure 22). While not shown here, it should be noted that this sensitivity was in actuality driven by the post-2013 regime effect for unproven females (i.e., first-time breeders) estimated by Linden et al. (2023b). This coefficient was additive to all stage 5 through stage 10 coefficients (β_5 - β_{10}); by itself, the regime effect had an absolute difference of ~25 for EMP. Given uncertainty in the mechanism behind this reproductive regime effect, whether related to sublethal injury or changes in realized prey availability/nutrition, additional research to understand this phenomenon should be a high priority.

9. FUTURE DIRECTIONS

This report represents the fruition of 5 years of intensive work by the team of co-authors but is meant, in some ways, to be a starting point rather than an ending point. With this initial PET constructed and operational, we can now begin to envision how it can grow, improve, and be put to work.

9.1 Vision for this Model

We view the NARW PET as a living model, a tool that is readily available, can be customized to address new questions, and improves over time. Several expectations are embedded in this vision. First, we expect the model to be evaluated consistently over time to identify the components that are working well and those that are not consistent with subsequent observations. This evaluation will allow us to identify how to improve the model. Second, we expect the model to be updated both regularly as new data come in and irregularly as new insights arise. Many of the datasets we relied on are updated annually, so annual updates to the model that simply update the parameters with the new data are a reasonable expectation. Of course, this relies on the stability of those ongoing datasets. But it would also be valuable to continually seek to improve the datasets to fill some of the gaps noted in earlier sections. Third, we expect that new management questions will arise fairly often and that the model will be updated periodically to answer new questions.

9.2 Using this Model in the Context of Management of Right Whales

The NARW PET was designed for specific applied purposes associated with the assessment and conservation of NARWs by federal, state, provincial, and other authorities. These applied purposes include: status assessment, notably against recovery metrics (as defined by the U.S., Canada, and the IUCN); comparison of the relative efficacy of management approaches to achieve recovery of NARWs; and communication with partners and the public about the demography of, threats to, and management needs for NARWs. We hope that the model can serve these purposes increasingly better over time. Deliberate and effective communication with management agencies, affected industries, and the public may help convey how this model can be used and engender dialogue that both improves the model and improves how it is used.

One possible way the utility of the NARW PET could be expanded is by carefully linking it to the Decision Support Tool developed by NOAA as part of the 2021 Atlantic Large Whale Take Reduction Plan Rule (NMFS 2021). The Decision Support Tool was designed to estimate how specific management actions would reduce entanglement risk; the PET is designed to estimate how reduction in entanglement risk is expected to change the trajectory of the population. Thus, these models could be integrated, with the coupling point between the 2 models being the degree of threat reduction. Future development of both models toward this end may be valuable, as well as consideration of how the PET model can be used with other assessment efforts (e.g., vessel strike mortality risk by Garrison et al., 2022).

Another possible use of the NARW PET is to conduct a power analysis for optimizing monitoring design. One of the difficulties in a statistical power analysis is that the purposes often focus on means objectives (like the precision of a survival estimate); the analyses leave open the question of how important any degree of precision is. By coupling a traditional power analysis with a population model, questions grounded in the value-of-information can be asked (Runge et

al. 2011); for example, how much would an improved sampling design increase our ability to assess the status of NARWs or choose among different management strategies?

One of the uses of the PET we considered but have not yet developed is analysis that derives recovery metrics from long-term recovery goals. For instance, if the overarching recovery goal were to achieve a PQE of less than 5% over 100 years, what combination of survival rates, reproductive rates, entanglement rates, vessel-strike rates, and so on would be needed? Another extension would be to use the model to estimate PBR rates, possibly through a management strategy evaluation approach like that used by Punt et al. (2020).

The PET could also inform various NARW recovery efforts. For example, PVAs are known to strengthen endangered species recovery efforts (e.g., Carroll et al., 2019) and are often used in conjunction with recovery plan implementation teams (e.g., Runge 2021). Given the interest in this effort by the regional U.S. implementation teams as noted above, this tool is expected to inform their efforts to assist NMFS with the implementation of the NARW recovery plan.

9.3 Future Model Development

There are many ways that the detailed structure of the NARW PET could be enhanced, its capabilities expanded, and the underlying demographic analyses improved. Following is a preliminary, but not exhaustive, list of potential developments that could be considered in future versions of the model.

As Section 8.4.5 outlines, there is considerable uncertainty about how the threats owing to climate change, as mediated by prey and whale distribution, could manifest. We envision collaborative work with other scientists, perhaps through an expert panel process, to (a) synthesize what is known about the link between climate change and *Calanus* distribution, the adaptive capacity for NARWs to change their distribution in response to prey, and the effects of prey availability on NARW demography; (b) articulate the key uncertainties in these processes; and (c) design prey scenarios that represent this understanding and capture the range of uncertainties.

Most of the parameters to which the model results were most sensitive arose from the entanglement and vessel-strike submodels. Improving these models may include changes to data collection, changes in how observations (e.g., injury states) are classified, how predictor variables are developed, and how the empirical analyses are structured.

Continued improvements in the empirical analyses associated with entanglement and vessel strike could also be coupled with development of threat scenarios that are more specific and mechanistic. This coupling could include a closer connection between the population evaluation model and other decision support tools being used to evaluate potential management interventions.

Currently, the NARW PET has an annual time step and a rangewide geographic resolution. More refined temporal and spatial resolutions could be considered. For example, because of the migratory patterns of NARWs, a seasonal temporal resolution (summer/winter) could be coupled with regional geographic resolution (e.g., Canada, northern New England, the mid-Atlantic, Georgia/Florida). This refinement would be a challenging modification, not least because the sub-annual survival analysis would need to include many parameters associated with the observation process (e.g., regional detection probabilities), but the increased resolution would allow more nuanced management questions to be asked.

As discussed in Sections 3.5.3 and 8.4.2, there is growing evidence that NARW demography may depend on latent individual health conditions. Because the PET is an individual-based model, the inclusion of an individual health index is possible (indeed, this sort of

functionality is one of the unique benefits of individual-based models). The prerequisite for adding a health index to the model would be the development of a dynamic model that predicts how the health of an individual changes over time, as a function of such factors as reproductive events (successful or not), injury, prey conditions, and environmental stress, and, in turn, how the individual's health affects probabilities of reproduction and mortality. Investigating evidence for a latent health index is promising and interesting work in its own right; we hope that the potential for inclusion in the PET motivates continued work in this direction.

One of the stressors that is suspected of having both direct and indirect effects on marine mammal demography is noise in the environment (Section 3.5.5). In this version of the NARW PET, we have explored one mechanism by which noise might affect right whale demography—through changing the accessibility of prey. If current levels of noise from shipping and other human activities are impairing foraging efficiency of NARWs, our model suggests that noise mitigation (e.g., quieter ships, ship speed limits) would have the biological effect of “restoring” prey accessibility to levels of prey availability during periods of population growth (Figures 19 and 20). We encourage research to test whether NARW foraging behavior is affected by existing noise sources because ocean noise levels respond so quickly to mitigation. In future versions of the model, other mechanisms and greater specificity in the mechanisms could be developed, perhaps in conjunction with development of an individual health index.

The effects of contaminants (Section 3.5.6) and disease (Section 3.5.7) were not included in the model described herein except implicitly to the extent that they contribute to the baseline levels of mortality and reproduction. Future versions of the model could include mechanisms for such threats.

9.4 Future Scenarios

For applied purposes, perhaps some of the most important future extensions of the NARW PET will be the development of new scenarios to examine other threats or management interventions. Cooperative work between management agencies and scientists would be a valuable way to identify important questions to embed in such scenarios.

Extensive offshore wind development is being planned along the continental shelf of the eastern U.S. (Quintana-Rizzo et al. 2021) in waters that are also used by NARWs during some periods of the annual cycle, and there is uncertainty about the potential impact this could have on NARW dynamics. We envision the development of a set of wind development scenarios, again perhaps through an expert panel process, that encompass a set of hypotheses about how wind development could affect demographic rates of whales, both with and without management mitigations.

Adding more detailed mechanisms by which noise might affect NARWs would also allow the development of a set of scenarios that explores uncertainty around the effects of noise, as well as the potential threat that additional activities that generate noise could cause. For instance, offshore wind development and offshore oil-and-gas exploration both can use seismic surveys to identify suitable locations for turbines or wells (Fields et al. 2019; McCauley et al. 2017; Richardson et al. 2017). Scenarios could be developed to explore the population consequences of such acoustic disturbance.

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Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

FIGURES AND TABLES

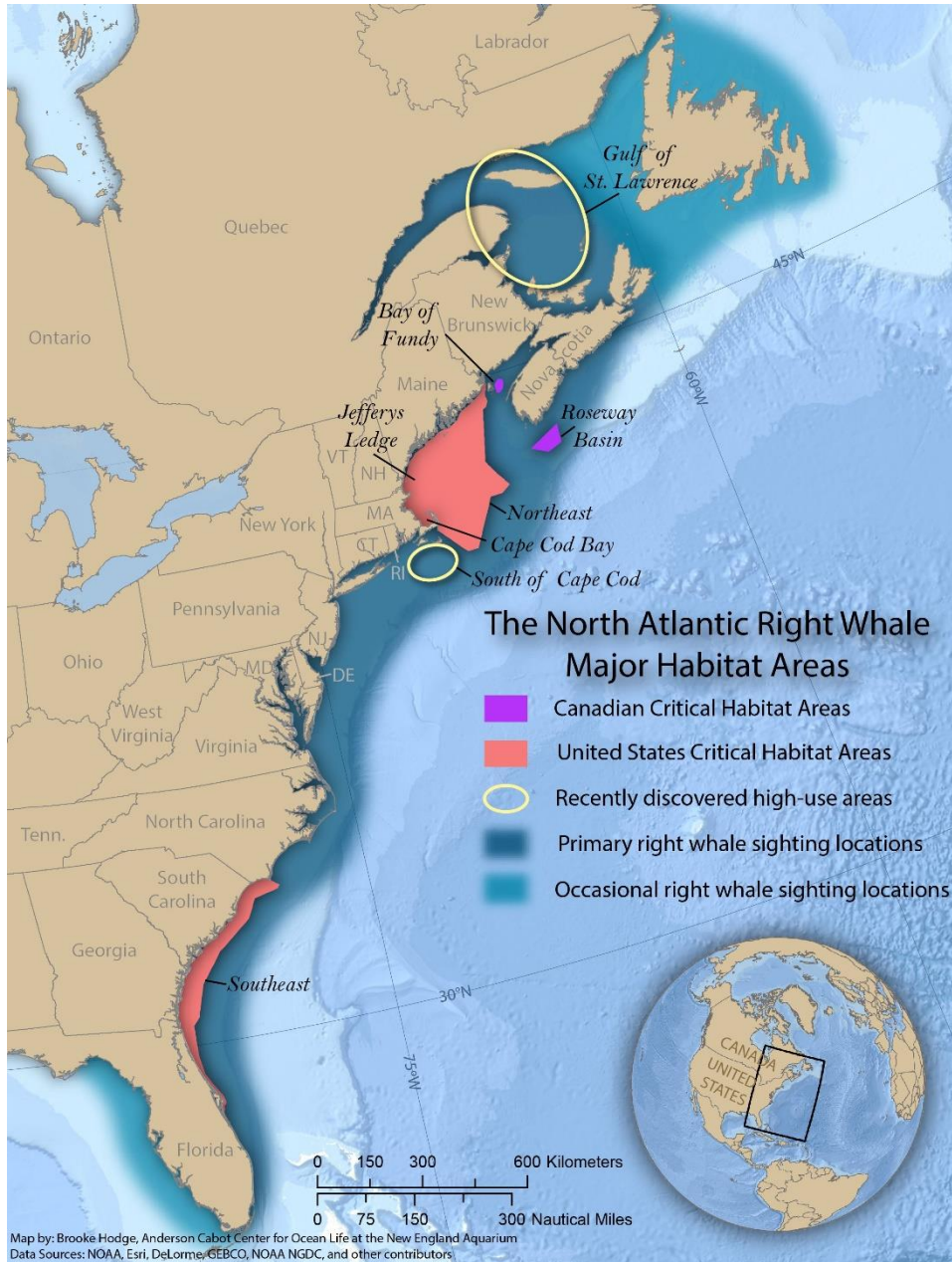


Figure 1. Map of North Atlantic Right Whale habitat areas. Additional locations mentioned in the text include: the Gulf of Maine (between Cape Cod and Nova Scotia); the Scotian Shelf (southeast of Nova Scotia); the Labrador Sea (north of Newfoundland and Labrador); Georges Bank (in the Gulf of Maine, just southwest of Nova Scotia). Source: Brooke Hodge, Anderson Cabot Center for Ocean Life at the New England Aquarium.

