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Research article

Estimating the effects of stressors on the health, survival and reproduction of a critically endangered, long-lived species

Enrico Pirotta[1], Robert S. Schick[2], Philip K. Hamilton[3], Catriona M. Harris[1], Joshua Hewitt[4], Amy R. Knowlton[3], Scott D. Kraus[3], Erin Meyer-Gutbrod[5], Michael J. Moore[6], Heather M. Pettis[3], Theoni Photopoulou[1], Rosalind M. Rolland[3], Peter L. Tyack[7] and Len Thomas[1]

[1]Centre for Research into Ecological and Environmental Modelling, Univ. of St Andrews, St Andrews, UK
[2]Marine Geospatial Ecology Lab, Nicholas School of the Environment, Duke Univ., Durham, NC, USA
[3]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, MA, USA
[4]Dept of Statistical Science, Duke Univ., Durham, NC, USA
[5]School of Earth, Ocean and Environment, Univ. of South Carolina, Columbia, SC, USA
[6]Biology Dept, Woods Hole Oceanographic Inst., Woods Hole, MA, USA
[7]School of Biology, Scottish Oceans Inst., Univ. of St Andrews, St Andrews, UK

Correspondence: Enrico Pirotta (ep343@st-andrews.ac.uk)

Quantifying the cumulative effects of stressors on individuals and populations can inform the development of effective management and conservation strategies. We developed a Bayesian state–space model to assess the effects of multiple stressors on individual survival and reproduction. In the model, stressor effects on vital rates are mediated by changes in underlying health, allowing for the comparison of effect sizes while accounting for intrinsic factors that might affect an individual's vulnerability and resilience. We applied the model to a 50-year dataset of sightings, calving events and stressor exposure of critically endangered North Atlantic right whales *Eubalaena glacialis*. The viability of this population is threatened by a complex set of stressors, including vessel strikes, entanglement in fishing gear and fluctuating prey availability. We estimated that blunt and deep vessel strike injuries and severe entanglement injuries had the largest effect on the health of exposed individuals, reinforcing the urgent need for mitigation measures. Prey abundance had a smaller but protracted effect on health across individuals, and estimated long-term trends in survival and reproduction followed the trend of the prey index, highlighting that long-term ecosystem-based management strategies are also required. Our approach can be applied to quantify the effects of multiple stressors on any long-lived species where suitable indicators of health and long-term monitoring data are available.

Keywords: cumulative effects, health, multiple stressors, North Atlantic right whale, population consequences, state space modelling

Introduction

Increasing human activities in the ocean and on land generate multiple, diverse stressors that can affect wildlife populations through a variety of pathways (Simmons et al. 2021). Some stressors, such as hunting or fishing, have direct, immediate effects on the survival and reproduction of individuals, while others, such as habitat degradation or chemical pollution, affect vital rates through protracted changes in different aspects of individual health (Kophamel et al. 2022, Pirotta et al. 2022). Assessing this suite of effects using purely empirical approaches is often challenging, especially for species that are already at risk, because low population density implies low statistical power and precludes invasive research techniques. For long-lived, wide-ranging species, the difficulties in monitoring individuals for sufficient time to detect an effect also limit the utility of observational approaches for addressing pressing conservation needs (Taylor et al. 2007). In these situations, information about the mechanisms through which stressors operate, and lead to adverse outcomes, can be incorporated into more process-driven analyses (Pirotta et al. 2022). In particular, theoretical frameworks outlining the conceptual cascades between exposure to stressors and the long-term effects on individual vital rates and, ultimately, population dynamics can be used to guide model structure (Ankley et al. 2010, National Academies 2017, Pirotta et al. 2018, Wilson et al. 2020). These mechanistic pathways describe the accumulation of effects into multiple variables that comprise an individual's health status (e.g. energetic, immune, organ or endocrine status). Health variables are informed using indicators that, thanks to technological advancements, can increasingly be measured even in wild animals (Ryan et al. 2007, Kophamel et al. 2022).

Quantifying the cumulative effects of anthropogenic stressors on populations is critical for the development of effective management strategies (Brown et al. 2014, Côté et al. 2016, Tyack et al. 2022). Stressors may differ in the risk they present to a population, the possibility of mitigation and the desirability of the activities that generate them. For example, some stressors result from activities with broad environmental and societal benefits (e.g. renewable energy developments), while others are legacies of past activities that may not be easily reduced in short timeframes (e.g. persistent organic pollutants). Being able to quantify and compare the size of stressor effects will inform alternative management scenarios; specifically, predictions help prioritize efforts to mitigate those stressors that have the greatest potential for reducing the risk for a population to an acceptable level (Pirotta et al. 2022).

North Atlantic right whales *Eubalaena glacialis* (hereafter, right whales) are exposed to many anthropogenic stressors due to their distribution in the coastal waters of the US and Canada, and have thus been nicknamed 'the urban whale' (Kraus and Rolland 2007). Right whales typically forage in waters off New England and the Canadian Maritimes in the spring, summer and fall (Kenney et al. 1995, Baumgartner et al. 2003, Mayo et al. 2018, Davies et al. 2019). Recent climate-driven shifts in right whale prey distribution are linked to increased use of southern New England (Quintana-Rizzo et al. 2021) and the Gulf of St. Lawrence (Crowe et al. 2021), and a shift out of previously used habitats such as the Great South Channel and the Bay of Fundy (Meyer-Gutbrod et al. 2022). Their wintertime distribution is less understood, but a subset of the population migrates to calving grounds off the coast of the southeast US (Keller et al. 2012). When conditions are good, adult females can give birth to a calf every three years (Kraus et al. 2001), but average birthing intervals tend to be much longer (Meyer-Gutbrod et al. 2015, Christiansen et al. 2020).

Due, in part, to their coastal habitat, right whales were harvested by whalers for centuries and their population was decimated (Reeves et al. 1999). Despite targeted conservation measures and a slow recovery until 2010, the species is now declining and listed as Critically Endangered (Cooke 2020). A complex set of stressors threatens their viability (Moore et al. 2021). Individuals are struck by vessels, which can lead to death or serious injury (Sharp et al. 2019). They frequently get entangled in fishing gear, which can cause mortality (Knowlton et al. 2012) or have sublethal effects depending on injury severity (Knowlton et al. 2022). When fishing gear remains attached to the whale for prolonged periods of time, increased drag imposes additional locomotion and energetic costs that may compromise the ability to survive or reproduce successfully (van der Hoop et al. 2017). Energy budgets are also affected by variability in the distribution and availability of their copepod prey (primarily *Calanus finmarchicus*), which has been linked with female reproductive success (Meyer-Gutbrod et al. 2015). Likely as a result of energetic effects, total body lengths have decreased over time (Stewart et al. 2021), which further impacts reproductive output (Stewart et al. 2022). Whales are also exposed to anthropogenic noise (Hatch et al. 2012), chemical pollutants and biotoxins (Doucette et al. 2012), which can compromise health (e.g. through chronic stress; Rolland et al. 2012). However, assessing exposure levels and linking them to measurable health variables is more challenging (Moore et al. 2021).

