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Fishing gear entanglement threatens recovery of critically endangered North Atlantic right whales

Amy R. Knowlton[1] | James S. Clark[2] | Philip K. Hamilton[1] |
Scott D. Kraus[1] | Heather M. Pettis[1] | Rosalind M. Rolland[1] |
Robert S. Schick[2,3]

[1]Anderson Cabot Center for Ocean Life, New England Aquarium, Central Wharf, Boston, Massachusetts, USA

[2]Nicholas School of the Environment, Duke University, Durham, North Carolina, USA

[3]Centre for Research into Ecological and Environmental Modelling, School of Mathematics and Statistics, University of St Andrews, St Andrews, UK

Correspondence
Amy R. Knowlton, Anderson Cabot Center for Ocean Life, New England Aquarium, Central Wharf, Boston, MA, USA.
Email: aknowlton@neaq.org
Robert S. Schick, Marine Geospatial Ecology Lab, Nicholas School of the Environment, Duke University, Durham, NC, USA.
Email: rss10@duke.edu

Abstract

North Atlantic right whales frequently become entangled in fishing gear, which can negatively affect their reproductive output and probability of survival. We estimated individual whale health from a hierarchical Bayesian model fit to photographic indices of health. We reviewed 696 whales sighted from 1980 to 2011 and assigned 1196 entanglement events to 573 individuals in six categories of increasing injury severity and estimated monthly median health scores (0–100 scale) for the duration of their life within the study period. We then quantified the relationship between entanglement injury events and their severity with survival, reproduction, and population health. *Severe* entanglements resulted in worse health for all whales—males and females with *severe* injuries were eight times more likely to die than males with *minor* injuries. Females with *severe* injuries that survived had the lowest birth rates. Though the relationship between entanglement and fecundity was complex, we found that as the health of reproductively active females declined, their calving intervals increased. Unimpacted whale health scores declined significantly over three decades, 1980s, 1990s, and 2000s, suggesting food limitations may be contributing to population-wide health declines. Decadal health scores of entangled whales showed a more notable reduction in health suggesting a clear and perhaps synergistic effect.

KEYWORDS
entanglement, fixed fishing gear, health, injury severity, reproduction, survival

1 | INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*; hereafter NARW) has faced a millennium of hunting pressure (Reeves et al., 2007); all that remains of this

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Amy R. Knowlton and Robert S. Schick contributed equally to this work.

long-lived, critically endangered species is a small and vulnerable population that recently declined from close to 500 individuals in 2010 to fewer than 350 in 2020 (Pace III et al., 2017; Pettis et al., 2022). Although protected from hunting by international regulations which came into force in the 1930s (Reeves et al., 2007), the NARW now faces multiple stressors in the highly industrialized waters of the western North Atlantic where this remnant population is primarily distributed. These stressors include collisions by vessels and entanglements in fishing gear (Kraus & Rolland, 2007). As compared to southern hemisphere right whales (*Eubalaena australis*), which inhabit less industrialized waters, NARW has shown limited recovery as a result of these human impacts (Corkeron et al., 2018). This species is also facing the more recent effects of climate change including shifting and less predictable food resources (Record et al., 2019).

Entanglements of NARW typically occur in fixed fishing gear, including lobster and crab pots, and gillnets after the whale collides with ropes in the water column (Johnson et al., 2005). The resulting injuries can range from superficial wounds with no attached gear to cases in which the line becomes tightly wrapped multiple times around the whale, resulting in deep wounds, impaired feeding, and energetic costs caused by increased drag (Cassoff et al., 2011; Knowlton et al., 2016; Knowlton & Kraus, 2001; van der Hoop et al., 2017; Lysiak et al., 2018). NARW are entangled frequently—a 30-year assessment of entanglement scars (1980–2009) showed 82.9% of the population has been entangled at least once, and some individuals as many as seven times (Knowlton et al., 2012). While most gear interactions result in only scars, the rate of serious entanglements (those with attached gear or severe injuries) has been increasing (Knowlton et al., 2012) and entanglements are now the leading cause of serious injury and mortality in this species (Henry et al., 2019; Kraus et al., 2016; Pace III et al., 2021). There is no sign of abatement in the frequency or severity of entanglement despite decades of dedicated management efforts in the United States (Henry et al., 2019; Kraus et al., 2016; Pace III et al., 2014). Entanglements also occur in Canadian waters (Wimmer & Maclean, 2021), where, until recently (Davies & Brillant, 2019), there had been little effort to change how the fisheries operate in relation to reducing large whale entanglements.

Assessing the sub-lethal effect of fishing gear interactions on individual and population health has been difficult due to the challenges of collecting blood or other health data from large free-ranging whales although an assessment of fecal glucocorticoids showed that chronic entanglements lead to highly elevated stress levels in this species (Rolland et al., 2017). Another recent study found evidence of stunted growth in young right whales (<10 years old) that were observed with attached gear or whose mothers had attached gear or severe entanglement injuries while nursing (Stewart et al., 2021) indicating an additional sub-lethal effect. This stunted growth effect has also impacted the reproductive output of females (Stewart et al. 2022). Here we apply another tool—photographic evidence of health—to assess how entanglements are affecting right whale health. Pettis et al. (2004) developed the Visual Health Assessment (VHA), which is an approach for monitoring the health of individual whales over the course of their lifespan by ranking photographic observations of health for four categories: body condition, skin condition, the presence of cyamids in the blowholes, and the presence of rake marks around the blowholes. Within each health category, ordinal classes describe the severity of the health status (Pettis et al., 2004). In addition, Pettis et al. (2017) assessed the rate at which a whale's health, measured by assessing body condition, can change, including those that are entangled. Robbins et al. (2015) assessed survival in 50 right whales carrying fishing gear, and found that declining health, as evidenced by graying skin, higher cyamid levels, or signs of emaciation, was predictive of reduced survival.

To expand the utility of the VHA scoring efforts, Schick et al. (2013) developed a state-space model to estimate a continuous latent health state in individual right whales using the VHA data. In addition, information from observed rates of change in body condition (Pettis et al., 2017) was used to inform health progression (Schick et al., 2016). The model is hierarchical in that inference, with uncertainty, was made on the true monthly health state of the animal; parameters that govern the relationship between the observed photographic class and the underlying state were estimated at the population level. The model also included estimates of the geographic location of the animal (resolved to a regional level), as well as estimates of survival. Further details are provided in Schick et al. (2013), Rolland et al. (2016), and Schick et al. (2016).