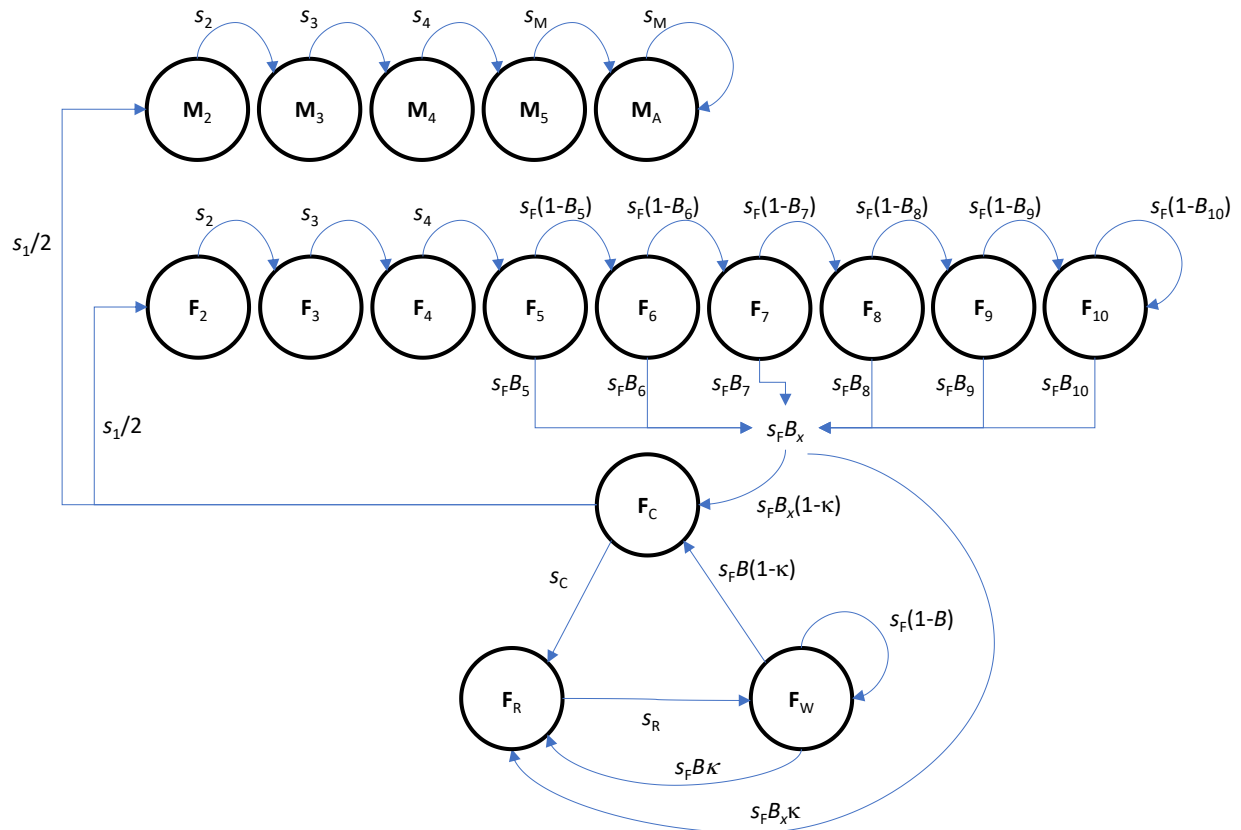


Figure 2. Demographic model structure for the North Atlantic right whale (*Eubalaena glacialis*). Individuals are classified into stages based on sex, age, and breeding class. First-year calves (F_1 and M_1) are represented as part of a mother-calf pair (F_C) in this diagram. Primiparous females who lose a calf transition to the adult resting stage (F_R); note that the primiparous transitions to adult are shown collectively for all primiparous ages to increase clarity in the diagram.

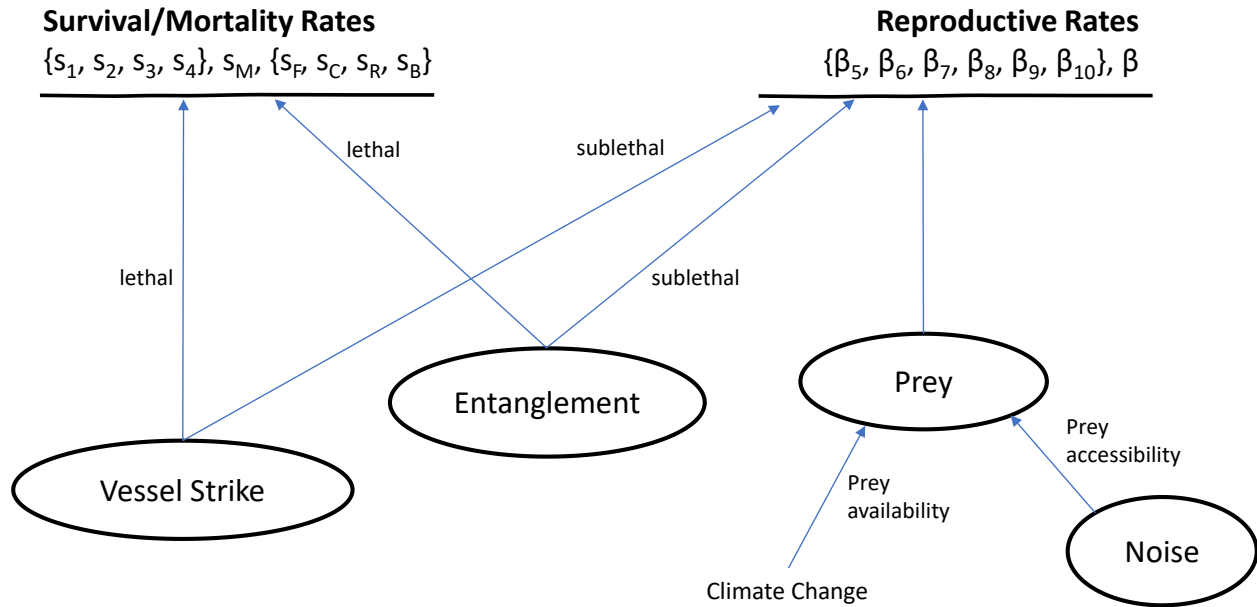


Figure 3. Submodels for the North Atlantic right whale (*Eubalaena glacialis*) and their links to the demographic rates.

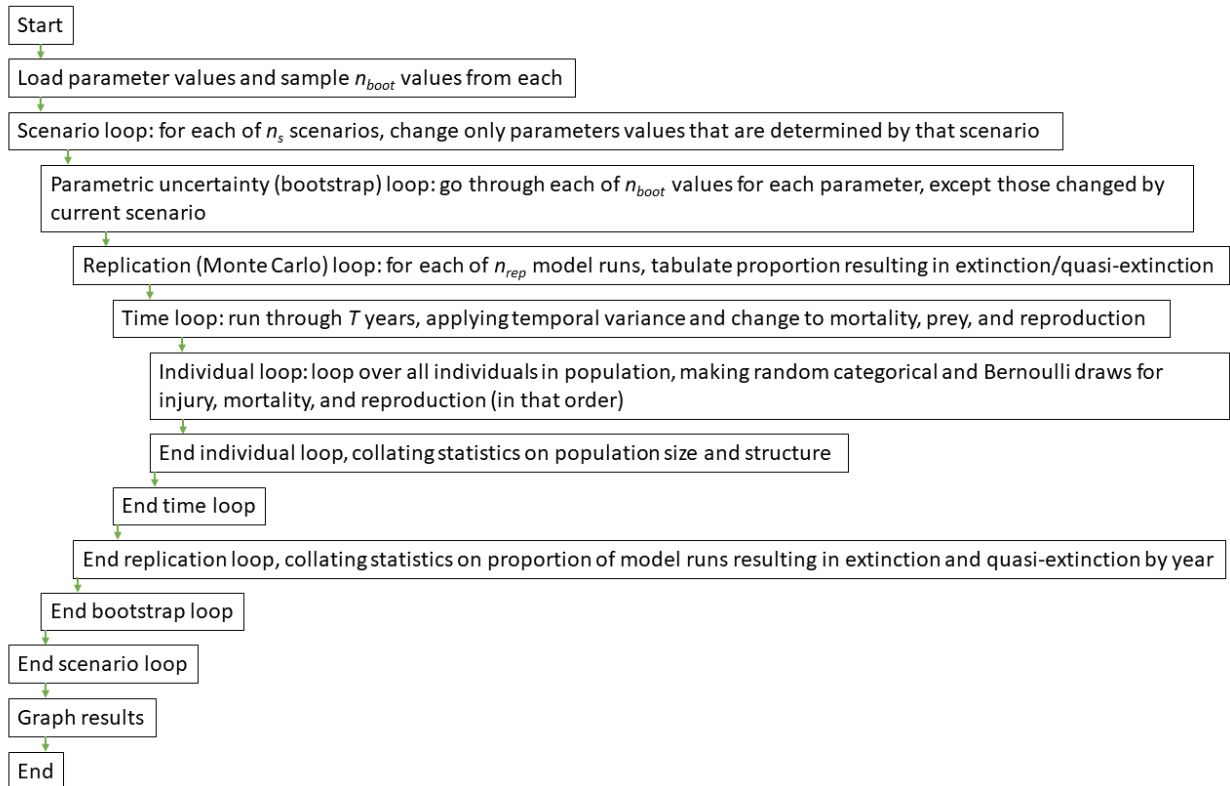


Figure 4. Nested flow process for North Atlantic right whale (*Eubalaena glacialis*) Population Evaluation Tool model. We programmed the model flexibly, but for the results presented in this report, n_{boot} was 1000, n_{rep} was 1 (eliminating the replication loop), and T was 100.