While several studies have detected changes in right whale vital rates associated with some of these stressors (Rolland et al. 2016, Meyer-Gutbrod et al. 2021, Knowlton et al. 2022), their effects have never been evaluated and compared within the same integrated model. In this study, we build upon the methods to estimate right whale health and anthropogenic effects in Schick et al. (2013), Rolland et al. (2016) and Knowlton et al. (2022), using a 50-year dataset of right whale sightings, calving events and exposure to stressors to inform a Bayesian state–space model for individual health, survival and reproduction. The model includes the effects of multiple key stressors on underlying health, allowing a direct comparison of their effects in the context of other life-history events that may challenge an individual. The availability of long-term individual data makes this a powerful case study to illustrate the development of a process-driven approach that explicitly outlines components of the mechanistic cascade between exposure to specific stressors and vital rates through changes in health.

Material and methods

Data

A long-term dataset (1970–2020) of on-survey and opportunistic sightings of individual right whales is curated by the New England Aquarium, and access is provided through the North Atlantic Right Whale Consortium (NARWC) (<www.narwc.org/narwc-databases.html>). Photographs of individual whales taken at each sighting are matched to an existing catalogue to assign an individual ID. Photographs are also used to support a visual health assessment (VHA) based on four categorical variables, which are scored using an ordinal scale: body condition and the presence of rake marks forward of the blowholes are scored as one of three categories (poor, fair or good), while the presence of cyamids around the blowholes and skin condition are scored using two categories (poor or good). Ancillary data are available on the sex, age class and calving status of each individual (Pettis et al. 2004). More details on the sighting and VHA data are provided in Schick et al. (2013) and Pettis et al. (2017). Researchers at the New England Aquarium also collate and process information on anthropogenic traumas. Specifically, for all entanglements in fishing gear, data include when the injury was first detected, the last sighting pre-injury, whether fishing gear was still attached to the animal, the first subsequent sighting without gear (if gear was attached) and the severity of the injuries (minor, moderate or severe) (details in Knowlton et al. 2012, 2022). Similarly, for vessel strikes, data include the date of detection of an injury, the last sighting pre-injury and the type of injury (superficial, shallow or deep cuts, or blunt injury, which was scored if a necropsy found evidence of internal trauma). Finally, for the temporal variation in prey abundance, we used data from the Continuous Plankton Recorder (CPR) survey in the Gulf of Maine (1961–2017), which previous studies found to be associated with right whale reproduction (Meyer-Gutbrod et al. 2015). Specifically, a time series of annual anomalies of late-stage *Calanus finmarchicus* abundance was calculated following Pershing et al. (2005) (hereafter prey abundance index). More details of the CPR data and the resulting prey index are provided in Meyer-Gutbrod et al. (2015).

Data processing

All data streams were initially processed at a monthly scale and then summarised over fixed three-month intervals for the analysis (Dec–Feb, Mar–May, Jun–Aug, Sep–Nov). During each month in the study period, an individual could be sighted or not, and, when sighted, scores were available for none, some or all four VHA variables. Individuals with a short sighting history (≤ 6 months) or no VHA information were removed from further analyses. Females could be sighted with calves, but the start and duration of each lactation period were uncertain. As an average estimate, we assumed lactation lasted from January to December of a calving year (Hamilton and Cooper 2010); except when a calf was first sighted in the later part of the previous year, in which case those months were also included (note that the birth year for these calves was assigned to the subsequent year). In the Supporting information we explore the use of an alternative estimate, where a female was only assumed to be lactating between the first and last sighting with a calf. Similarly, we assumed that a calf transitioned to juvenile status (i.e. no longer depending on the mother for nutrition) in the Dec–Feb interval at the end of the birth year. A female was marked as pregnant in the year before a calving year and as resting in the following year (Rolland et al. 2016). In all other years, and after sexual maturity, she was considered available to reproduce. Maturity was defined as a known age of nine years or greater, the year before the first observed calving event, or a sighting history greater than eight years (Hamilton et al. 1998). Some individuals are known to be females but have never been seen with a calf over a variable number of years after their estimated maturity (Moore et al. 2021, Bishop et al. 2022). Females of unknown maturity status and females with too short a sighting history to determine available calving years or a lagged relationship with health were excluded from the reproduction component of the analysis.

For each entanglement event, we calculated the most likely estimate of its start date as the expected date given the last sighting without gear or injury, the first sighting with gear attached or an injury, and the probability of becoming entangled on each day (derived from Knowlton et al. 2012; Supporting information). Similarly, we estimated the date when the gear was most likely to have been shed (our aim was to place these dates in the correct three-month period; for details, see the Supporting information, where we also explore the results of using a minimum and maximum estimate of entanglement duration). For vessel strikes, we assumed that an event occurred within the same three-month period of its detection (but see the Supporting information for the results when we assumed that a strike occurred just after the last pre-injury sighting).

The final dataset included 74 907 sightings of 729 individual whales (314 known females, 364 known males and 51 individuals of unknown sex) from 1970 to 2020 where information on ID and sighting date was available. These resulted in 53 517 three-month modelled intervals, 33% of which had some associated VHA data. Data prior to 1980 were scarce, which likely affected the uncertainty around estimated health in early years. Fifty-nine percent of individuals (427) were first sighted as calves and were thus of known age. VHA data were available until 2019, but sighting data until November 2020 were included in the analysis because they contributed to inform survival. Of the 238 known sexually mature females with a sufficiently long sighting history, 178 were observed with at least one calf. The data included 1706 entanglement events (130 with gear attached, and 1576 where only scarring was observed) and 81 vessel strikes, while the prey abundance index was missing for five years (1975, 1976 and 2018–2020).

Model overview

We developed a state–space model for the health, survival and reproduction of individual whales over the course of their sighting history, building on the state–space model by Schick et al. (2013). State–space models comprise a process model for the time series of latent variables representing the state of the system, and one or more observation models describing how these hidden quantities are observed or measured to generate the available data (Auger-Méthé et al. 2021). This approach was suitable for our application because we were interested in estimating the underlying health of an individual, which varies over time and can only be observed imperfectly using health markers. State–space models are also particularly conducive to the incorporation of mechanistic knowledge (Auger-Méthé et al. 2021), which is useful to inform predictions of how the system will behave in the future under varying conditions. Here, the process model included the effects of covariates on health (juvenile status, lactation status and the stressors under analysis) and the relationships between health and the two vital rates (survival and calving), while the observation model linked underlying health to each of the four variables of the VHA, and survival to individual sightings (Fig. 1).

Process model

We modelled the latent health of an individual ($i = 1, 2, ..., N$, where $N = 729$) in a three-month time step ($t = 2, 3, ..., T_i$), $h_{i,t}$, as a function of health in the previous time step and a series of intrinsic ($Z_{j,i,t}$, with $j = 1, 2$) and extrinsic ($W_{k,i,t}$, with $k = 1, 2, ..., 9$) covariates:

$$h_{i,t} \sim \text{Normal}\left(h_{i,t-1} + \sum_{j=1}^{2} \alpha_j \times Z_{j,i,t} + \sum_{k=1}^{9} \beta_k \times W_{k,i,t}, \sigma \right) \quad (1)$$

where α_j and β_k indicate the effects of each intrinsic and extrinsic covariate, respectively, and σ is the process standard deviation. Preliminary analyses suggested that the model was mixing poorly when σ was estimated from the data. The final model thus uses the fixed value $\sigma = 0.1$, which is the upper range of σ's estimated value (0.08–0.10) to improve mixing of additional parameters (see details in the Supporting information, where we also explore the use of a smaller or larger value of σ).