For this study, we apply the Schick et al. (2013) model to link these individual health estimates and fishery entanglement interactions, quantify the effect of entanglement on subsequent NARW health and life history and compare these findings on a decadal scale to the overall population health. Herein, we provide the first quantitative summary of the effects of entanglement in fishing gear on NARWs—one of the most well-studied and imperiled large whale species in the world (Cooke, 2020).

2 | METHODS

Individual NARWs can be identified by natural markings on their heads (Kraus et al., 1986) and have been

monitored throughout much of their range since 1980 (Kraus & Rolland, 2007). All photographed sightings of right whales that were contributed to the North Atlantic Right Whale Consortium's Identification Database have been reviewed and—if a match was confirmed—linked to a cataloged individual. All photographed sightings of identified individual right whales were combined within a sighting season and habitat area into a "batch" and a detailed assessment of this suite of images was carried out to look for human-related scarring (Knowlton et al., 2012), and to conduct a VHA (Pettis et al., 2004) for that batch. Using the technique developed by Schick et al. (2013) and applied to the VHA data, we estimated health on a monthly scale for each individual whale.

To explore entanglement effects on health, we combined these health estimates with photographic data on entanglements (either of still-attached gear or scars from a prior entanglement where the entangling gear was shed) to assess the effects of the varying levels of entanglement severity on an individual (Knowlton et al., 2016). We then evaluated how each entanglement event affected survival and reproduction in six ways: (1) documenting changes in estimated health during and following the entanglement; (2) comparing the health of entangled animals in specific demographic classes as a function of entanglement severity; (3) examining the effect of entanglement on survival according to injury severity and by sex; (4) determining the number of months that the health of reproductive females who experienced an entanglement was below the calving threshold health value identified by Rolland et al. (2016); (5) examining the effect of entanglement on calving intervals; and (6) comparing the health of unimpacted and entangled whales by decade. We begin by describing the data followed by the methods used in each analysis. Although entanglement data exists for the period after 2013, there was a dramatic shift in NARW distribution in 2011 (Record et al., 2019) which confounded the Schick et al. (2013) model outputs for subsequent data. Therefore, we analyzed entanglement effects for the three decades of time when NARW movement patterns were more stable.

2.1 | Visual health assessment data

A total of 16,569 batches of 696 individual right whales photographed from 1980 to 2013 were reviewed and coded for VHA. All four parameters—body condition, skin condition, rake marks, and cyamids around the blowholes were used in the model to estimate latent health. Briefly, in the state-space model, there is an observation model for each of these ordinal VHA categories. This component of the state-space model links the observed score to the estimates of latent health. We use a multinomial logit formulation to evaluate the range of true health over which we may observe each of the ordinal values. In the observation model, we estimate both the center of these breaks between classes, as well as the slope of the curves describing the conditional probability of true health given these parameters. Here, we use informed priors to determine where in the latent heath range we estimate breaks from one of the observed ordinal classes to the next. See Schick et al. (2013) for further details.

We updated the monthly individual health curves described in Rolland et al. (2016) using sighting and health data for these 696 individual right whales.

2.2 | Entanglement data

Entanglement events were documented through a detailed assessment of all photographs of each individual whale following methods described by Knowlton et al. (2012). Entanglements were documented through 2011 with VHA scoring carried out through 2013 to help define the effects post-entanglement. A total of 1196 entanglement interactions involving 573 whales were categorized according to injury severity and the presence or absence of entangling gear (Table 1). Injury severity was coded as *minor*, *moderate*, or *severe* based on the extensiveness and the depth of the injuries (Appendix S1; see Knowlton et al., 2016, supplementary materials). Six entanglement injury categories were used in these analyses: (1) *minor no gear*, (2) *minor with gear*, (3) *moderate no gear*, (4) *moderate with gear*, (5) *severe no gear*, and (6) *severe with gear*, and compared to unimpacted whales (i.e., the period of time before a given individual experienced its first entanglement). For each case, we determined the timeframe within which the entanglement occurred and the duration of time when the gear was attached. In some cases, we could not determine the likely start of the entanglement event, for example, when we lacked sufficient photographic evidence of the animal in an uninjured state. When this happened in known age whales, who are typically born in the winter months off the southeastern U.S. coast, we bounded the started the entanglement timeframe on December 1 prior to their calving year, as this represents the beginning of the calving season (Kraus et al., 1986). Many whales endured multiple entanglements but, in this study, each entanglement event was evaluated independently.

2.3 | Analyses

The following analyses are focused first on describing how entanglements affect modeled health as a function

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TABLE 1 Summary of the data by entanglement category and reproductive status with mean and maximum duration (in months) of the *entanglement health windows*

Reproductive status	Entanglement category	Total # of events	Average length (months)	Maximum length (months)
Reproductive female	Minor no gear	92	4	4
	Minor gear	4	10	11
	Moderate no gear	27	4	4
	Moderate gear	7	17	56
	Severe no gear	4	4	4
	Severe gear	5	10	13
Nonreproductive all	Minor no gear	828	4	4
	Minor gear	21	11	61
	Moderate no gear	140	4	4
	Moderate gear	21	15	112
	Severe no gear	13	3	4
	Severe gear	34	15	77

Note: Reproductive female is a female from first pregnancy (as evidenced by successful calving) onward; nonreproductive all includes all males, females before first pregnancy, and juveniles.

of severity level and demographic groupings, and then we apply these findings to explore how health affects survival and fecundity. Lastly, we assess how the health of unimpacted whales (individuals prior to their first entanglement event) in relation to entangled whales has changed over three decades.

2.4 | Effect of entanglement category on health and recovery

To characterize the relative health effect and recovery for the six entanglement categories (Table 1), we assessed individual health at three time points: (1) at the uninjured sighting prior to the entanglement detection of a whale (if this timeframe was greater than 12 months, health was assessed at 12 months), (2) either the first date observed with new scars or, for those whales with attached gear, the last date seen carrying gear (this latter date reflects health when the whale was closer to the start of recovery if the gear was later shed), and (3) 12 months after either entanglement scar detection or the last date observed with attached gear. The goal of this assessment was to capture glimpses of health at similar points of time around the injury detection date, especially to investigate recovery. A 12-month period would ensure an impacted whale had experienced an annual feeding cycle which should support recovery. Slope graphs were created to depict the median health scores at these three different points of time for all events falling into each of the six entanglement categories.