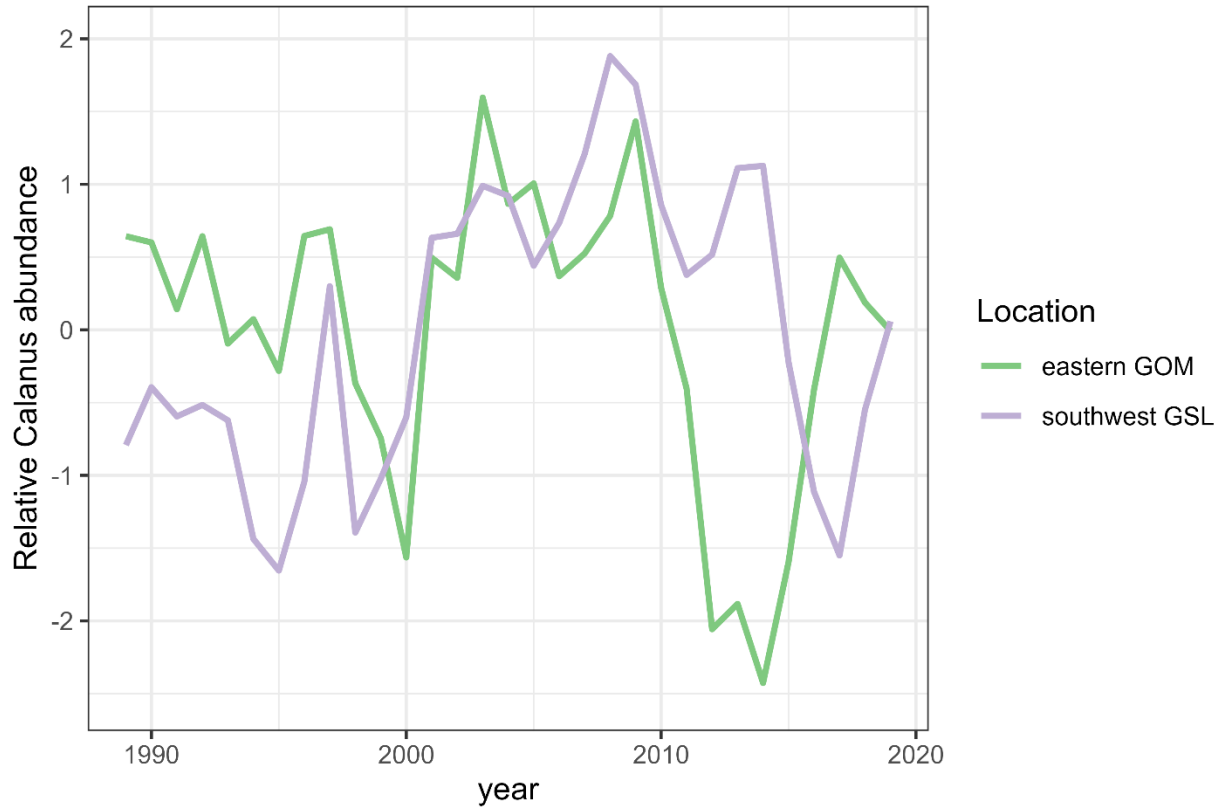


Figure 5. Prey availability index (log prey availability in mg dry weight per square meter) for the North Atlantic right whales (*Eubalaena glacialis*) in the western Atlantic Ocean, 1986-2019. GOM = Gulf of Maine; GSL = Gulf of St. Lawrence.

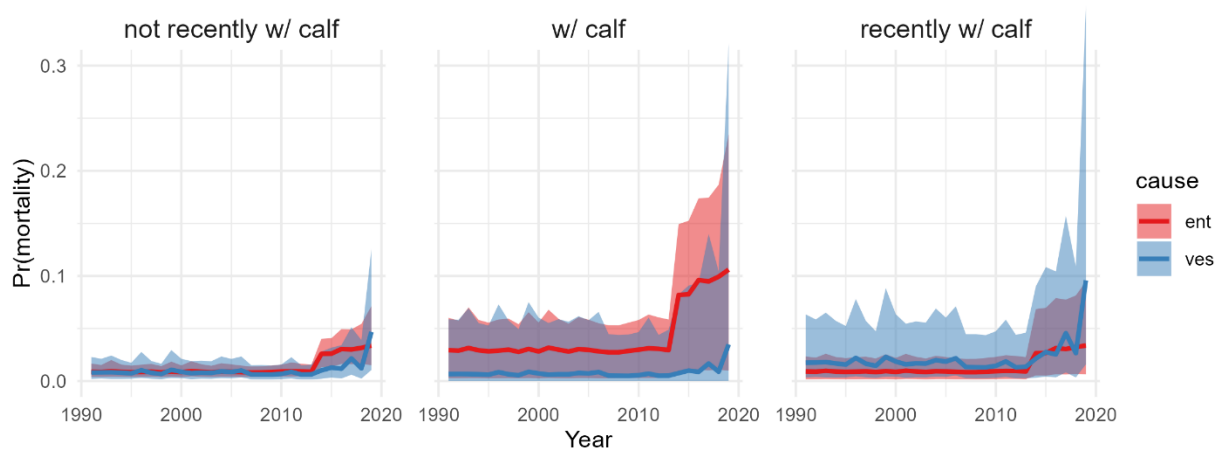


Figure 6. Marginal probability of mortality for North Atlantic right whales (*Eubalaena glacialis*) across time due to both entanglement (ent) and vessel strike (ves) for adult whales in 1 of 3 reproductive states, including individuals not recently with a calf (males and waiting females), females with a calf (F_C), and females recently with a calf (i.e., in resting state; F_R).

Average prey conditions, no severe injury 2013-2019

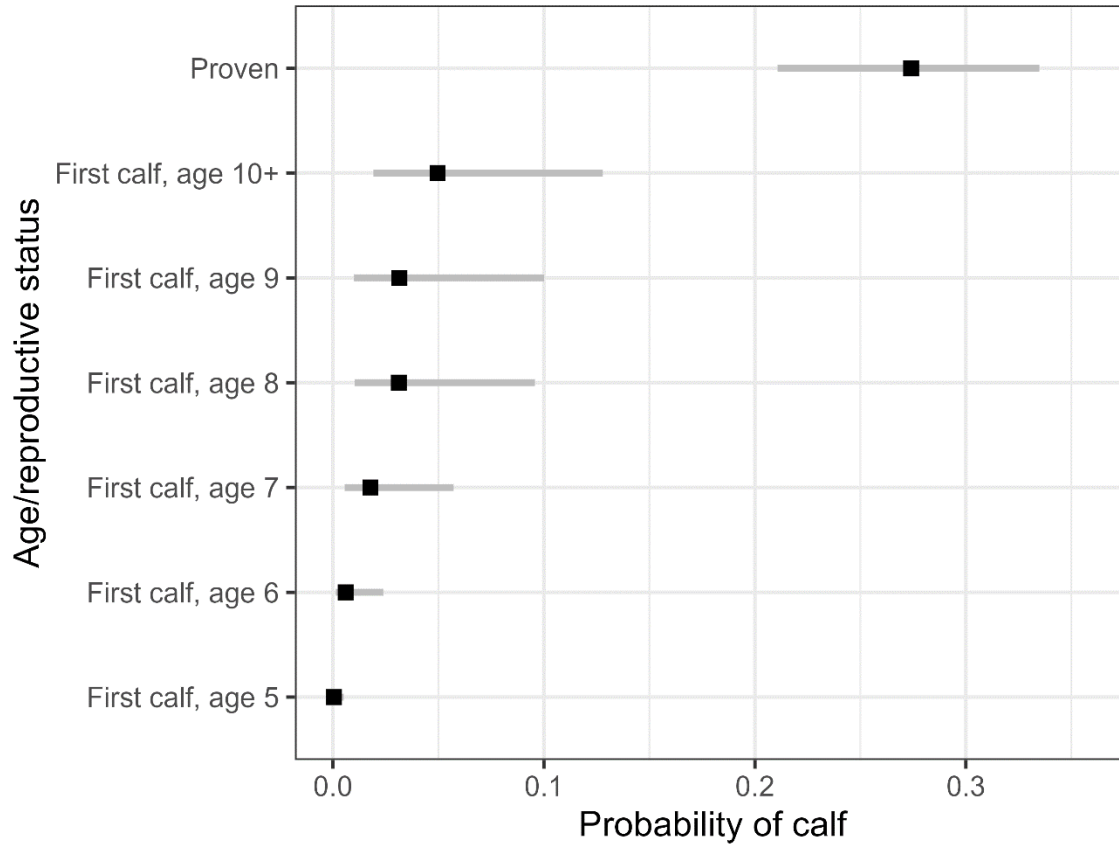


Figure 7. Expected probability of calving for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females in the waiting state (F_w , individuals that have previously given birth) and as a function of age for nulliparous female NARWs that are not severely injured during 2013-2019. The gray bars show the 95% credible intervals for the estimates.

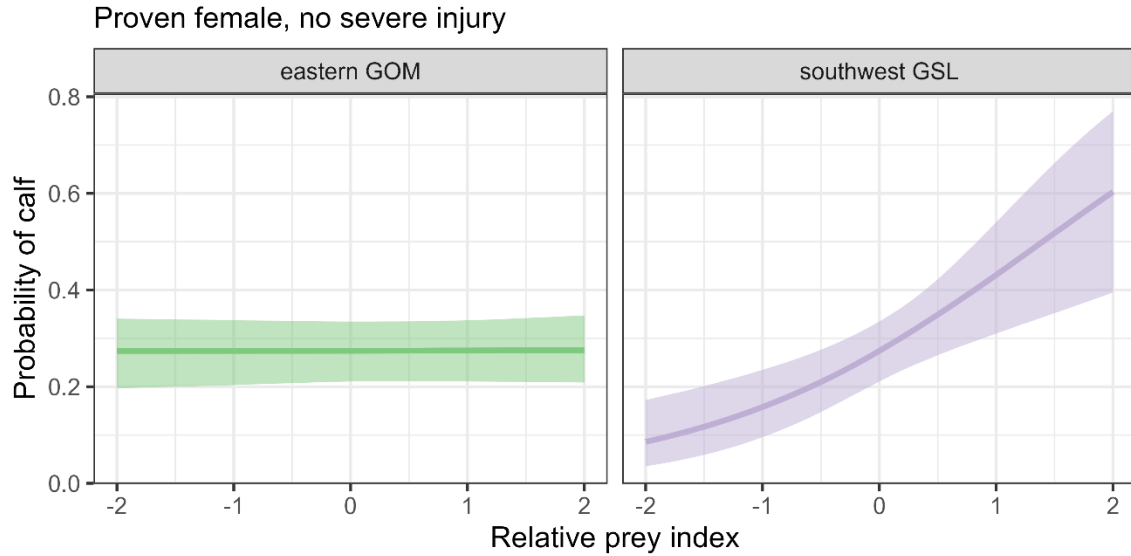


Figure 8. Expected probability of calving for uninjured, proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females in the waiting state (F_w , individuals that have previously given birth) and as a function of prey indices in the eastern Gulf of Maine (GOM) and the southwest Gulf of St. Lawrence (GSL).

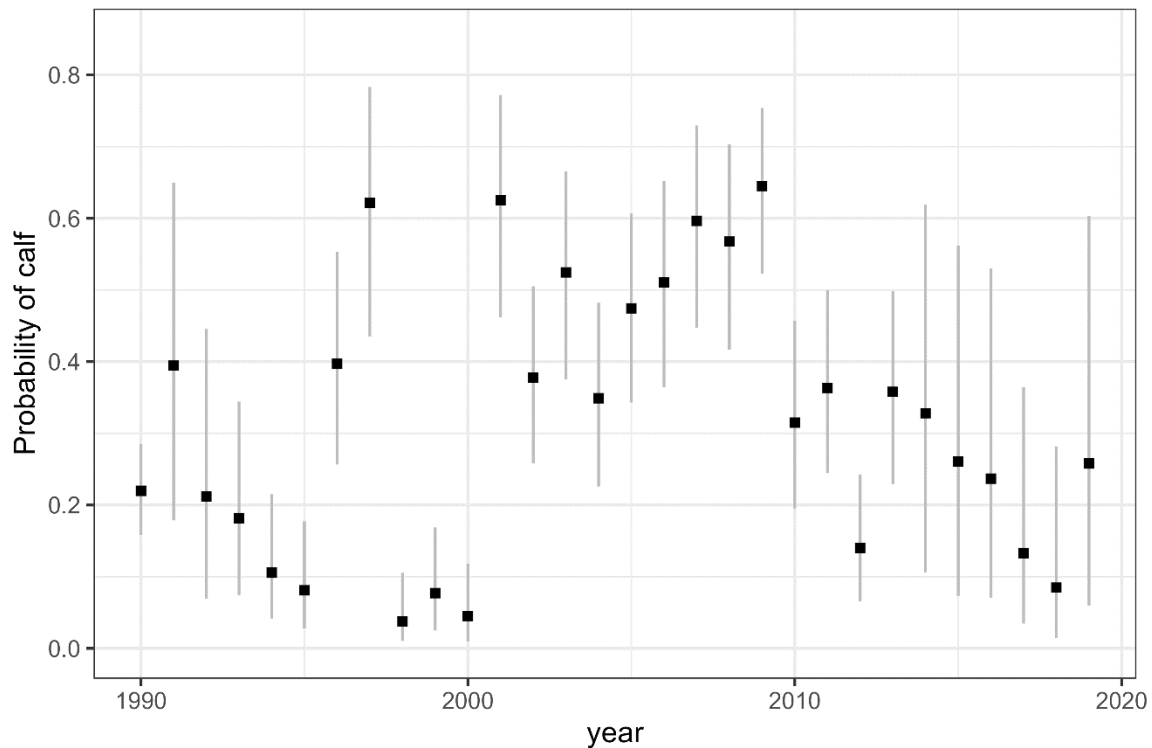


Figure 9: Temporal variation in expected probability of calving for uninjured, proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females in the waiting state (F_w , individuals that have previously given birth) as a function of the prey indices and temporal variation across time.