Intrinsic covariates included the effect of the transition from calf to juvenile status (i.e. $Z_{1,i,t} = 1$ in the Dec–Jan–Feb interval at the end of the birth year, and 0 otherwise) and the proportion of a three-month interval spent in lactation status (i.e. $Z_{2,i,t}$ varied between 0 and 1 depending on how many months in an interval a female was nursing a dependent calf). The former was modelled to affect only one interval because we expected a juvenile to suffer an initial drop in health when weaned but subsequently recover as time progressed. In contrast, lactation was modelled to affect the health of a female in all intervals during which she was delivering milk, because a female incurs an energetic cost throughout the lactation period. Extrinsic covariates included the effect of
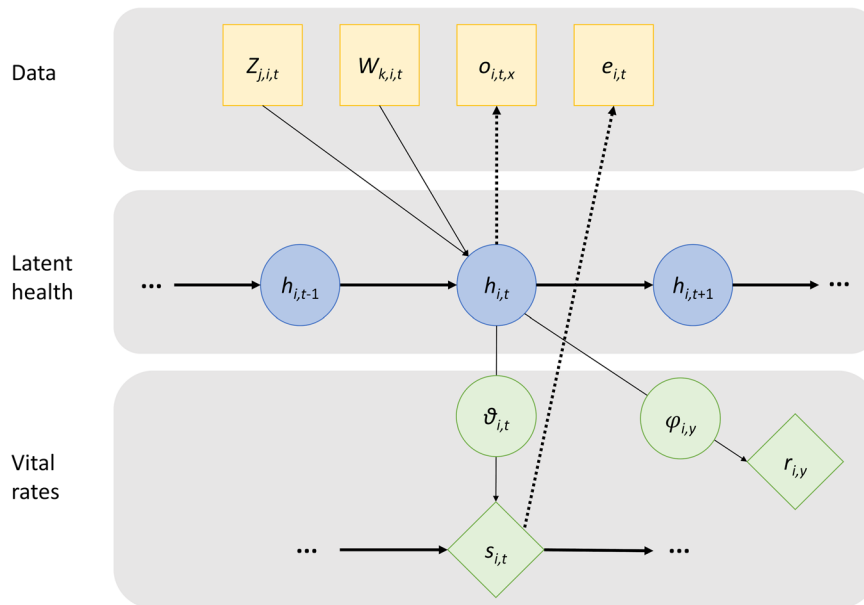

Figure 1. Schematic representation of the model. The yellow boxes indicate the data streams, including intrinsic ($Z_{j,i,t}$) and extrinsic ($W_{k,i,t}$) covariates affecting health (solid arrows; j and k indicate each intrinsic and extrinsic covariate, respectively), and the observation models (VHA data $o_{i,t,x}$, where x indicates each of the four VHA variables, and sightings $e_{i,t}$; dotted arrows). The blue circles represent the time series of latent health, $h_{i,t}$, for individual i at time t. Health affects survival probability $\vartheta_{i,t}$ in time step t and calving probability $\varphi_{i,y}$ in available years y (green circles), which determine the time series of the two vital rates (survival $s_{i,t}$ and calving $r_{i,y}$, green diamonds).

entanglements, vessel strikes and the prey abundance index. Specifically, entanglements can result in an individual carrying gear for prolonged periods (i.e. $W_{1,i,t}$ varied between 0 and 1, indicating the proportion of time the gear was attached over a three-month period), but can also cause immediate effects on health that differ with the severity of the event (a factor with three levels, indicated by dummy variables $W_{2,i,t}$, $W_{3,i,t}$ or $W_{4,i,t}$, which could take value 1 in the interval when an event occurred depending on whether it was scored as minor, moderate or severe, respectively, and were 0 otherwise; see the Supporting information where we explore a differential effect of entanglements on males and females). Vessel strikes can also cause an immediate effect on health that differs depending on the injury type (a factor with four levels, indicated by $W_{5,i,t}$, $W_{6,i,t}$, $W_{7,i,t}$, $W_{8,i,t}$, which could take value 1 or 0 in the interval when a strike occurred, depending on whether the injury was scored as blunt, or deep, shallow or superficial cuts, respectively). Finally, the annual prey abundance index ($W_{9,i,t}$) in the Gulf of Maine was modelled to affect individual health in the Jun–Jul–Aug interval (see the Supporting information for details of preliminary analyses that included the influence on all three-month intervals). There were missing values in this covariate, which were assigned a uniform prior between the minimum and maximum observed values.

Latent health corresponded to the probability of surviving to the end of the current time step, $\vartheta_{i,t}$, on the complementary log–log (cloglog) link scale:

$$\text{cloglog}\left(\vartheta_{i,t}\right) = h_{i,t} \tag{2}$$

$$s_{i,t} \sim \text{Bernoulli}\left(\vartheta_{i,t} \times s_{i,t-1}\right) \tag{3}$$

where survival $s_{i,t} = 1$ when the individual was alive, and 0 when it was dead. A cloglog link was preferred over other link functions because it improved mixing in preliminary explorations. Survival was set to 1 for all time steps between the first and last sighting of an individual and to 0 when an individual was found dead. Survival status was unknown and estimated for intervals between the last sighting and an observed death, or for one year after the last sighting (in the Supporting information we investigate the use of a longer period). Note that, because of model formulation, predictions of latent health should only be considered when an individual is estimated to be alive.

If individual i was female, the probability of giving birth to a calf on a year y when she was available to calve (i.e. alive, sexually mature, not pregnant and not resting; $\varphi_{i,y}$) was modelled as a sigmoid function of health at some lag (l) prior to y:

$$\varphi_{i,y} = g_i \times \left(\frac{m_i}{1 + e^{-\delta \times \left(h_{i,l} - \mu\right)}} \right) \tag{4}$$

$$r_{i,y} \sim \text{Bernoulli}\left(\varphi_{i,y} \times s_{i,y}\right) \tag{5}$$

where $r_{i,y} = 1$ when the individual was seen with a calf on year y, 0 when it was sighted on that year but never with a calf, and NA otherwise; m_i is the maximum calving probability for that individual (i.e. the asymptote of the sigmoid relationship), δ drives the steepness of the sigmoid relationship and μ is the value of health at which calving probability is 50% of the maximum. The binary variable g_i indicates whether an individual is part of the cohort of reproductive females (i.e. females that have already calved or may do so in the future). This was set to 1 for any female who was observed with at least one calf, while it was estimated for other females. In particular:

$$g_i \sim \text{Bernoulli}\left(\nu\right) \tag{6}$$

where ν is the average probability of individuals being part of the cohort of reproductive females. The individual random effect on the asymptote was modelled as a truncated normal distribution with mean λ and standard deviation χ:

$$m_i \sim \text{Truncated Normal}\left(\lambda, \chi\right)\left[0,1\right] \tag{7}$$

We assumed that the probability of calving was affected by health at the end of pregnancy (i.e. in the Sep–Oct–Nov interval prior to the calving year), while in the Supporting information we report the results when assuming that this probability was affected by health during the previous feeding season (Jun–Jul–Aug) or at the start of pregnancy (Dec–Feb–Jan of the previous year). We also explore a direct effect of the prey abundance index on calving probability in the Supporting information.