2.5 | Comparison of entanglement effects on different demographic groups

To further analyze the health effects of entanglements on different demographic groups, we created *entanglement health windows* for each entanglement event to assess health scores for a period of time bracketing the date when each event was first detected and the likely duration (if the gear was attached) to capture the presumed injury effect period (Appendix S2). *Entanglement health windows* for events that resulted in scars only, that is, the animal was not carrying gear, included health scores at the month of detection and up to a maximum of 3 months prior (if the whale was sighted within 3 months of detection, the *entanglement health window* was narrowed to that timeframe). For events with attached gear, the *entanglement health window* included health scores at the time of detection and up to 3 months prior, through the period that the whale carried the gear, and 3 months past the last date observed with attached gear. For each entanglement event, the health scores for all the months in the given *entanglement health window* were averaged, and the average for all events within each entanglement category were displayed as boxplots.

For the analyses, we grouped animals by demographic categories, following Rolland et al. (2016). The first group, "reproductive females" includes females from their first successful pregnancy year (i.e., the year prior to giving birth to a calf) onward. The second group, "nonreproductive all" includes adult males, juveniles, and adult females prior to their first pregnancy. Both groups

were compared to unimpacted individuals (whales in the given demographic grouping recorded in the period prior to their first entanglement detection). We summarized the health during *entanglement health windows* and compared the six different entanglement categories and the reference category of the monthly health estimates of unimpacted individuals.

2.6 | Effect of entanglement on survival

The survival component of the model in Schick et al. (2013) is based on the capture-recapture model from Dupuis (1995) and Clark et al. (2005). Model output includes an estimated monthly survival probability for each individual whale not known to have died. Twenty-four whales killed by ship strike and five entangled carcasses not seen entangled when alive were removed from this analysis. To compare survival between entanglement categories, we estimated individual survival probability from the end of the last entanglement experienced by each individual whale for a period of 6 years. By the end of the 6-year assessment period, animals experienced one of four fates: (1) they survived; (2) they were removed ("right-censored") from the study at a given point (due to shortened life history data); (3) they experienced a known death; or (4) they experienced an estimated death event, that is, it was not estimated to survive to the next month. Capture-recapture models obtain information on survival probability from a random effect on individual detection—the probability that an individual with a high detection rate has died increases with the elapsed time since last sighted. The temporal extent of the modeling stopped in December 2013, at which point survival was right-censored. Time to death or censoring was calculated as the difference (in months) between the end of the last entanglement event documented for an individual and the death or censoring event. From the monthly estimates of survival probability, we constructed survival curves grouped by sex and entanglement injury categories, resulting in three curves (*minor*, *moderate*, and *severe*) for both males and females. We tested the differences between the curves using a Cox proportional hazards model, where the time to event (death) was a function of sex and entanglement severity. Analyses were performed with the survival package in R (Therneau, 2020; Therneau & Grambsch, 2000).

2.7 | Proportion of time below calving threshold

For reproductive females, we assessed the percentage of months within *entanglement health windows* that fell below an estimated health score of 67, the score

below which no calvings have been detected (Rolland et al., 2016). First, we took the average health scores for each *entanglement health window* in the six entanglement categories and compared those to the average health score of unimpacted reproductive females. We defined unimpacted reproductive females as those who have had a successful pregnancy but had not yet experienced an entanglement. To account for uncertainty in the health estimates in this process, for each animal, we drew 1000 health estimates from posterior predictive distribution, whose parameters were the posterior monthly health and standard deviation. For each of these 1000 predictions, we compared the predicted health vector to tally the number of months below the threshold.

2.8 | Effect of entanglement on fecundity

To investigate whether entanglements of different injury severity levels affect fecundity, several investigations were conducted. This was a retrospective analysis, whereby we first estimated health and survival following Schick et al. (2013), and then intersected observed entanglement and fecundity evidence with the posterior estimates. We used two types of regression analyses to examine the effect of latent health and entanglement status on (1) the probability of becoming pregnant in any given available year, that is, all years except the calving year and resting year after each calving and not including the year before their first calving event, as a function of scaled estimated health, entanglement severity, year, number of months during the interval where health was below 67 (this was scaled to reflect the differing length of the windows across individuals), and decade and (2) the length of time between pregnancy events as a function of the same covariates. To scale health, we took the estimated latent health on the 0–100 scale, and simply used the scale function in R to center and scale the estimated values. For the first analysis, we conducted a binomial generalized linear model (GLM) with pregnancy status as a 0/1 variable, and scaled latent health, entanglement severity, scaled year, decade (as a factor variable), and time since the last entanglement as covariates. In the second analysis, we conducted a) a normal GLM on the time between pregnancies (in years). The first of these analyses examine the annual probability of getting pregnant but does not consider a time-dependent response. The second analysis examines whether the health and increasing entanglement severity covariates affect the length of the interval between observed pregnancies. That is, we do not censor animals that are alive but not actively calving.
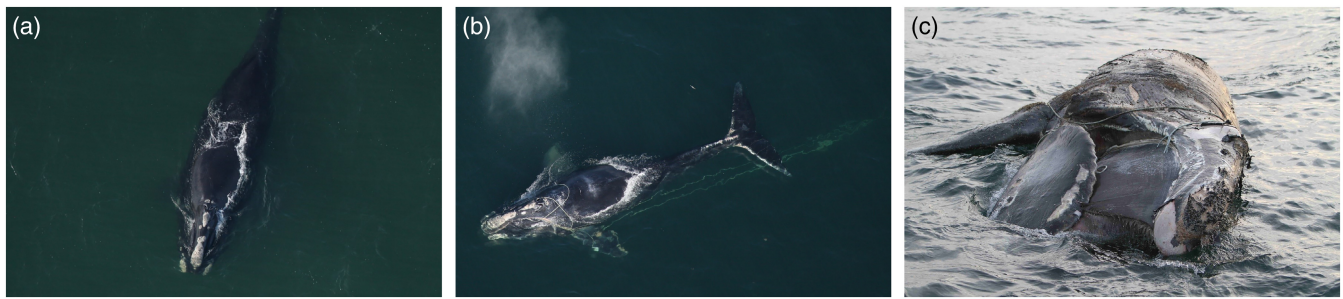
FIGURE 1 Timeline for entanglement of #3911, a 2-year-old female. She was last seen in good health with no gear on February 23, 2010 (a), with attached gear and severe injuries on December 25, 2010 (b) and was found dead on February 1, 2011 (c) after a disentanglement effort was unsuccessful (Moore et al., 2013). Photo credits: Florida Fish and Wildlife Conservation Commission, taken under NOAA research permits #594-1759 and #932-1905/MA009526