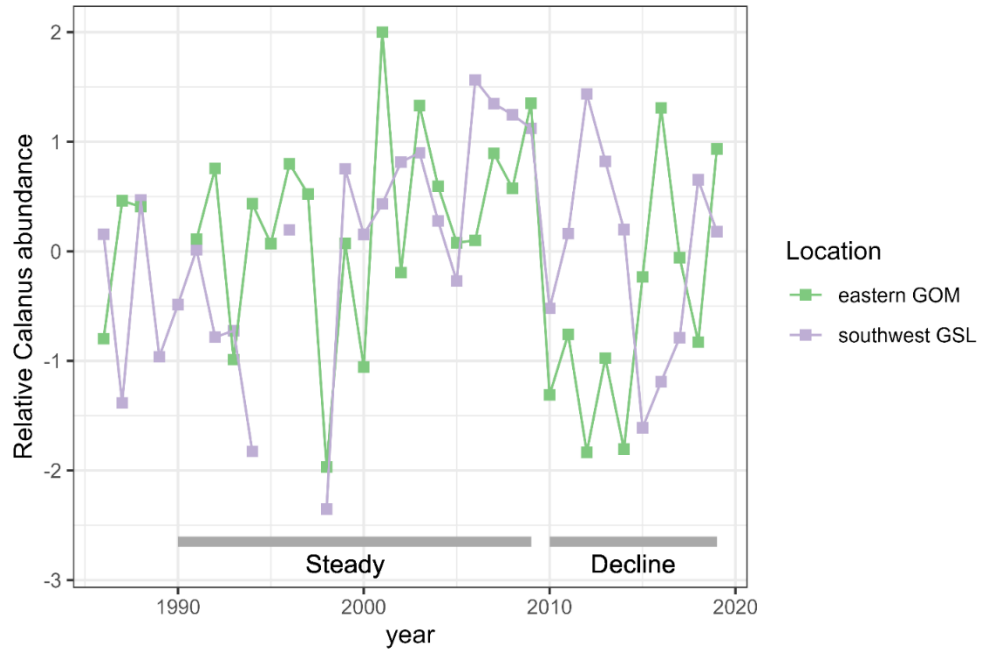
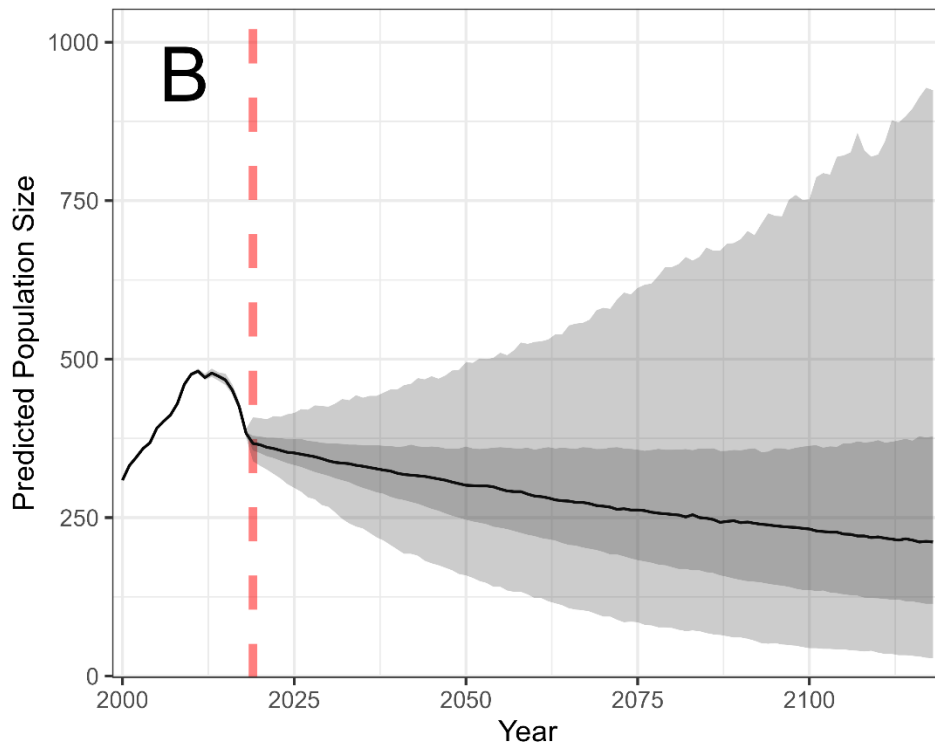
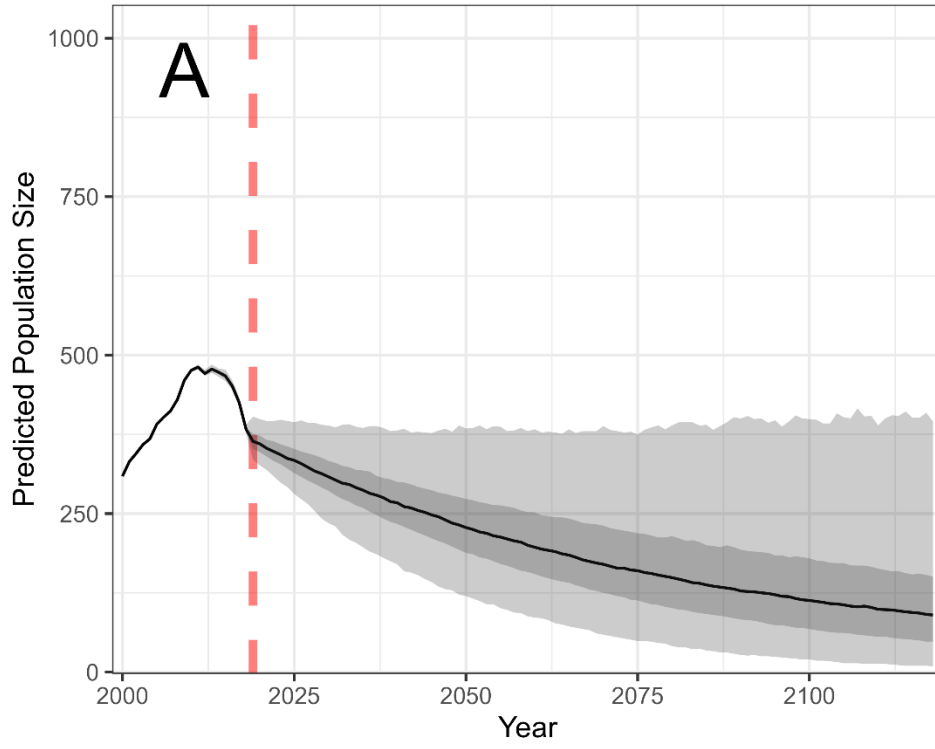


Figure 10. Relative *Calanus* abundance in the southwest Gulf of St. Lawrence (GSL) and the eastern Gulf of Maine (GOM). The “steady” period (1990-2009) and the “decline” period (2010-2019) are illustrated.



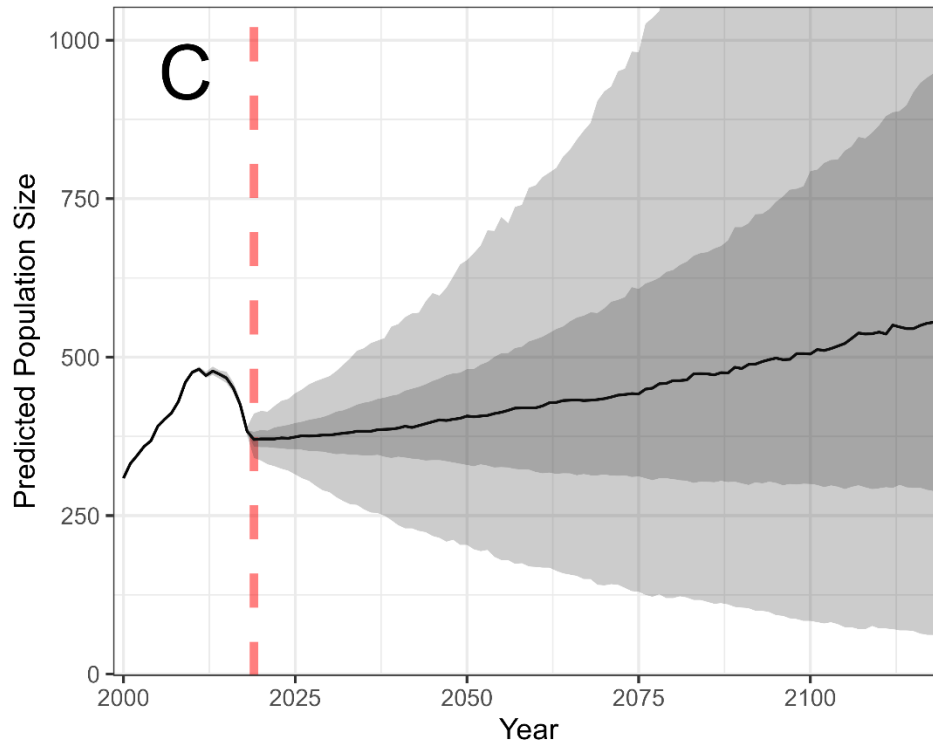


Figure 11. Historical and projected total North Atlantic right whale (NARW; *Eubalaena glacialis*) population size over time, 2001-2119. (A) Baseline 1 scenario (status quo). (B) Baseline 2 scenario (25% entanglement reduction). (C) Baseline 3 scenario (50% entanglement reduction). The period before 2019 (vertical dashed line) shows the historical estimates for the NARW population size; the period after 2019 shows the projections from the population projection model. The bold line shows the median value; the light gray shaded area encompasses the 2.5% and 97.5% quantiles (thus the 95% projection interval) while the dark gray area encompasses the 25% and 75% quantiles (thus the 50% projection interval)