Observation model

The probability of sighting an individual alive in a time step was equal to sighting probability ρ multiplied by its survival state (i.e. whether the individual was currently alive),

$$p_{i,t} = \rho \times s_{i,t} \tag{8}$$

A sighting then emerged from a random Bernoulli draw:

$$e_{i,t} \sim \text{Bernoulli}\left(p_{i,t}\right) \tag{9}$$

Note that, under this formulation, $e_{i,t} = 0$ when an individual was sighted as dead.

The four ordinal variables comprising the VHA (indicated below by subscript x) provided irregular observations of an individual's health. For each variable, a lower category was assumed to correspond to poorer health. Skin condition and cyamid presence have two categories, while body condition and rake marks have three categories. Cyamid presence was only assessed for non-calf individuals, i.e. individuals

older than one year, because calves tend to have high levels of cyamids from the interaction with the mother during lactation (Knowlton unpubl.). The probability of observing the first category of each variable ($\eta_{i,t,x,1}$), corresponding to the poorest health score, was expressed as a function of health using a logistic formulation, i.e.:

$$\text{logit}\left(\eta_{i,t,x,1}\right) = \gamma_{x,1} + \omega \times h_{i,t} \tag{10}$$

where $\gamma_{x,1}$ is an intercept parameter and ω controls the effect of health on the probability of observing this category. For variables with two categories, the probability of observing the second category was simply:

$$\eta_{i,t,x,2} = 1 - \eta_{i,t,x,1} \tag{11}$$

For variables with three categories, the probabilities of observing the second and third category were expressed using an ordinal logit formulation, i.e.:

$$\text{logit}\left(Q_{i,t,x}\right) = \gamma_{x,2} + \omega \times h_{i,t} \tag{12}$$

$$\eta_{i,t,x,2} = Q_{i,t,x} - \eta_{i,t,x,1} \tag{13}$$

$$\eta_{i,t,x,3} = 1 - Q_{i,t,x} \tag{14}$$

where $\gamma_{x,2}$ was constrained to be greater than $\gamma_{x,1}$. For increasing health, the probability of observing higher categories was expected to increase, i.e. we expected ω to be negative (also note that ω was the same across health variables). Given the number of categories for a variable (c), up to 3 ordinal observations (one per month) $o_{i,t,x,1:V_{i,t,x}}$ resulted from a multinomial draw with probabilities $\eta_{i,t,x,1:c}$, where $V_{i,t,x}$ was the number of observations for that variable in that time step:

$$o_{i,t,x,1:V_{i,t,x}} \sim \text{Multinomial}\left(\eta_{i,t,x,1:c}, V_{i,t,x}\right) \tag{15}$$

Bayesian inference

The model was fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC) algorithms implemented in software JAGS ver. 4.3.0, run through package runjags (Denwood 2016) for R (www.r-project.org). The data were vectorized to improve computation times. Prior distributions for all model parameters are listed in the Supporting information. Five chains were started at different initial values and iterated in parallel for 100 000 iterations after the adaptation phase (5000 iterations). Given reasonable initial values, burn-in was rapid and convergence was achieved within the adaptation phase, so that all subsequent samples could be

used to approximate the posterior distribution. Chains were thinned by retaining 1 in 10 iterations to ensure manageable object sizes. Convergence and mixing were assessed by visually inspecting trace and density plots. We also ensured that the Brooks–Gelman–Rubin diagnostic fell below 1.1 and that the Monte Carlo error was less than 5% of the sample standard deviation. The selected number of chains and iterations led to an effective sample size > 400 for all parameters (Lunn et al. 2013). The R code to run the model is available via the Open Science Framework (https://osf.io/ert85/).

Results

The process model returned a time series of estimated health for each individual. The time series had a median duration of 64 three-month intervals, ranging between 7 and 200 (i.e. between 1.75 and 50 years). Across individuals, health underwent a gradual increase up to 1990, followed by a sharper decline until 2000. Health then stabilised, although a new decline might have started in the last decade (Fig. 2a). This trend shows some similarities to the trend in the prey abundance index (Fig. 2b). Individuals that did not experience any entanglement or vessel strike were in better health, on average, but the temporal trend was broadly comparable to individuals that did (Fig. 2c). The observation models indicated that all VHA variables contributed to inform underlying health.

Survival (i.e. the inverse cloglog transformation of health) was high at the three-month scale, but varied more widely when raised to the power of 4 and converted to the yearly scale (the posterior mean ranged between 0.14 and > 0.99, although remaining above 0.91 in 95% of time steps across individuals). The probability of sighting an individual when alive in a three-month interval was estimated to be 0.370 (95% confidence interval: 0.366–0.375). Calving probability in available years declined to zero for individuals in poor health ($h_{i,t} < 1$), increased rapidly over intermediate health values, and reached a mean asymptotic probability of 0.38 (95% confidence interval: 0.29–0.44) when in good health ($h_{i,t} > 1.7$), although inter-individual variation was large (0.09–0.72; Fig. 3a). Because survival and calving probability are both linked to health, it is possible to express calving probability as a function of survival probability (Fig. 3b): individuals with annual survival probability < 0.9 were estimated rarely to breed, while maximum calving probability occurred at mean survival probability of approximately 0.97. The trend in annual survival was comparable to that of health and highlighted the decline in recent years (Fig. 4a). However, calving probability in available years was estimated to have decreased consistently over the study period, with only a brief period where the decline slowed down in the early 2000s (Fig. 4b).