2.9 | Effect of entanglement on population health

To further investigate the reported declines in health and reproductive output over time documented by Meyer-Gutbrod and Greene (2018) and Rolland et al. (2016), the health of individuals in each decade—1980s, 1990s, and 2000s—was broken out by category of unimpacted, and *minor*, *moderate*, and *severe* injuries with average health scores summarized during the *entanglement health windows* that originated during the given decade. We ran a GLM on these data to examine the impact of entanglement status (as a factor variable—unimpacted vs. entangled), decade, and an interaction between the two.

3 | RESULTS

3.1 | Health in relation to entanglement severity

The health of right whales that experienced an entanglement event declined as injury severity increased (see Figure 1 for an individual case example). The most dramatic decline was observed among whales in the *severe with gear* category (Figures 2 and 3). Whales with severe entanglement injuries—both with attached gear and without—were in worse health than unimpacted whales (Figure 2). Statistically, for the non-reproductive all group, health declines with entanglement. The amount of decline was lowest in *minor no gear*, *minor with gear*, *moderate no gear*, and *moderate with gear* injuries with large declines in the *severe no gear* and *severe with gear* categories (Appendix S3). The *p* values for all but the *minor with gear* and *moderate with gear* were significant. For reproductive females, all entanglement categories were negative with generally higher

negative health estimates than the nonreproductive group although no pronounced increase in the *severe no gear* and *severe with gear* categories were seen in the estimates. This may be due to the smaller sample sizes in certain categories and the wider range of standard errors; only the *minor no gear* and *moderate no gear* categories were significant.

3.2 | Recovery from entanglements

No health declines were detected in the *minor no gear*, *minor with gear*, or *moderate no gear* categories (Figure 3). For *moderate with gear* and *severe no gear* and *severe with gear* categories, health declined in all cases and was especially precipitous for *severe with gear* cases. Also, the medians of estimated health scores for each of these three categories showed no recovery 12 months after the entanglement.

3.3 | Effects of entanglement on reproductive females

Females who had never experienced an entanglement or had experienced a *minor no gear* entanglement had median health values below the calving threshold of 67 in only 9.5% and 12.7% of the months assessed, respectively (Figure 4; Appendix S4), whereas those whales in the *minor with gear* category were below the threshold in 18% of assessed months. Whales in the *severe with gear* category were below the calving threshold in 76.9% of the assessed months. There is considerable variability in the estimates of numbers of months below 67, which may be influenced by how the entanglement coincides with their reproductive cycle and is likely affected by the sample sizes in the different categories.
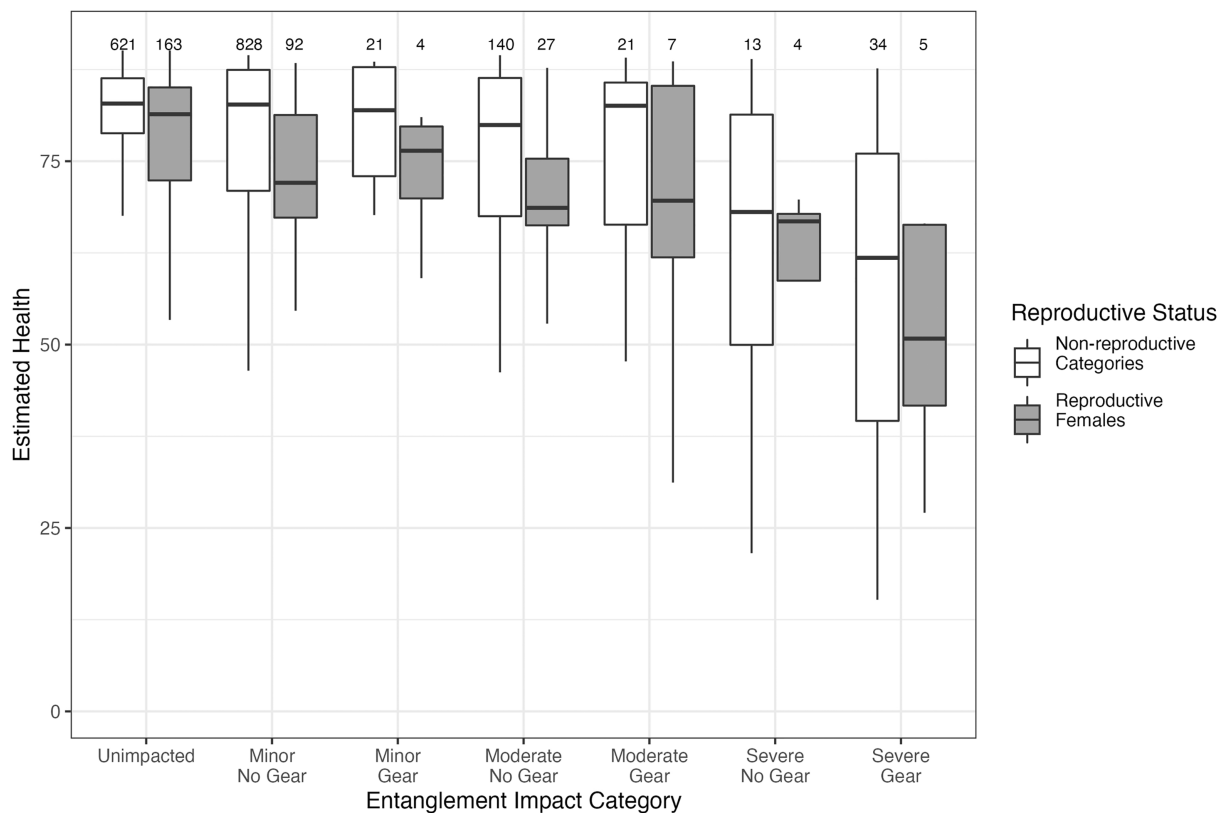
FIGURE 2 Boxplots of health scores categorized by entanglement impact categories and demographic groupings show that health during entanglement health windows declines with increasingly severe injuries, with the impact significantly worse for reproductively active females (Appendix S2). The boxes contain the middle 50% of the measurements collected in each category, the line through the box is the median, and the whiskers show the 95% confidence interval. The numbers above the bars represent the number of cases assessed in each impact category

3.4 | Effects of entanglement on calf production

Results from the binomial regression indicated that animals in better health were more likely to successfully calve. The coefficient relating *severe* entanglements and calving was negative but was not significant owing to a wide standard error (Table 2). The role of time was also significant—as the years of the study progressed, animals were less likely to calve in any given year. On the decadal scale, where the 1980s were the reference category, animals were significantly less likely to calve in the 1990s and significantly more likely to calve in the 2000s (Table 2). As with the binomial regression, the coefficient describing the relationship of the interval between calving and entanglement severity shows an increase in the interval, but the result was not significant (Table 2).