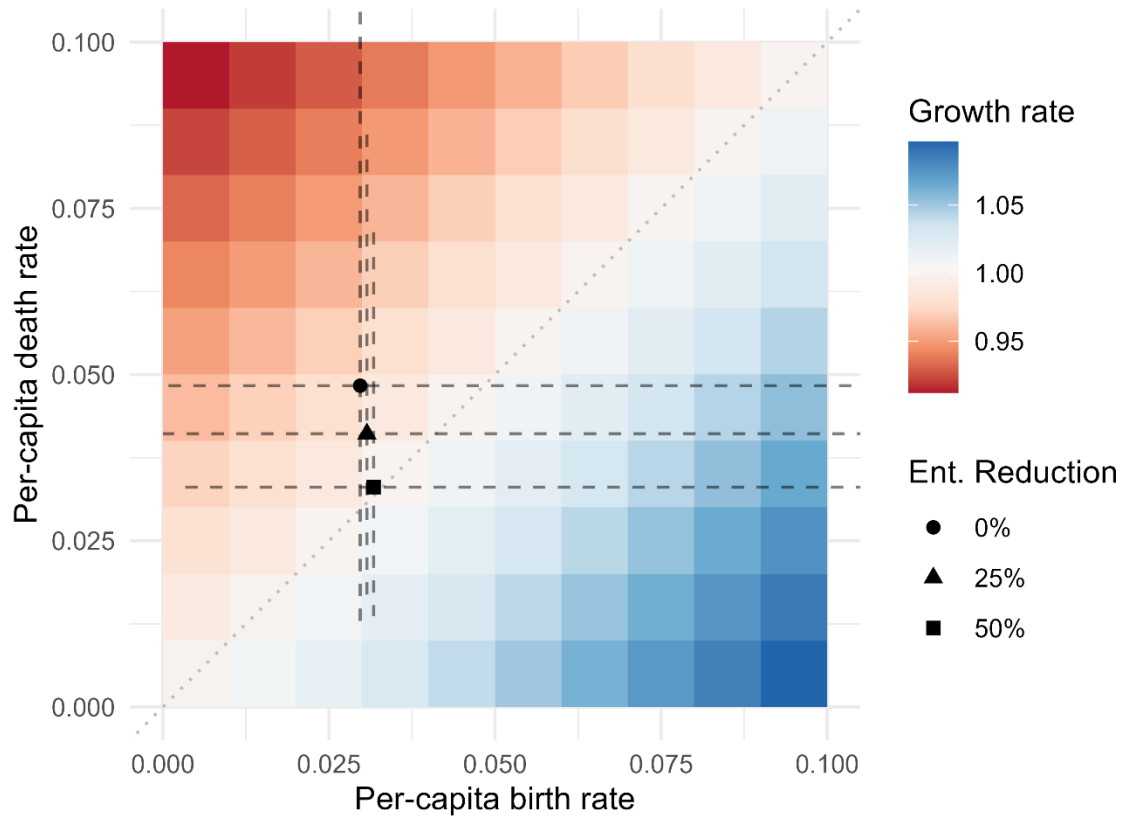
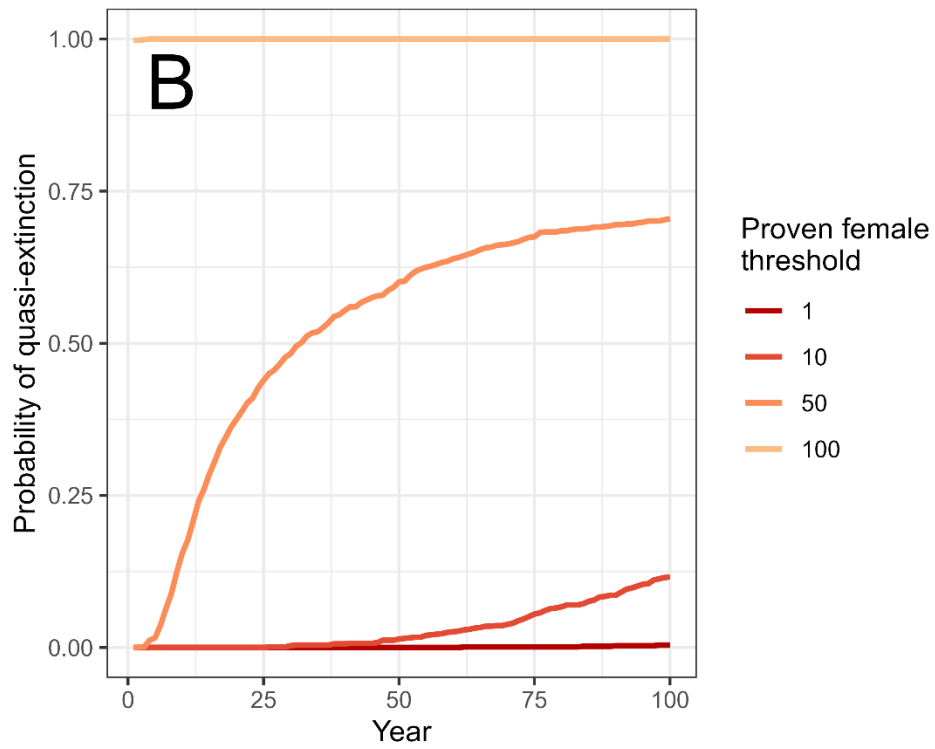
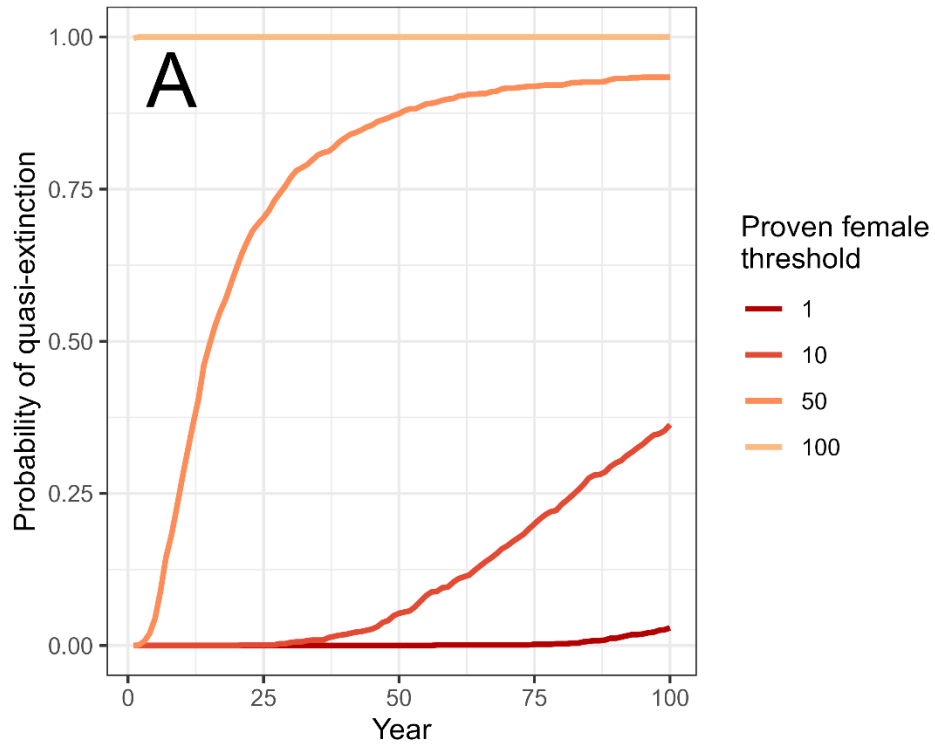


Figure 12. Realized per-capita rates of birth and death for the North Atlantic right whale (NARW; *Eubalaena glacialis*), with the resulting growth rates, for each baseline, as represented by the amount of entanglement reduction (Ent. Reduction): baseline 1 (0%), baseline 2 (25%), and baseline 3 (50%). Error bars indicate 95% credible intervals.



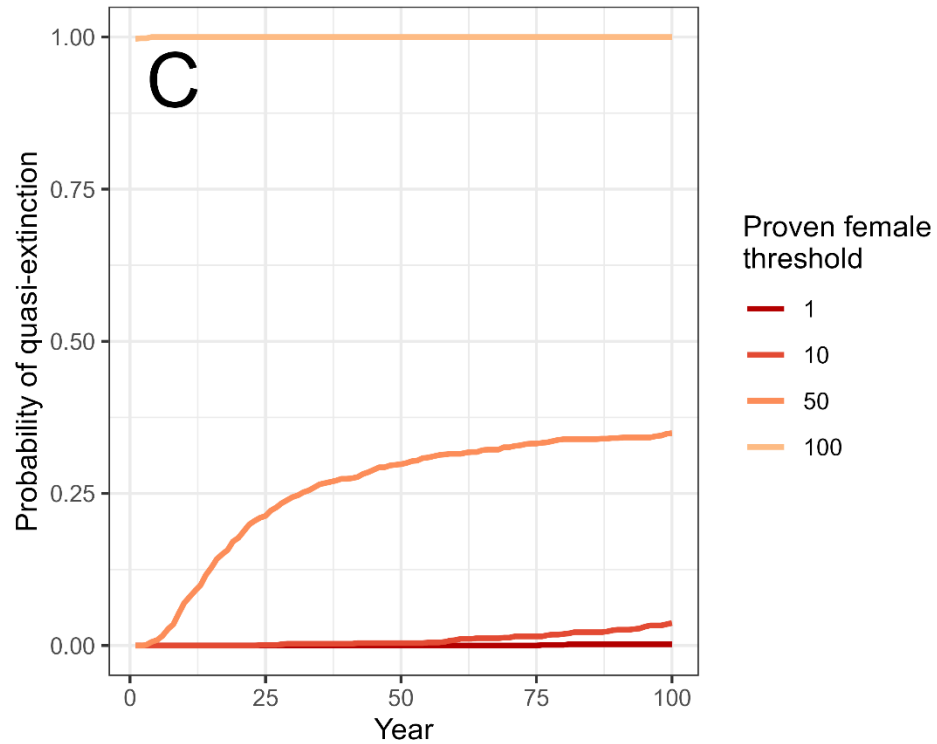


Figure 13. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) under various thresholds during the 100-year forward projection. (A) Baseline 1 scenario (status quo). (B) Baseline 2 scenario (25% entanglement reduction). (C) Baseline 3 scenario (50% entanglement reduction).

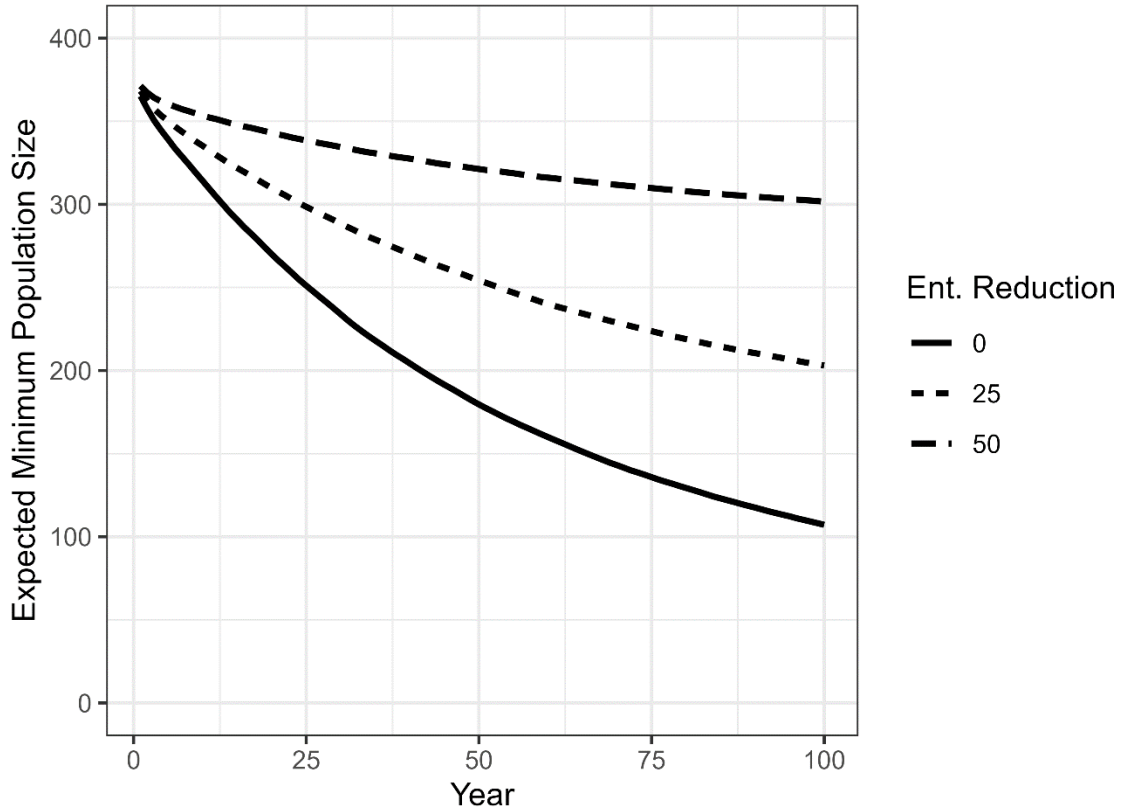


Figure 14. Expected minimum population size for North Atlantic right whales (NARWs; *Eubalaena glacialis*) during the 100-year forward projection for each baseline, as represented by the amount of entanglement reduction (Ent. Reduction): Baseline 1 scenario (status quo); Baseline 2 scenario (25% reduction); and Baseline 3 scenario (50% reduction).