The effects of intrinsic and extrinsic covariates are summarised in the Supporting information and Fig. 5. Because the relationships between health and vital rates were nonlinear, the consequences of these effects for survival and
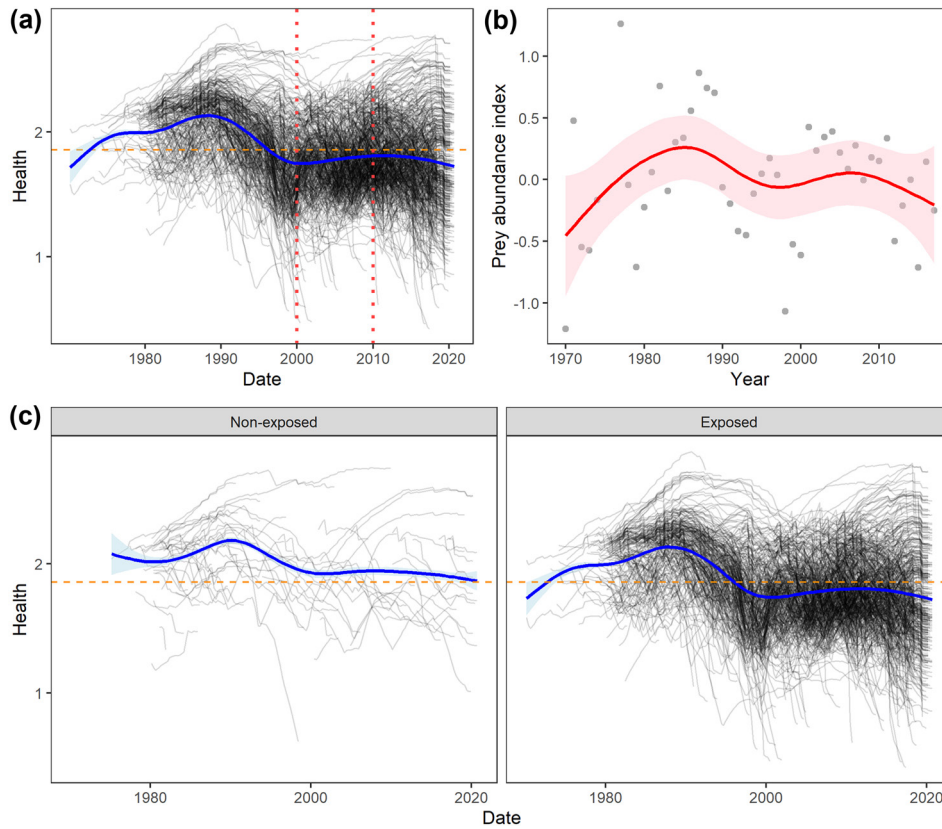
Figure 2. Estimated health of individuals (a and c) and prey abundance index (b) over the study period. In (a and c), each grey line corresponds to the estimated health trajectory for one individual, when median survival was 1 (i.e. the individual was estimated to be alive). In (c), the time series are plotted separately for individuals that experienced entanglements or vessel strikes ('exposed') and individuals that did not ('non-exposed'). The dashed orange line indicates the mean estimated health across all individuals. The time series were smoothed for plotting using a cubic spline. In (a), the dotted red lines indicate salient moments in the recent history of the species: the end of a period of health decline in the 1990s, and the start of a new decline around 2010.
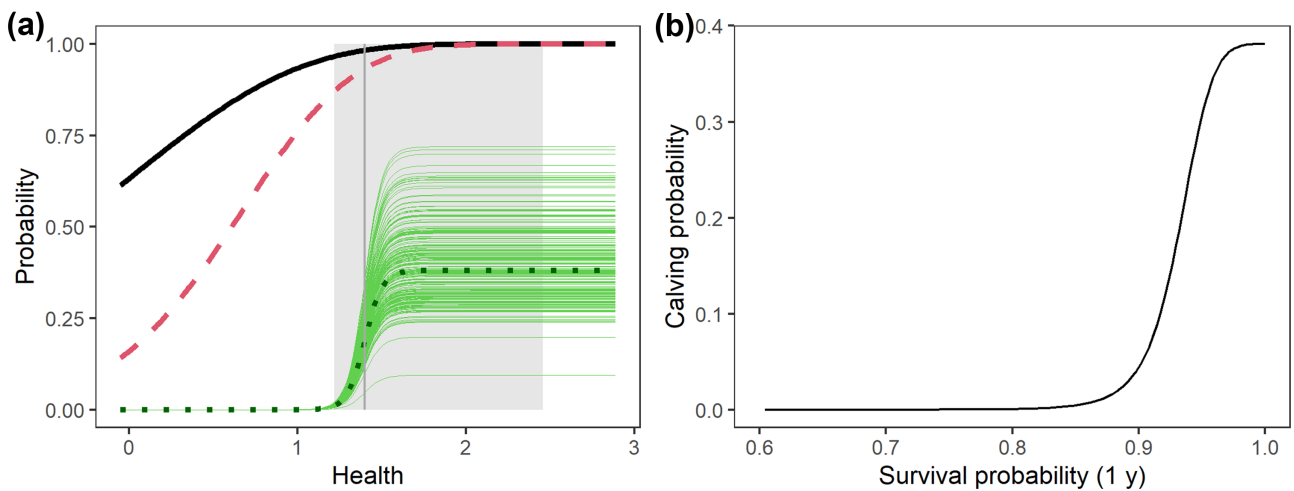

Figure 3. In (a), estimated relationships between health and three-month survival probability (black, solid line), annual survival probability (red, dashed line) and calving probability (mean and individual random effects; dotted and solid green lines, respectively); the shaded area represents the range of 95% of the posterior mean health estimates, while the vertical grey line indicates the health value corresponding to half of the asymptotic calving probability across individuals. In (b), relationship between annual survival probability and mean calving probability.
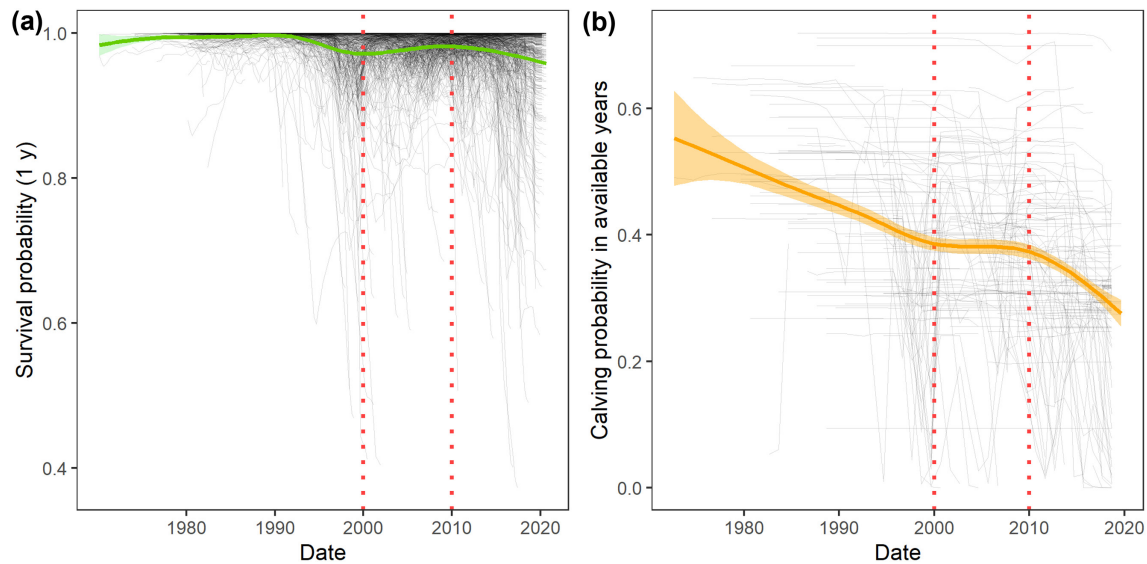
Figure 4. Individual annual survival probability (a) and calving probability in available years (b) over the study period. Each grey line corresponds to the time series of estimated vital rates for one individual, when median survival was 1 (i.e. the individual was estimated to be alive). Survival and calving probabilities were computed from estimated health and their time series were smoothed using a cubic spline. The dotted red lines indicate salient moments in the recent history of the species: the end of a period of health decline in the 1990s, and the start of a new decline around 2010.