3.5 | Survival costs of entanglement

Comparing the effects of entanglement on survival using males with a *minor* entanglement as the baseline, or reference case, both males and females with *severe* entanglements

were eight times more likely to die (Appendix S5). Only 44% of males and just 33% of females with *severe* injuries survived longer than 36 months (Figure 5). Entangled females had poorer survival than males in all three categories (Figure 5). The difference in survivorship narrowed as entanglement severity increased, suggesting males with *minor* and *moderate* injuries fared much better than females, whereas *severe* injuries are equally impactful for both sexes (Appendix S6). Using a Cox proportional hazards model, where males with *minor* entanglements are the reference class, results indicate that the survival of females is significantly lower than males (Table 3). There was no difference in survival between males with *minor* and *moderate* injuries. Females with *minor* injury have significantly lower survival than males with a *minor* injury. Females with *moderate* injury have lower survival, though this difference was not as pronounced. Differences in survival are strongest in the *severe* category, regardless of sex.

3.6 | Population-wide health

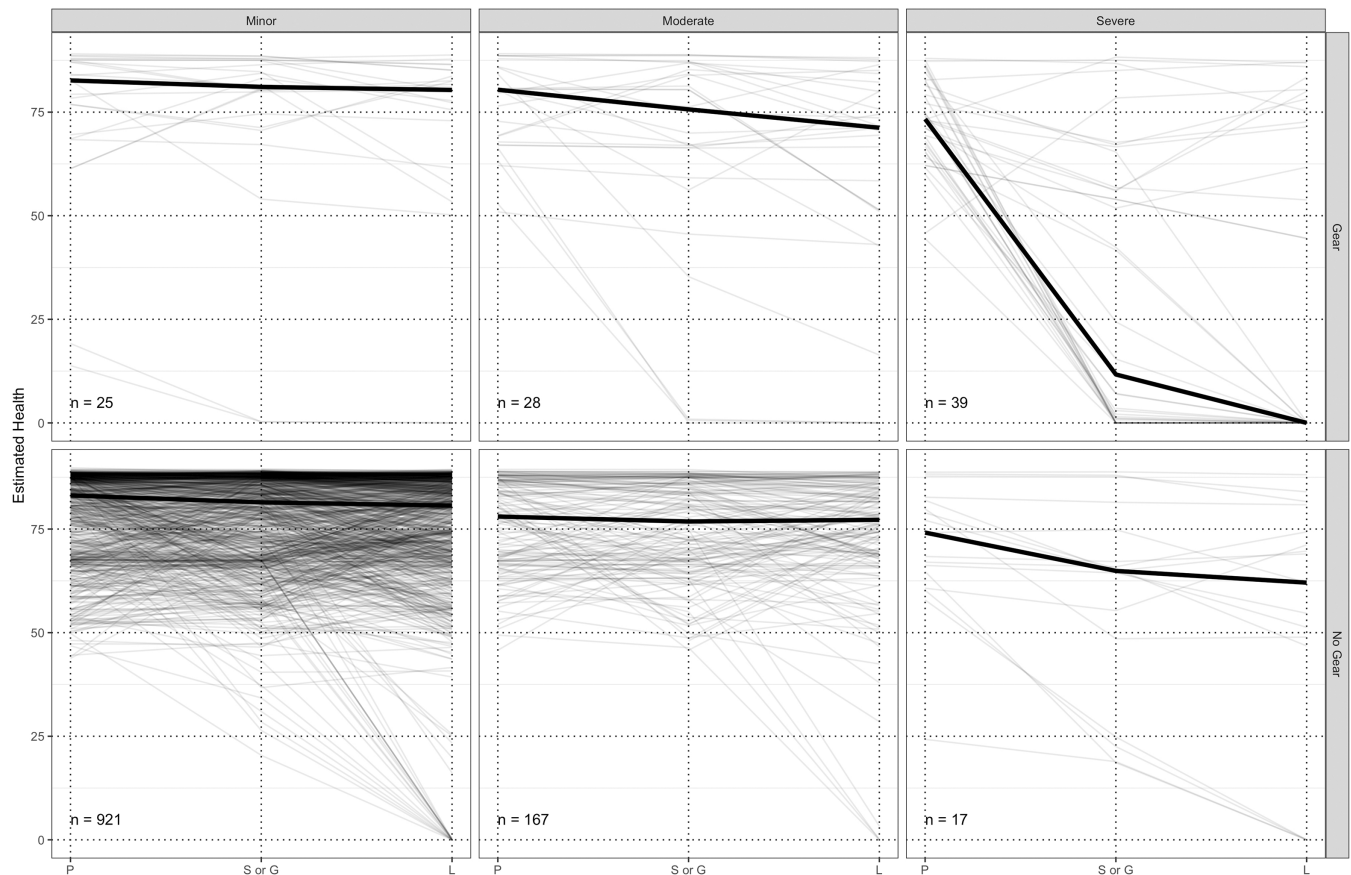A decadal comparison of health indicated a significant decline in average median health scores during each