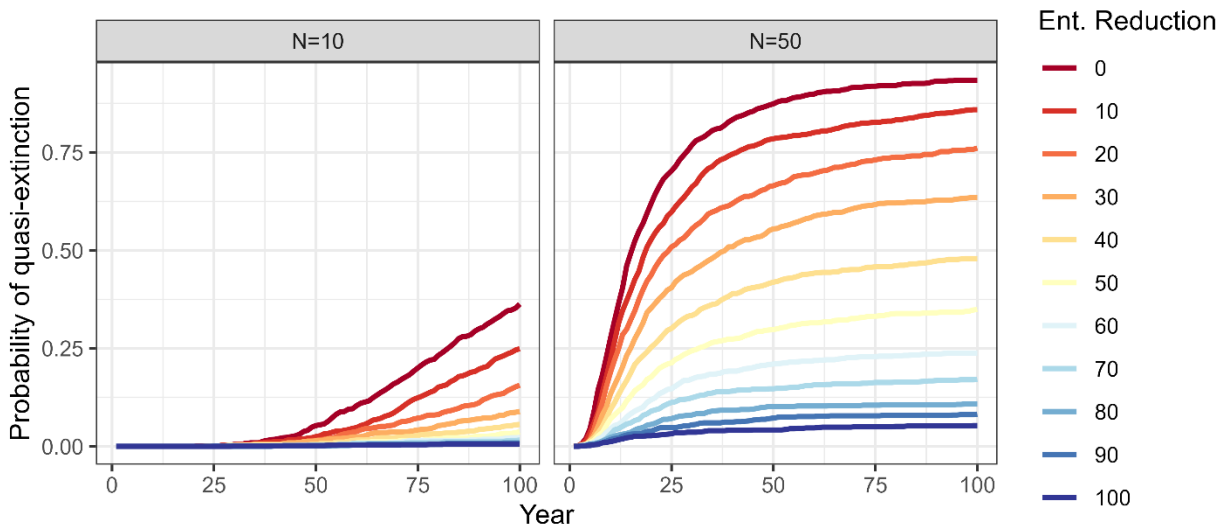


Figure 15. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals under various levels of entanglement risk reduction (Ent. Reduction).

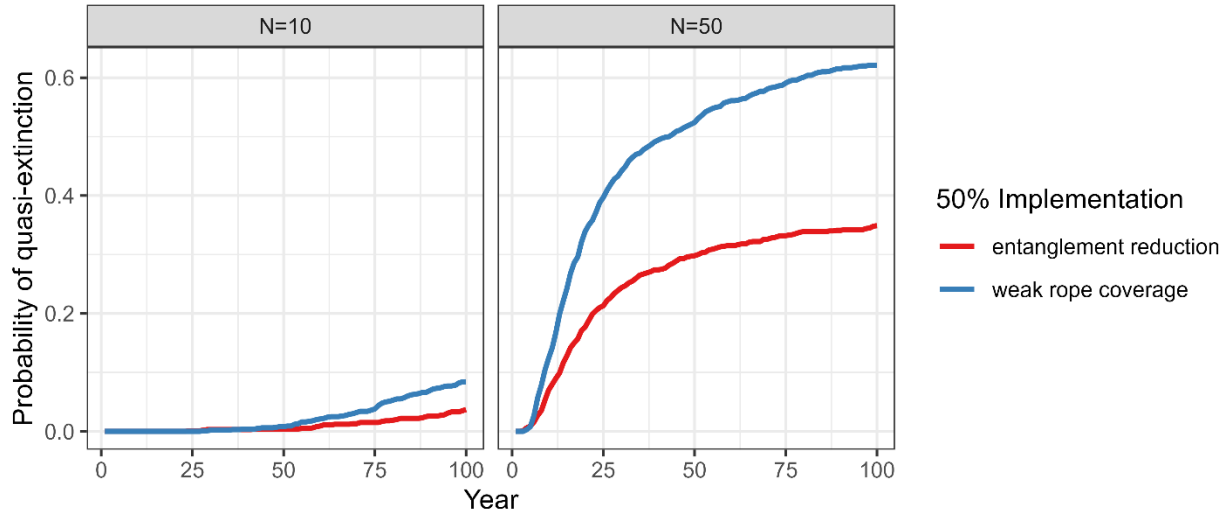


Figure 16. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals under a 50% implementation of weak rope technology or entanglement risk reduction.

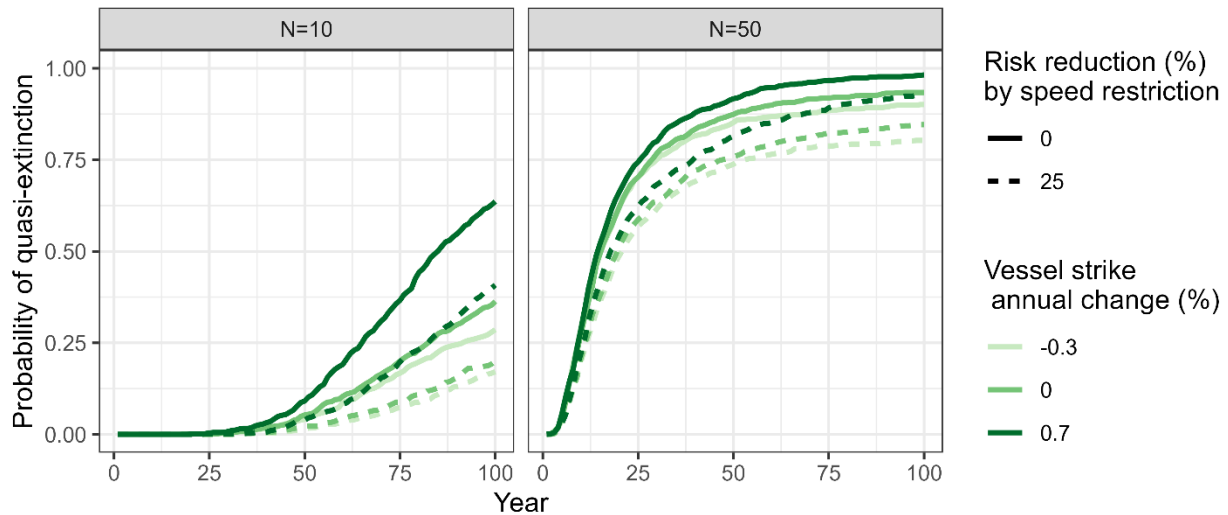


Figure 17. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals as a function of the annual rate of change in vessel strike risk and implementation of a speed restriction resulting in 25% reduction in risk, without any reduction of entanglement risk (thus, compare to baseline 1).

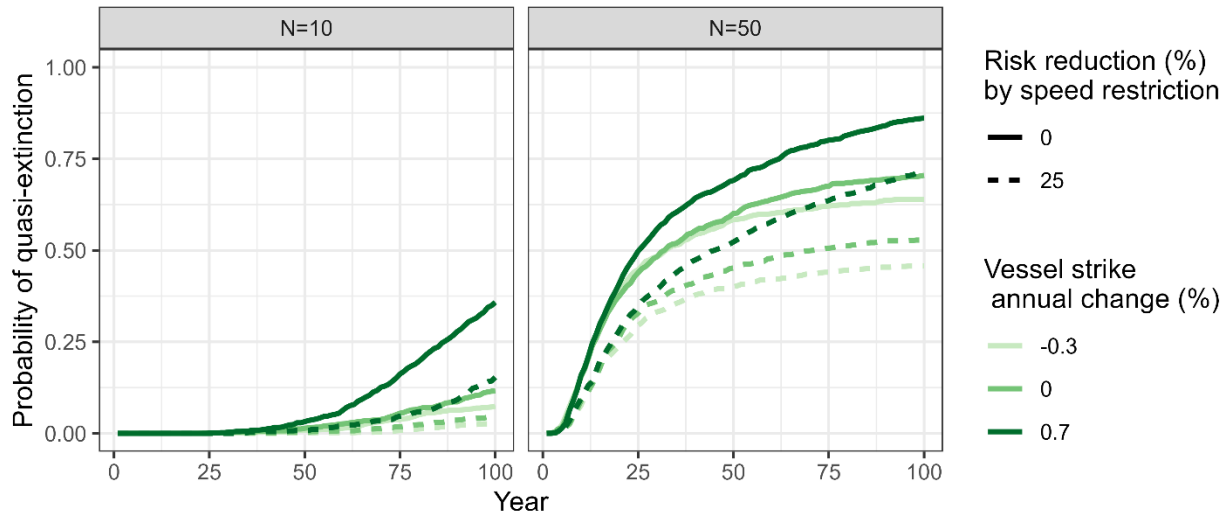


Figure 18. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals as a function of the annual rate of change in vessel strike risk and implementation of a speed restriction resulting in 25% reduction in risk, along with a 25% reduction in entanglement risk (thus, compare to baseline 2).

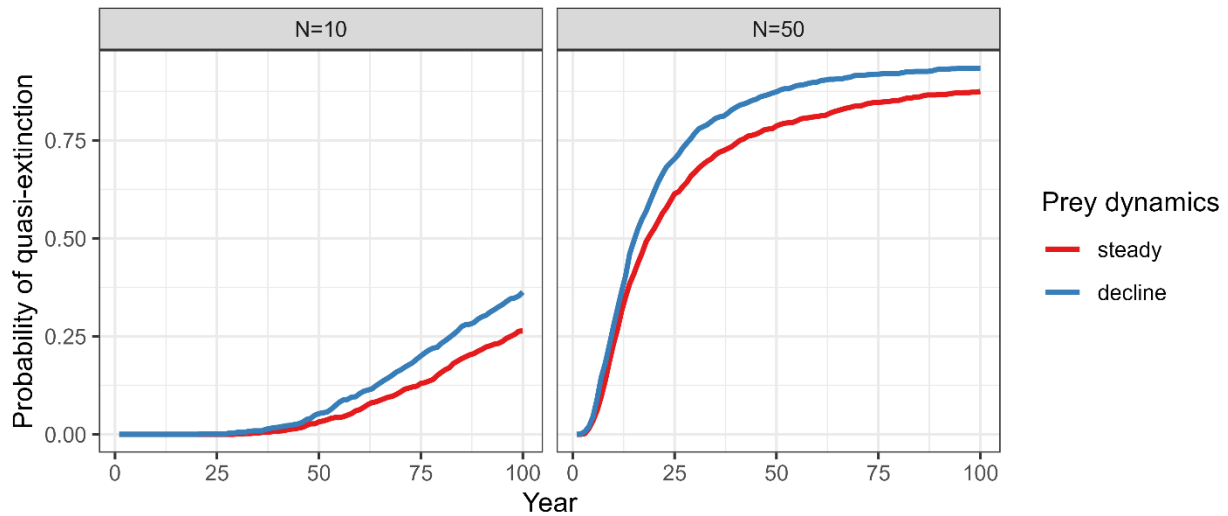


Figure 19. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals under 2 regimes of prey availability dynamics: steady, following historical patterns (1990-2009); and decline, representing post-2010 conditions.