calving probability varied depending on health (i.e. an individual in good health was less affected by a stressor than an individual in poorer health). Here, we discuss all effects with respect to $h_{i,t} = 1.4$, as this health value corresponds to half of the asymptotic calving probability across individuals and is the value at which effects are maximised. For ease of interpretation, we also convert effects to the resulting change in annual survival and, where relevant, calving probability in available years (with the mean asymptote), reporting the mean effect and the posterior 95% confidence interval. The transition from calf to juvenile caused a drop in health that corresponded to a 0.04 (0.03–0.06) decrease in annual survival. Lactation also exerted a cost to health: an average lactation event, lasting 3.67 three-month periods, resulted in a 0.05 (0.03–0.06) drop in the mother's annual survival. The prey abundance index was associated with a variation in annual survival between 0.919 (0.912–0.925) and 0.944 (0.940–0.948) (given a mean survival probability of 0.933 when the index was 0, which represents the average prey value over the reference period). In terms of reproduction, a poor prey year could result in a reduction in calving probability in an available year from a mean of 0.19 to as low as 0.10 (0.07–0.14), whereas in a good prey year it could increase to 0.27 (0.24–0.29). Entanglement events had a prolonged effect on health when the gear remained attached to the body: if the animal carried the gear for an entire three-month period, its annual survival probability declined by approximately 0.004 (0.001–0.007) and its calving probability by 0.03 (0.01–0.05). However, the 95% confidence interval for this effect was bound at 0, suggesting that there was a small probability (< 2.5%) that it was 0. The posterior distribution of the immediate effects of minor and moderate

entanglement events overlapped with 0, while it did not for severe events. Severe entanglements led to a change in health that corresponded to a drop in annual survival probability by 0.21 (0.17–0.25). The protracted effect of carrying gear showed some posterior negative correlation with the immediate effects of minor, moderate and severe events (−0.47, −0.24 and −0.23, respectively). Vessel strikes led to a drop in annual survival of 0.61 (0.43–0.76), 0.19 (0.10–0.29) or 0.08 (0.01–0.17) when associated with blunt, deep or shallow wounds, respectively. The effect overlapped with 0 for strikes associated with superficial wounds.

As a result of these effects, the health trajectory varied widely among individuals, reflecting their time series of life-history events, anthropogenic traumas and variation in prey availability (Fig. 6, Supporting information).

Discussion

We developed a Bayesian state–space model for the survival and reproduction of individuals in a long-lived species, where the cumulative effects of intrinsic and extrinsic factors on these vital rates are mediated by changes in individual health. We then applied the model to quantify the consequences of a set of key stressors on the individual life-history performance of critically endangered North Atlantic right whales.

The latent health of an individual acts to integrate the effects of stressors operating along different response pathways and at different temporal scales (Pirotta et al. 2022; e.g. the protracted effect of reduced energy acquisition in years of poor prey availability, compared to the immediate effect of a deep injury resulting from a vessel strike). Explicitly
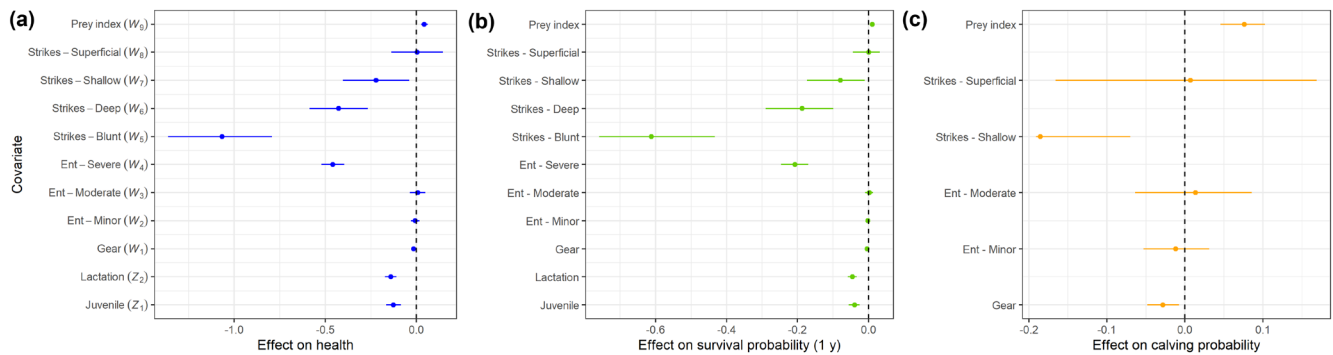
Figure 5. Effect sizes (posterior mean and 95% confidence intervals) of intrinsic and extrinsic covariates on individual health in a three-month interval (a), annual survival probability (b) and calving probability in an available year (c). Stressors resulting in a large effect on annual survival probability (< -0.1) are excluded from panel (c), because these are likely or known to lead to death. The effects of lactation and of the transition from calf to juvenile are also excluded from panel (c), because these do not apply to females in years when they are available to calve. The effect of attached gear is reported assuming that this lasted for an entire three-month interval. The effect of lactation is reported for the average duration of a lactation event (3.67 three-month periods). The effect of the prey index is reported for the best prey year in the time series ($W_9 = 1.3$) in comparison to the average prey year ($W_9 = 0$). In a, variable names are reported in brackets.

modelling health therefore makes it possible to compare the effect sizes of these diverse stressors, while integrating the influence of other intrinsic factors that might affect an individual's vulnerability and resilience in different phases of its life. In particular, model results showed that a newly weaned juvenile or a female that is nursing a dependent calf may be at a greater risk of incurring life-history consequences from exposure to anthropogenic stressors, concurring with Rolland et al. (2016). These demographic classes are generally expected to be more vulnerable to the effects of stressors across long-lived vertebrates (Eberhardt 2002), because their life-history stage imposes a higher allostatic load, and could therefore be the focus of targeted conservation efforts (Horvitz et al. 1997). The results also supported the existence of a tradeoff between survival and current reproduction, with females rarely breeding when estimated survival probability was below 0.9, which is in line with previous work on right whales (Rolland et al. 2016) and with predictions from life-history theory for long-lived species (Stearns 1992, Eberhardt 2002).

Our analysis found an association between the prey abundance index and health, suggesting that the protracted effects of limited prey could affect the ability of a female to reproduce in a given year and, if prolonged, even have consequences for survival. Vessel strikes and entanglements had the greatest immediate effect on the health of exposed individuals, causing a decline that could be rapidly lethal, with the ultimate outcome dependent on the severity of the event, consistent with Knowlton et al. (2022). The only strike-related blunt wounds detected were associated with mortality (Sharp et al. 2019), and the estimated drop in survival probability was strong enough to capture this lethal outcome. However, this large effect does not account for the fact that most sublethal blunt injuries are never observed. In addition to immediate effects, carrying fishing gear for prolonged periods of time also had some sub-lethal, protracted consequences. This effect was estimated to be small, but the

posterior correlation of the corresponding parameter with the immediate effects of entanglement events suggests that these effects might be partly confounded. This is likely due to the immediate effect of an entanglement event capturing the decline in health across an entire three-month interval and, in addition, leading to lower health in subsequent time steps as the individual recovers. As a result, the immediate effects also contribute to explain the protracted consequences of entanglement events, and it is unclear if some of the decline in health currently attributed to these parameters should be apportioned to the parameter representing the protracted effect of carrying the gear.

Previous work has estimated a reduction in reproductive success following years of limited prey abundance, as well as higher levels of mortality resulting from entanglements and vessel strikes (Knowlton et al. 2012, 2022, Meyer-Gutbrod et al. 2015, Robbins et al. 2015). Estimates of increased drag costs have also led to a hypothesized reduction in reproduction resulting from protracted entanglements (van der Hoop et al. 2017), and entangled whales have elevated glucocorticoids, which can affect reproduction (Rolland et al. 2017). More broadly, these stressors are known to be important drivers of mortality and fecundity across marine megafauna (Lewison et al. 2004, Schoeman et al. 2020). However, using a model to integrate multiple stressors and quantify their effects in the same currency (here, the latent health variable) is important for designing effective and pragmatic management measures. Such measures should aim to reduce the cumulative risk to a species by ensuring survival and reproduction rates that support positive population growth rates and, in the case of North Atlantic right whales, the species' recovery (Moore et al. 2021, Pirotta et al. 2022).