FIGURE 3 As entanglement injury severity increases, the health of entangled animals worsens with no sign of recovery. Here we depict the health scores prior to, during, and after entanglement events. The six panels represent the median group category health score (black line) and individual health scores (gray lines) for the six entanglement impact categories. On the x-axis, P refers to either the date prior within 12 months detected without scars or gear or a maximum of 12 months prior to the detection date if the prior observation date is greater than 12 months, S or G is the first sighting with scars (S) or last date with gear (G), and L is 12 months after the S or G date

decade—1980s, 1990s, and 2000's for both unimpacted whales and entangled whales with *minor*, *moderate*, and *severe* injuries combined (Appendix S6). Each decade showed slightly different patterns (Figure 6). In the 1980's, the median health scores were similar across all the categories although the *minor* and *moderate* categories showed greater variability. Only one *severe* entanglement was documented in that decade. In the 1990s, *minor* entanglements showed a similar median and variability as the 1980's but *moderate* events had a notably lower median score than the 1980's and the *severe* events, which were more numerous, showed dramatically lower health scores well below any of the other categories. For the 2000s, the median scores for both *minor* and *moderate* were below unimpacted and again the *severe* scores were well below any of the other categories. The unimpacted category declined significantly over each decade (Appendix S6) but the median scores remained high, ranging from a median of 81.6 in the 1980s to 75.7 in the 2000s, which for reproductive females is well above

the calving threshold of 67 (Rolland et al., 2016). The median health estimate for all entanglements combined was higher than unimpacted in the 1980s (82.0 vs. 81.6) whereas in the 1990s and 2000s, the health estimate for the entangled group was lower than unimpacted (76.1 vs. 78.6 in the 1990s and 74.9 vs. 75.7 in the 2000s indicating that entanglements are playing a role in population health declines (Rolland et al., 2016) as the frequency of moderate and severe injuries increase.

4 | DISCUSSION

This study documents the negative effects of entanglements on the health and survival of NARW. By coupling longitudinal monitoring data on NARW with a unique modeling approach utilizing visual health assessment data (Schick et al., 2013), we investigated the effects of *all* entanglements, including cases with only scars which comprise the majority of documented entanglement
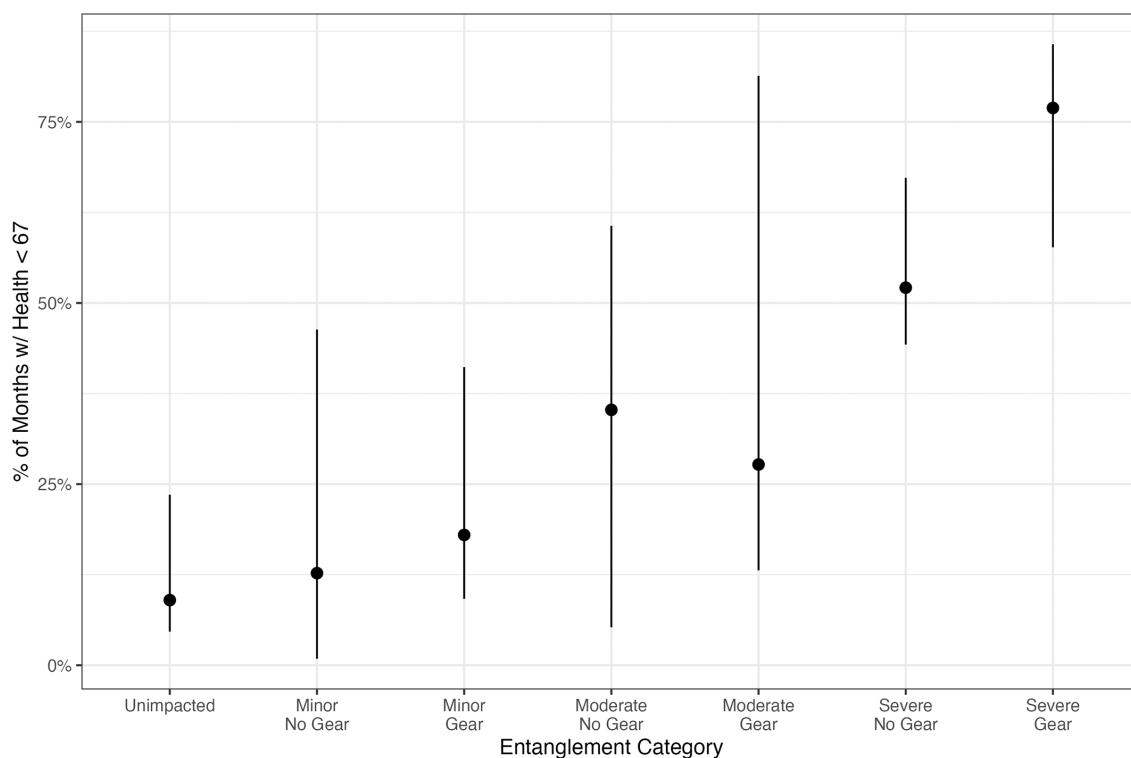
FIGURE 4 As entanglement severity increases reproductively active females have longer periods of time within their entanglement health windows with health scores below the calving threshold of 67 (Rolland et al., 2016). The graph represents the median (dots) and inter quartile range of percentages below the threshold. See Appendix S3 for the number of events and the number of months used to calculate these percentages

TABLE 2 Estimated regression parameters for effects of health and entanglement on the probability of getting pregnant, and the interval between successful pregnancies

Regression	Covariate	Coefficient	Standard error	p-value
Probability of becoming pregnant	Intercept	−1.137	0.348	.001
	Health	0.124	0.064	.053
	Minor	0.777	0.277	.005
	Moderate	0.804	0.486	.098
	Severe	−13.859	366.317	.97
	Year	−0.716	0.194	.0002
	Decade: 1990	−0.564	0.276	.041
	Decade: 2000	1.395	0.446	.002
	Decade: 2010	0.833	0.611	.172
Length of time between pregnancies	Intercept	3.603	0.236	<<.001
	Health	−0.07	0.527	.8935
	Decade: 1990	1.304	0.327	<<.001
	Decade: 2000	0.71	0.287	.014
	Decade: 2010	0.634	0.372	.09
	Severity	0.047	0.039	.223