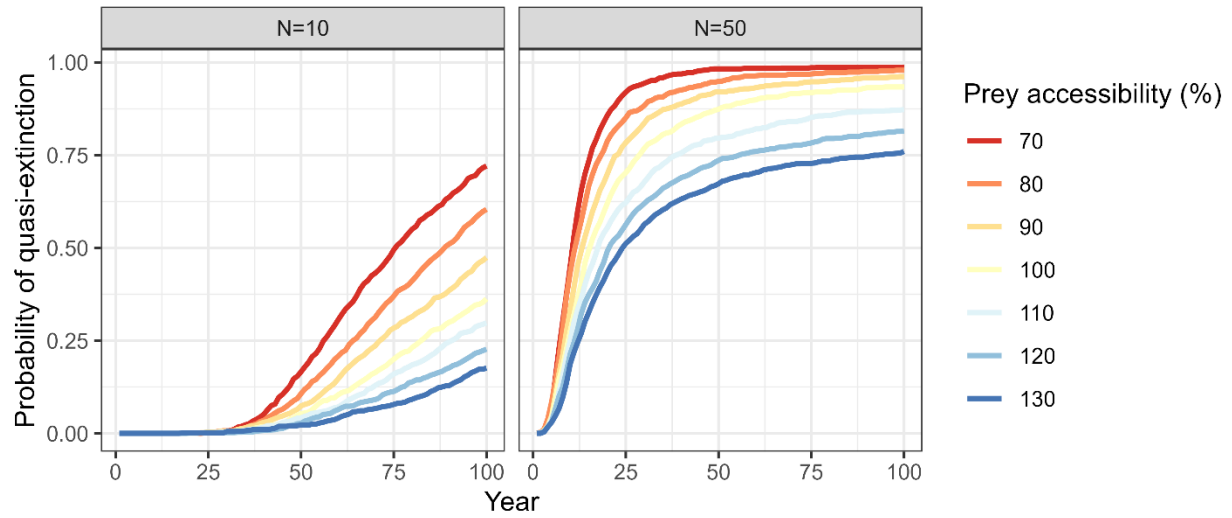


Figure 20. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females (individuals known to have produced calves) at thresholds of N=10 and N=50 individuals under various changes prey accessibility compared to the baseline 1 scenario.

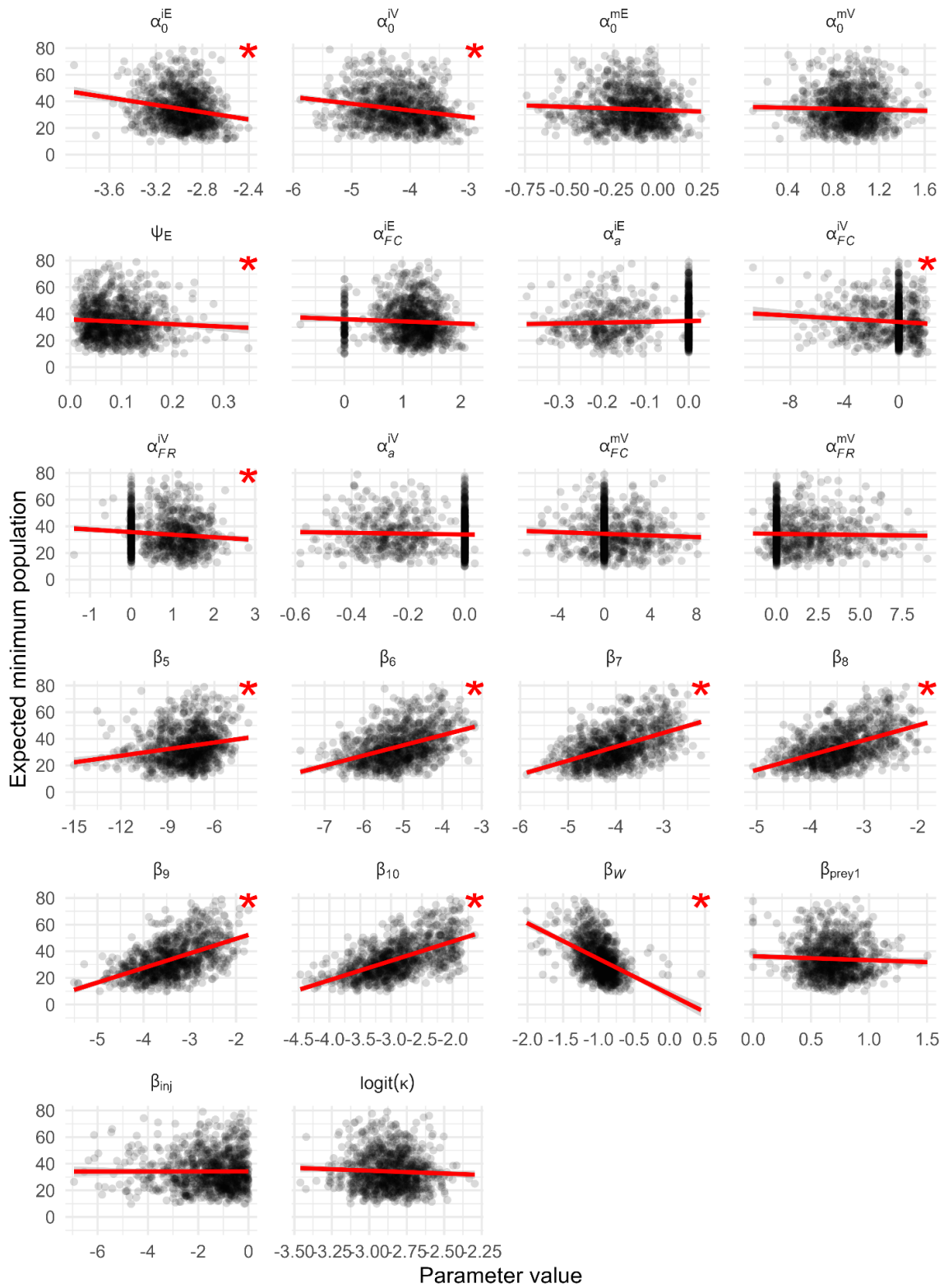


Figure 21. Expected minimum population size for North Atlantic right whales (NARWs; *Eubalaena glacialis*) as a function of the value of an individual parameter, for each of 1,000 replicates. Red lines represent the estimated regression lines, and red stars indicate regression coefficients deemed notable (p-value ≤ 0.05). For parameter definitions, see Table S1.

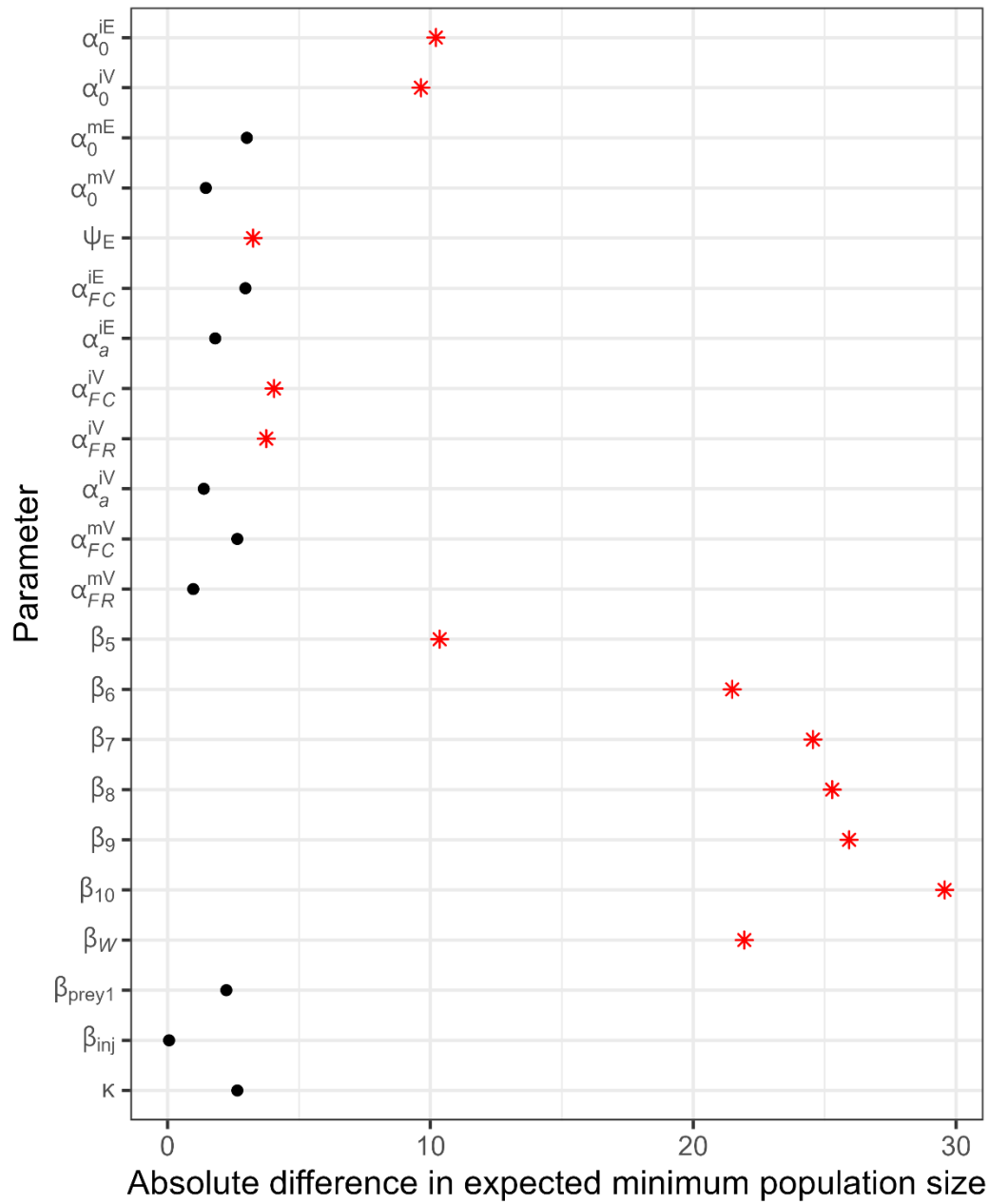


Figure 22. Absolute difference in expected minimum population size for North Atlantic right whales (NARWs; *Eubalaena glacialis*) between lower and upper 95% values for each parameter in the population projection model. Red stars indicate regression coefficients deemed notable (p-value ≤ 0.05). For parameter definitions, see Table S1.

Table 1. Probabilities of population decline or increase of various magnitudes for North Atlantic right whales (NARWs; *Eubalaena glacialis*) for each baseline scenario. The first 3 statistics correspond to metrics used by the International Union for the Conservation of Nature (probability [Pr] of the total population size declining by 30%, 50%, or 80% in 100 years). Also shown are the probability that the population size doubles within 35 years and the probability that the number of mature animals exceeds 1,000 within 100 years.