Our analysis confirmed that reducing the risk of entanglements or vessel strikes would have substantial, immediate benefits on the survival of right whales. These are stressors for which mitigating solutions already exist and should be urgently implemented to prevent lethal and sub-lethal
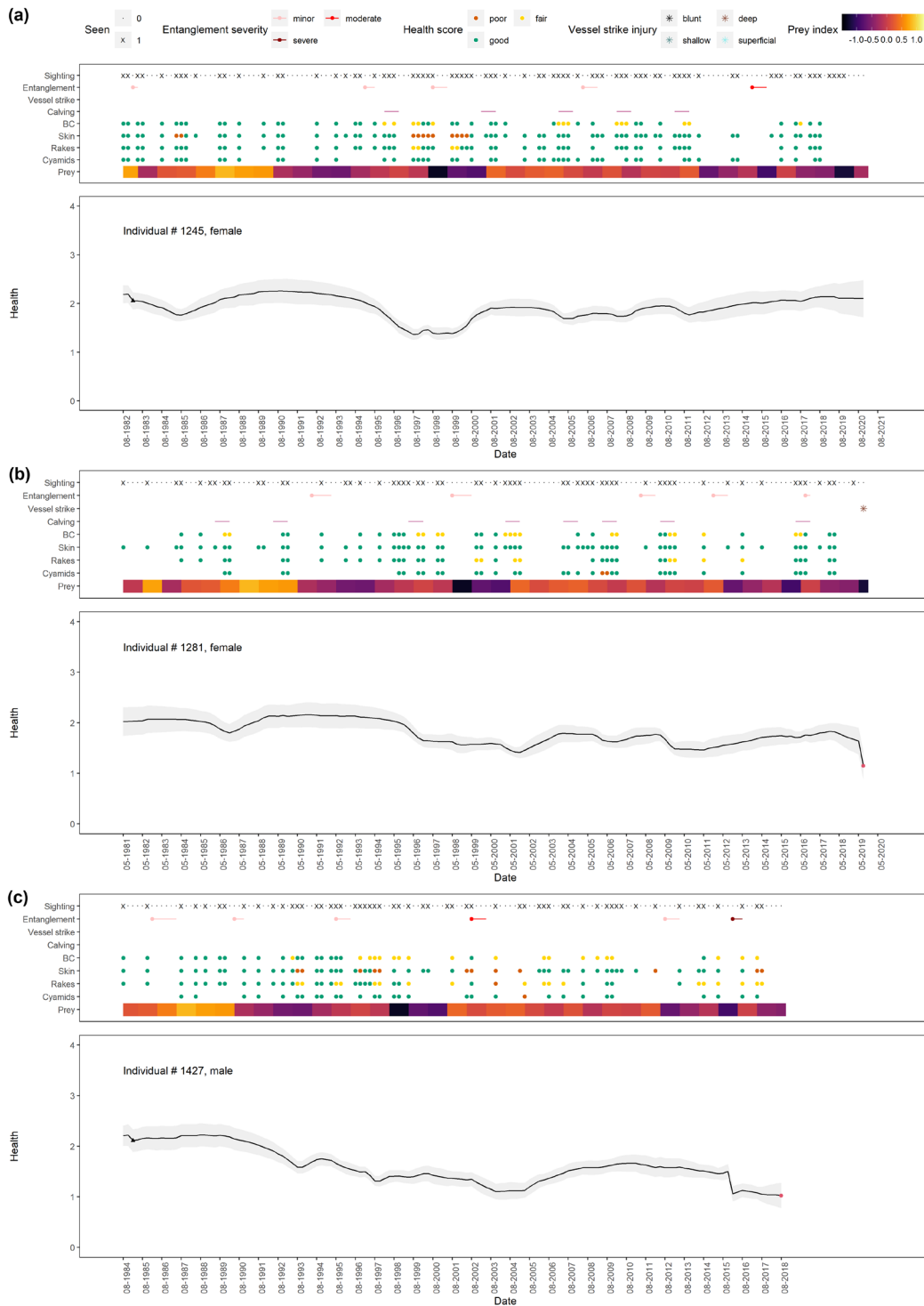
Figure 6. Time series of data streams (top panel) and estimated health (black line and grey ribbon in bottom panel, reporting the posterior mean and standard deviation) for three individuals. Health is the cloglog transformation of survival probability at the three-month scale (for reference: health values of 2.5 and 0 correspond to survival probability > 0.999 and 0.63, respectively). The estimated time of death (i.e. posterior median survival = 0) is represented as a red dot along the health time series, where available. Entanglement events are represented by a dot followed by a segment indicating the most likely estimate of the duration over which the gear remained attached to an animal (coloured by severity). Vessel strikes are indicated by a star in the same interval in which the injury was detected (coloured by injury type). Calving events are represented as segments covering the lactation period. Scores for the four visual health assessment variables (body condition, skin condition, rake marks and cyamid presence) were averaged and rounded over a three-month interval for plotting. Each plot also reports the individual number from the North Atlantic Right Whale Catalog (http://rwcatalog.neaq.org) and the sex.

consequences (Moore et al. 2021). However, the long-term trends in population health, survival and calving were not fully driven by the exposure of individuals to these events. Explicitly modelling individual health allowed us to detect the smaller effects of protracted stressors, such as prey abundance. The prey index we used has several limitations: it is derived from data collected in a specific region on only one of the target prey species and it does not reflect fine-scale patch distribution nor the recent trends in other portions of the range, which have led to changes in whale movements (Meyer-Gutbrod et al. 2021). As such, it should be interpreted as a coarse proxy of the overall quality of right whale habitat in a given year, rather than a precise metric of the abundance of prey in specific areas. Nonetheless, our results highlight the need for an ecosystem-based approach to contextualise management efforts within the current environmental regime (Meyer-Gutbrod et al. 2015). Climate-driven ocean warming and changes in circulation in the northwest Atlantic (Seidov et al. 2021) have had cascading consequences on right whale copepod prey (Record et al. 2019), which resulted in changes in the foraging ecology, movements and habitat use of the population (Meyer-Gutbrod et al. 2021, 2022). Quantifying and tackling this pervasive stressor will require robust, spatially explicit data on right whale prey and broader ecosystem dynamics, and widespread policies to address climate change and its effects on prey availability (Tulloch et al. 2019). In the short term, addressing the threats of entanglement and vessel strikes remains essential and will give the species greater resilience to respond to long-term environmental variation.