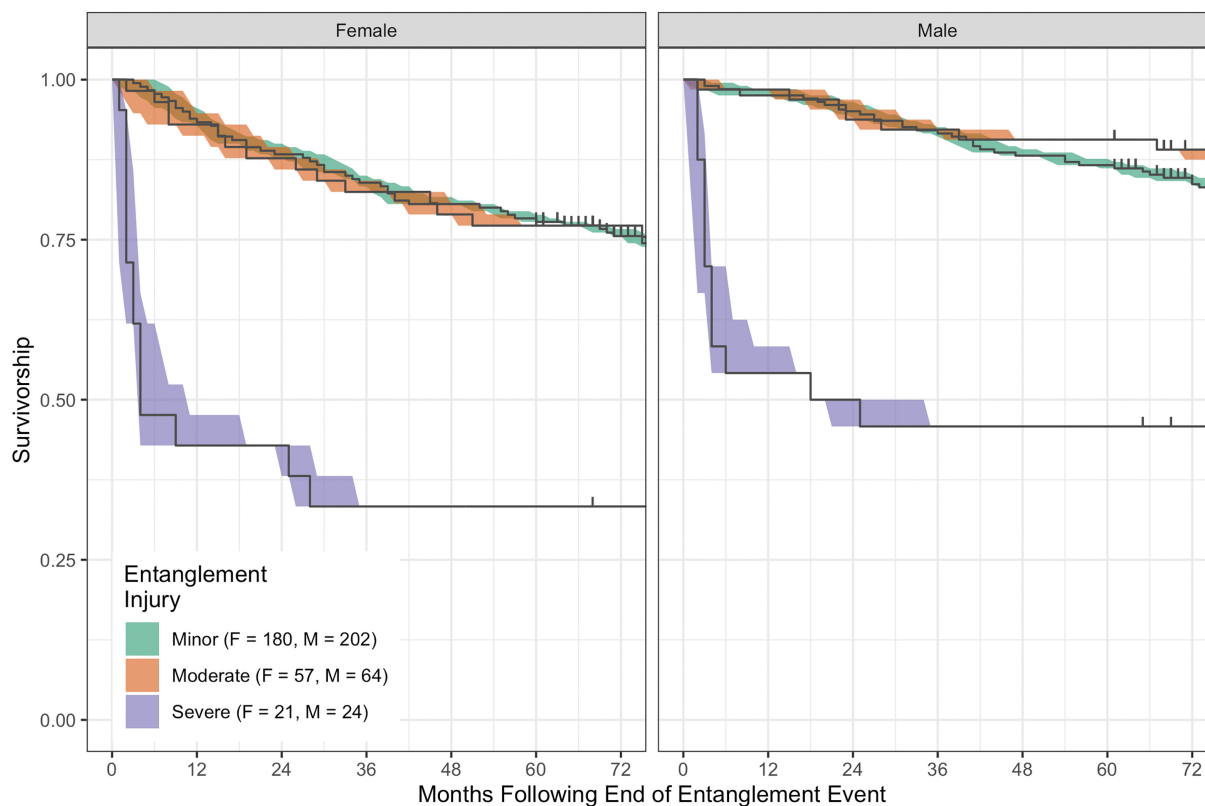*Note*: Decade: 1980 is the reference category.

FIGURE 5 Survival probability declines after entanglement and is consistently worse for females (Table 3; Appendix S4). The data shown include both with and without gear events. The lines depict the survival curves following the last entanglement of each individual. Colored regions indicate the uncertainty around the survival curves; specifically, the regions depict the upper and lower bounds of 1000 draw from the posterior distribution. Tick marks on each line indicate when whales were right-censored, that is, left the study because the modeling timeframe ended before an estimated death. The legend shows the number of individuals assessed for each injury category

TABLE 3 Estimated regression parameters from a cox proportional hazards test on the effects of sex and entanglement on survival

Entanglement class	Coefficient	Exponentiated coefficient	Standard error	_p_-value
Male—moderate	0.052	1.05	0.27	.85
Male—severe	1.81	6.1	0.28	<<.001
Female—minor	0.55	1.74	0.177	.002
Female—moderate	0.46	1.57	0.26	.08
Female—severe	1.86	6.45	0.27	<<.001

Note: Males with minor entanglements are the reference category. Results indicate significant differences between males and females, with female survival being lower than males.

events (Knowlton et al., 2012). Through an evaluation of all cases, we determined that sub-lethal effects are more pronounced than previously reported. Entanglements affect right whales in three ways: (1) they compromise individual health even when the gear is not present; (2) they reduce survival—especially in females; and (3) they reduce fecundity in females that survive.

An important finding of this study is the comparison of injury severity versus health. By categorizing each entanglement event into a severity level of _minor_, _moderate_, or _severe_ wounds and whether gear was attached or

not and further grouping by reproductive status, we learned that entanglement has a negative effect on both reproductive and non-reproductive groups although not all of these comparisons were significant. Yet the negative health estimates were more pronounced and significant for reproductive females in both _minor_ and _moderate no gear_ categories when compared with unimpacted reproductive females who already experience lower health scores due to the costs of lactation (Pettis et al., 2004; Rolland et al., 2016). As severity worsened and when entanglement events included attached gear,
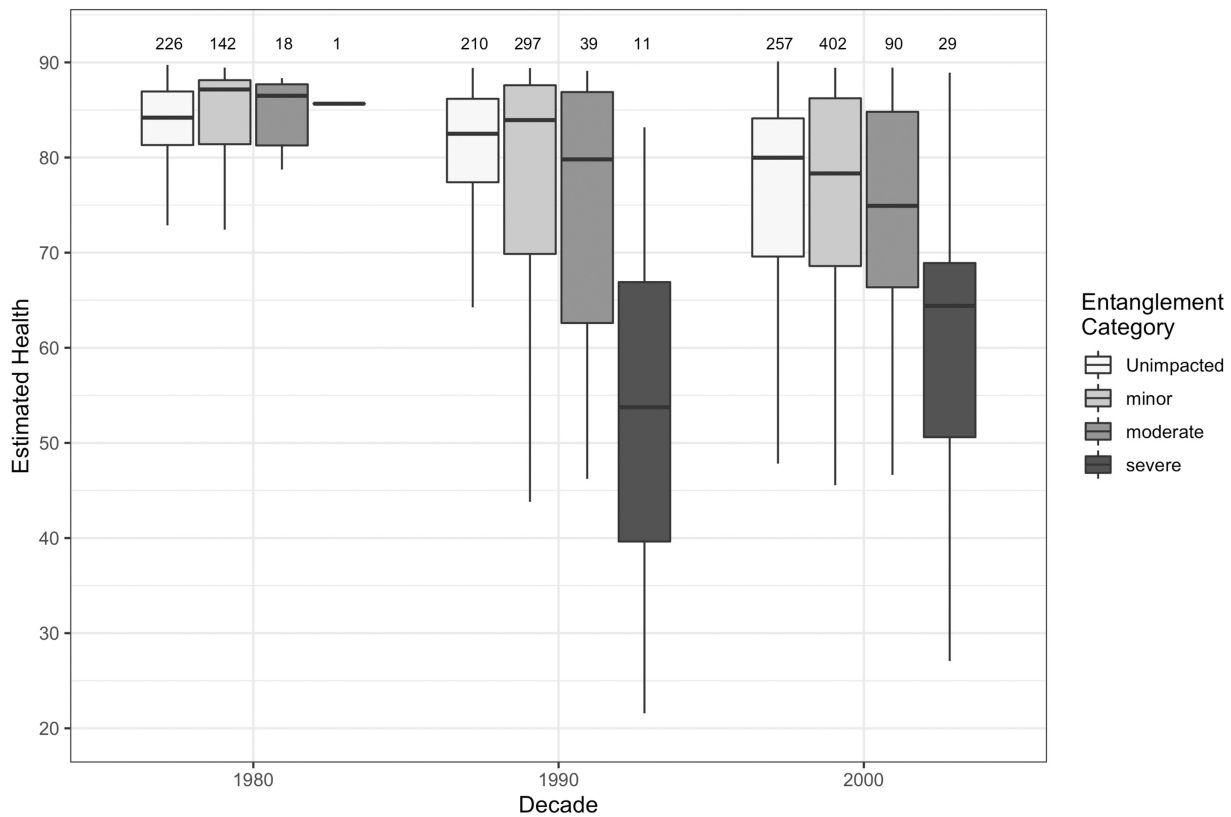
FIGURE 6 Summary of median health scores by decade for unimpacted whales prior to first entanglement detection and for entangled whales according to injury severity with health scores measured during each whale's entanglement health window. Values in each show the upper and lower whiskers (the most extreme point no more than 1.5 times the box range), the upper and lower hinge (approximately the first and third quantiles), and the median (Appendix S5)