Scenario	Pr(decline over 100 yrs)			Pr(doubling in 35 yrs)	Pr(>1,000 in <100 yrs)
	30%	50%	80%		
Baseline 1	0.972	0.829	0.435	<0.001	<0.001
Baseline 2	0.645	0.458	0.135	<0.001	0.005
Baseline 3	0.254	0.141	0.033	0.012	0.098

Table 2. Probabilities of quasi-extinction for proven North Atlantic right whale (NARW; *Eubalaena glacialis*) females after 100 years at a threshold of 50 individuals under removal of the primary threats to the population.

Threat Present?			Pr(Quasi-Extinction)
Low Prey	Entanglement	Vessel Strike	
Present	Present	Present	0.934
Absent	Present	Present	0.875
Present	Absent	Present	0.053
Present	Present	Absent	0.343
Absent	Absent	Present	0.034
Present	Absent	Absent	<0.001
Absent	Present	Absent	0.245
Absent	Absent	Absent	<0.001

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APPENDIX

Supplemental Table S1. Variables and parameters include in the North Atlantic right whale (NARW; *Eubalaena glacialis*) Population Evaluation Tool (PET) model. For single parameters, the mean and 95% credible interval (CI) from the posterior distribution is provided.

Variable	Sections	Description	Mean	95% CI
M_X	Core stage-structured model (4.1)	Male in stage X		
F_X	Core stage-structured model (4.1)	Female in stage X		
$N_{X,t}^M$	Core stage-structured model (4.1)	Number of males in stage X in year t		
$N_{X,t}^F$	Core stage-structured model (4.1)	Number of females in stage X in year t		
n_t	Core stage-structured model (4.1)	Number of whales in each stage at time t		
A	Core stage-structured model (4.1)	Representation of transition probabilities in matrix form		
$S_X, S_{i,t}$	Core stage-structured model (4.1) and mortality submodel (4.2.2)	Probability of survival for stage X or probability of survival for individual i in year t		
$B_X, B, B_{i,t}$	Core stage-structured model (4.1) and reproduction submodel (4.2.3)	Probability of reproduction, either for primiparous female in stage X , for adult females, or for female i in year t , respectively		
κ	Core stage-structured model (4.1) and reproduction submodel (4.2.3)	Probability of calf loss in the roughly 6 months between birth and the anniversary date of the model (July 1 st)	0.055	0.040, 0.072
$h_{i,t}^{mN}$	Mortality submodel (4.2.2)	Mortality hazard rate due to natural causes for individual i in year t		
$h_{i,t}^{mE}$	Mortality submodel (4.2.2)	Mortality hazard rate due to entanglement for individual i in year t		

$h_{i,t}^{mV}$	Mortality submodel (4.2.2)	Mortality hazard rate due to vessel strike for individual i in year t		
α_0^{mE}	Mortality submodel (4.2.2)	Log-scale intercept for mortality hazard rate due to entanglement	-0.150	-0.545, 0.108
α_0^{mV}	Mortality submodel (4.2.2)	Log-scale intercept for mortality hazard rate due to vessel strike	0.944	0.531, 1.329
α_a^{mE}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (entanglement) for the effect of age (below age 5)	0.000	0.00, 0.00
α_a^{mV}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (vessel strike) for the effect of age (below age 5)	0.036	0.00, 0.324
α_{FC}^{mE}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (entanglement) for the effect of being a female with a calf	-0.040	-1.055, 0.561
α_{FC}^{mV}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (vessel strike) for the effect of being a female with a calf	0.536	-3.431, 5.145
α_{FR}^{mE}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (entanglement) for the effect of being a resting female	0.035	-0.428, 0.715
α_{FR}^{mV}	Mortality submodel (4.2.2)	Mortality hazard rate coefficient (vessel strike) for the effect of being a resting female	1.073	-0.267, 5.859
ε_t^{mE}	Mortality submodel (4.2.2) and environmental stochasticity (4.4.2)	Random normal effect of year t on mortality log hazard rate for entanglement		
ε_t^{mV}	Mortality submodel (4.2.2) and environmental stochasticity (4.4.2)	Random normal effect of year t on mortality log hazard rate for vessel strike		
$a_{i,t}^\dagger$	Mortality submodel (4.2.2), entanglement submodel (4.2.4), and vessel strike submodel (4.2.5)	Age of whale i in year t if that age is below 5; otherwise 5		
$W_{i,t}$	Mortality submodel (4.2.2), reproduction submodel,	Wound status of whale i in year t (0 = no severe wound; 1 = severe entanglement)		

	entanglement submodel (4.2.4), and vessel strike submodel (4.2.5)	wound; and 2 = severe vessel strike wound)		
$\mathbf{a}_{i,t}$	Reproduction submodel (4.2.3)	Vector of indicator variables for the stage of individual i in year t		
$I_{i,t}^{FC}$	Mortality submodel (4.2.2), entanglement submodel (4.2.4), and vessel strike submodel (4.2.5)	Indicator variable (1 if true and 0 if false) for individual i being a female with a calf in year t		
$I_{i,t}^{FR}$	Mortality submodel (4.2.2), entanglement submodel (4.2.4), and vessel strike submodel (4.2.5)	Indicator variable (1 if true and 0 if false) for individual i being a resting female in year t		
β_w	Reproduction submodel (4.2.3)	Coefficient for the effect of a severe wound on female reproduction	-1.514	-4.715, -0.046
$I_{i,t}^i$	Reproduction submodel (4.2.3) and entanglement submodel (4.2.4)	Indicator variable for individual i having a severe injury in year t (same as $W_{i,t} > 0$)		
$\beta_{p,1}$	Reproduction submodel (4.2.3)	Coefficient for the effect of prey at location 1 on female reproduction	0.695	0.334, 1.093
$\beta_{p,2}$	Reproduction submodel (4.2.3)	Coefficient for the effect of prey at location 2 on female reproduction	0.004	0.000, 0.044
$P_{t,l}$	Reproduction submodel (4.2.3) and prey submodel (4.2.6)	Normalized prey rolling average abundance for year t in location l		
ε_t^r	Reproduction submodel (4.2.3) and environmental stochasticity (4.4.2)	Random normal effect of year t on reproduction		
β_{stage}	Reproduction submodel (4.2.3)	Vector of reproductive intercept coefficients based on stage		
β_5	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 5	-7.817	-11.540, -5.288
β_6	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 6	-5.119	-6.553, -3.742

β_7	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 7	-3.984	-5.133, -2.782
β_8	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 8	-3.422	-4.531, -2.259
β_9	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 9	-3.384	-4.558, -2.191
β_{10}	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage 10	-2.907	-3.953, -1.925
β_w	Reproduction submodel (4.2.3)	Reproductive intercept coefficient for stage W	-0.996	-1.446, -0.623
$\Psi_{i,t}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Matrix of transition probabilities between injury states		
$\psi_{i,t}^{i0,i}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Probability of uninjured whale i obtaining a severe injury (of some type) in year t		
$\psi_{i,t}^{i0,iE}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Probability of uninjured whale i obtaining a severe injury from entanglement in year t		
$\psi_{i,t}^{iE,i0}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Probability of healing from a severe entanglement wound obtained in a previous year		
$h_{i,t}^{iE}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Hazard rate for obtaining severe wound from entanglement		
α_0^{iE}	Entanglement submodel (4.2.4)	Log baseline hazard rate for entanglement injury	-2.968	-3.376, -2.626
α_a^{iE}	Entanglement submodel (4.2.4)	Coefficient for the effect of age on entanglement injury hazard	-0.071	-0.295, 0.000
α_{FC}^{iE}	Entanglement submodel (4.2.4)	Coefficient for the effect of being a female with a calf on entanglement injury hazard	1.085	0.000, 1.791
α_{FR}^{iE}	Entanglement submodel (4.2.4)	Coefficient for the effect of being a resting female on entanglement injury hazard	-0.064	-1.560, 0.807
ε_t^{iE}	Entanglement submodel (4.2.4) and environmental stochasticity (4.4.2)	Random normal effect of year t on entanglement injury hazard		
Δ_t^{iE}	Entanglement submodel (4.2.4), entanglement scenarios (6.3.1)	Injury hazard change factor (entanglement)		

$\psi_{i,t}^{i0,iV}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Probability of uninjured whale i obtaining a severe vessel strike injury in year t		
$\psi_{i,t}^{iV,i0}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Probability of healing from a severe vessel strike wound obtained in a previous year		
$h_{i,t}^{iV}$	Entanglement submodel (4.2.4) and vessel strike submodel (4.2.5)	Hazard rate for obtaining severe vessel strike wound		
α_0^{iV}	Vessel strike submodel (4.2.5)	Log baseline hazard rate for vessel strike injury	-4.196	-5.258, -3.336
α_a^{iV}	Vessel strike submodel (4.2.5)	Coefficient for the effect of age on vessel strike injury hazard	-0.106	-0.444, 0.00
α_{FC}^{iV}	Vessel strike submodel (4.2.5)	Coefficient for the effect of being a female with a calf on vessel strike injury hazard	-0.502	-5.228, 1.609
α_{FR}^{iV}	Vessel strike submodel (4.2.5)	Coefficient for the effect of being a resting female on vessel strike injury hazard	0.759	0.00, 1.943
ε_t^{iV}	Vessel strike submodel (4.2.5) and environmental stochasticity (4.4.2)	Random normal effect of year t on vessel strike injury hazard		
Δ_t^{iV}	Vessel strike submodel (4.2.5) and vessel strike scenarios (6.3.2)	Injury hazard change factor (vessel strikes)		
Δ^N	Prey submodel (4.2.6), noise submodel (4.2.7), and noise scenarios (6.3.4)	Noise (prey accessibility) factor		
\mathbf{c}_t	Prey submodel (4.2.6)	Log-scale Calanus prey availability in the two locations ($c_{t,1}$ and $c_{t,2}$) for year t		
\mathbf{c}_y^h	Prey submodel (4.2.6) and prey data (5.1.3)	Log-scale Calanus prey historical data from the two historical locations for the same year y		
$C_{t,l}$	Prey submodel (4.2.6)	Log-scale Calanus prey accessibility in year t and location l , adjusted by noise factor Δ^N		

$prey_{t,l}$	Prey submodel (4.2.6)	Non-normalized 3-year rolling average log prey biomass in location l ending in year t		
\overline{prey}_l^h	Prey submodel (4.2.6)	Historical mean of rolling average prey biomass in location l		
$SD(pre_y_l^h)$	Prey submodel (4.2.6)	Historical standard deviation of rolling average prey biomass in location l		
n_{boot}	Stochasticity and uncertainty (4.4)	Number of bootstrap runs for the PET model to propagate parametric uncertainty (currently set at 1000)		
n_s	Stochasticity and uncertainty (4.4)	Number of scenarios to run through		
n_{rep}	Stochasticity and uncertainty (4.4)	Number of replicates per bootstrap run (currently set at 1)		
T	Stochasticity and uncertainty (4.4)	Number of years to run each simulation (currently set to 100)		
σ^r	Environmental stochasticity (4.4.2) and reproduction analysis (5.3)	Temporal standard deviation for logit reproductive probability	0.899	0.587, 1.309
σ^{iE}	Environmental stochasticity (4.4.2) and mortality analysis (5.2)	Temporal standard deviation for injury log hazard rate for entanglement	0.155	0.009, 0.422
σ^{iV}	Environmental stochasticity (4.4.2) and mortality analysis (5.2)	Temporal standard deviation for injury log hazard rate for vessel strike	0.383	0.100, 0.751
N_t	Output metrics (4.5) and initial population size and structure (5.4)	Total abundance in year t		
N_t^P	Abundance (4.5.1)	Total “proven” females (the number of females alive that have successfully produced a first-year calf) in year t		
Q	Probability of quasi-extinction (4.5.2)	Quasi-extinction threshold		
C	Probability of population decline (4.5.4)	Critical threshold of population decline		
N_0	Probability of population decline	Total initial abundance	362	345-378

	(4.5.4) and initial population size and structure (5.4)			
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