In this study, we have ignored the potential interactions that could emerge from the combined effects of multiple stressors (Orr et al. 2020, Pirotta et al. 2022). For example, recent changes in prey availability and the associated changes in whale distribution have altered the exposure risk of individuals to vessels and fishing gear (Meyer-Gutbrod et al. 2021). Moreover, carrying fishing gear could interfere with the ability of an animal to search for prey patches and feed effectively. Multiple traumatic events in succession could also lead to a stronger decline in health than the additive effects we currently model. Assessing these combined effects is a primary goal for management and conservation (Pirotta et al. 2022) and a requirement of many regulatory frameworks (Tyack et al. 2022). Conceptually, it would be possible to introduce interaction terms in the presented model; however, these may be challenging to quantify empirically, as the temporal resolution of the data and the scale of the model are relatively coarse. Moreover, interactive effects could have a spatial component (e.g. the changing preyscape leading to variation in the exposure to stressors in different regions), but space is not treated explicitly in the model. Future work should therefore extend the model to include a spatial structure, to quantify the spatially explicit exposure to multiple stressors, and investigate specific mechanisms by which multiple stressor effects may combine. Knowledge of these interactions could contribute to guiding the selection of combinations of stressors that can be managed to promote

the species' viability (Pirotta et al. 2022). Specifically, these results could be incorporated into population modelling tools to predict the future trajectory of the population under alternative scenarios of stressor mitigation or removal.

Our model capitalised on the multi-decadal dataset available for this species and a large-scale collaboration among research groups (Moore et al. 2021). We used these data to test an approach that explicitly captures some of the mechanistic cascades through which stressors are expected to affect vital rates, thus differing from previous, purely empirical analyses. In particular, the VHA data were critical to inform the variation in latent health (Supporting information), especially at the extremes of an individual's health state. However, additional analyses (Supporting information) suggested that the resolution of these data might be insufficient to discriminate finely between intermediate health states, which ultimately restricts the ability to correctly capture all stressor effects. In particular, protracted effects that lead to reduced reproductive output without impacting survival might be partially missed using the current health data. In the Supporting information, we explored the trends of different components of calving probability: while the component associated with health showed a comparable trend to survival, there was large variability in the individual-specific asymptote of the sigmoid relationship (representing individuals' maximum calving probability), which continuously declined over the decades and was unrelated to latent health as currently informed (Supporting information). The relatively coarse and qualitative health data also presented problems for informing the degree of variation in health across time steps (as reflected in the need to fix the standard deviation parameter to improve MCMC mixing), which had some influence on the estimation of effect sizes. Health is a multi-faceted concept that emerges from the integration of multiple aspects of an animal's physiology, including its energy, endocrine, immune and organ status; however, theoretical and technological advancements are needed to develop additional indicators (Ryan et al. 2007, Kophamel et al. 2022), and to integrate existing ones into routine health assessments and into our model (Rolland et al. 2017). Additional data streams could be used to inform different components of health separately, thus capturing multiple response pathways explicitly. For example, biomarkers derived from blood samples can offer a suite of health indicators (Kophamel et al. 2022), but remote blood sampling in large whales remains challenging (Fauquier et al. 2020). Other emerging techniques include the characterisation of an individual's microbiome or its epigenetic make-up, which are expected to vary as a result of energetic, immune or inflammatory status and exposure to stressors (Apprill et al. 2017, Crossman et al. 2021). Regular sampling of reproductive steroid hormones and glucocorticoids in matrices such as feces or blubber also offer an integrated measure of reproductive status and chronic stress, provided that sufficient data are available to correctly quantify baseline levels (Rolland et al. 2017, Rolland and Moore 2018). Finally, photogrammetry has proven effective at measuring variation in individual body size and condition

(Christiansen et al. 2020, Stewart et al. 2021). It should be noted that there are other stressors (e.g. anthropogenic noise) that might affect vital rates by altering the connections among individuals (e.g. mating or feeding behaviour), whose effects are not mediated by health as currently modelled. Moreover, our model does not include the effect of pollutants. These are potentially important stressors for the population but data on individual exposure levels and their link to health markers are largely unavailable.

We investigated the sensitivity of the results to some of the uncertainties associated with model formulation and with the incidence of stressors. Uncertainty in the timing of traumas and deaths had some influence on the size of the estimated effects. This variation largely did not affect the prioritization of these stressors for management, although some of the weaker effects (e.g. the impact of minor entanglements) only appeared to be relevant under some sets of assumptions (Supporting information). Moreover, many deaths are never observed (Pace et al. 2021). This cryptic mortality could influence the estimated health trajectory in the last, unobserved time steps, as well as the estimated effects of stressors, because the associated cause of death is not recorded and, for traumas that have protracted effects, only survivors are resighted. The recent distribution shift has also likely resulted in a change in the probability of detecting individuals when alive, while we are modelling it to be fixed across the study period. These results highlight the need for more homogeneous, cross-boundary efforts to monitor this population over the entire year and across its range to ensure that the exposure to stressors and the death of individuals are detected more precisely. In general, for long-lived species, building mechanistic knowledge into the analyses of stressor consequences will not obviate the need for long-term, large-scale monitoring studies (Lindenmayer and Likens 2010).

In conclusion, the persistence of threatened marine and terrestrial species in the Anthropocene will depend on our ability to identify, quantify and reduce the effects of the many anthropogenic stressors they are exposed to. In order to do this effectively, quantifying the relative consequences of different stressors on demographic rates is an important first step towards the robust prioritisation of management solutions. For example, right whales are protected by extensive policies to reduce the risk of vessel strikes (Laist et al. 2014, van der Hoop et al. 2015) and fishing gear entanglement (Knowlton et al. 2012), but these management actions are often inadequate (Pace et al. 2021) and further lose efficacy when the population undergoes rapid demographic or distributional shifts (Davies et al. 2019, Meyer-Gutbrod et al. 2022). Modelling exercises that investigate the mechanisms underlying these shifts will be useful for updating protective policies across the population's range and complementing them with dynamic management systems (Koubrak et al. 2021). In this paper, we have shown how the estimation of stressor effects can be achieved for a critically endangered, long-lived species through long-term data and a modelling approach that incorporates an understanding of the mechanisms leading to adverse outcomes. Our findings suggest that effective management of these stressors is a priority for ensuring the survival of this species.

Author contributions

Enrico Pirotta: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Funding acquisition (supporting); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Robert S. Schick**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (supporting); Software (supporting); Visualization (supporting); Writing – review and editing (equal). **Philip K. Hamilton**: Data curation (equal); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Catriona M. Harris**: Funding acquisition (equal); Methodology (supporting); Project administration (lead); Supervision (supporting); Writing – review and editing (equal). **Joshua Hewitt**: Formal analysis (supporting); Methodology (supporting); Software (supporting); Writing – review and editing (equal). **Amy R. Knowlton**: Data curation (equal); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Scott D. Kraus**: Data curation (supporting); Funding acquisition (supporting); Investigation (equal); Writing – review and editing (equal). **Erin Meyer-Gutbrod**: Data curation (equal); Methodology (supporting); Writing – review and editing (equal). **Michael J. Moore**: Data curation (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Heather M. Pettis**: Data curation (lead); Funding acquisition (supporting); Investigation (equal); Writing – review and editing (supporting). **Theoni Photopoulou**: Formal analysis (supporting); Methodology (supporting); Software (supporting); Writing – review and editing (equal). **Rosalind M. Rolland**: Data curation (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Peter L. Tyack**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Supervision (lead); Writing

– original draft (supporting); Writing – review and editing (equal). **Len Thomas**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Project administration (supporting); Software (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Open Science Framework: https://osf.io/ert85/ (Pirotta et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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