health declined for all demographic groups in the *severe* cases and that decline was highly significant for the non-reproductive category. For all three injury categories, survival in relation to entanglement was much lower for females than for males. However, in the *severe* category, both females and males showed dramatic declines in survival. Similarly, as injury severity got worse, the health of reproductive females was more likely to be below the calving threshold of 67 (Rolland et al., 2016). These findings amplify the recent studies that suggest that human activities, especially entanglements, are the primary contributor to the current population decline (Corkeron et al., 2018; Kraus et al., 2016; Moore et al., 2021; Pace III et al., 2021). Further, significantly reduced survival in females in relation to entanglements shown here is consistent with Pace III et al.'s (2017) findings of lower survival for female NARWs.

The effects of entanglement on fecundity for those reproductive females that survived suggest a complex and non-linear interplay between entanglement, latent health, and time, as the mean health of successful calving females declined over time. While available animals in better health were significantly more likely to successfully calve and whales with minor and moderate injuries did not experience a reduction in the ability to calve, our findings suggest whales with *severe* entanglements were much less likely to be reproductively successful, though the latter relationship was not significant. We suspect that this is most likely due to significantly worse survival, that is, so few reproductive females actually survived a *severe* entanglement that there were relatively few instances to make this comparison. In those limited number of cases where females survived a *severe* injury and continued to reproduce, calving intervals were longer. It is important to note that the analysis of event duration is, by definition, looking at successful calving intervals, and does not factor in females that have been entangled and never go on to calve again (though the binomial regression does include these cases). Nevertheless, the results indicate that over the duration of the study, animals were less likely to calve and calving intervals have increased—both worrisome trends for the long-term survival of the species.

The decadal assessment shows that entanglements lead to lower health scores in comparison to the unimpacted category as the frequency of moderate and severe entanglements increases. In addition, the health of unimpacted NARW showed a significant decline in each decade suggesting this model is detecting food limitation, which has been described in other studies (Meyer-

Gutbrod & Greene, 2018; Rolland et al., 2016; Stewart et al., 2021), or other factors that could affect health. If food limitations or other factors were not occurring, we would have expected the unimpacted category to remain unchanged. Rolland et al. (2016) showed a health decline over the 30-year period with some dramatic health declines linked to poor calf output but indicated further work would be needed to tease out the role that anthropogenic events were having on that decline. What this assessment indicates is that the decline is likely the result of both the increasing rate of moderate and severe entanglements (Knowlton et al., 2016) as well as other factors. Other factors such as non-lethal vessel strikes, anthropogenic noise, and the cumulative effects of repeated entanglements experienced by individuals could also be playing a role in this decline but were not explored in this study.

This study measured the effects of entanglement only through 2011 despite the fact that entanglement and VHA data exist through 2019 and are updated annually. The movement components of the model developed by Schick et al. (2013) were based on a well-defined pattern of right whale movements between habitats which began to shift starting in 2010 (Record et al., 2019). Sensitivity analysis indicates the informed priors we used are no longer appropriate with more recent data after the apparent shift in habitat use (results not shown). This component of the model is being actively developed as part of a new research effort. However, the findings of this study provide a baseline characterization of the sublethal effects of entanglements, especially as injury severity increases. Since 2011, there continue to be high levels of entanglements, especially of moderate and severe injuries. Of 476 documented fishing gear entanglements from 2012 to 2019, 78 resulted in *severe* injuries (including 11 documented deaths) and 74 resulted in *moderate* injuries (Hamilton et al., 2020; NEAq unpublished data) indicating this issue is showing no signs of abatement despite efforts at mitigation (Pace III et al., 2014). As part of this ongoing research, our focus will be on ensuring that the effects of multiple human activities and climate change on this beleaguered species are better understood. Considering that some NARWs have experienced at least seven entanglements in their lifetime (Knowlton et al., 2012) as well as sublethal vessel strikes, there may be an even greater cumulative impact than we have noted here.

If we are going to save the right whales from imminent extinction, dramatic changes to how fixed fishing activities are presently conducted are required. Between ropes getting stronger (Knowlton et al., 2016) and expanded offshore fishing efforts overlapping with the NARW range, the fishing activity could lead to the ultimate demise of this species. There are solutions to this crisis including ropeless fishing methods (Myers et al., 2019) and reduced breaking strength ropes (Knowlton et al., 2016), both of which are available and could be integrated with area closures and fishing effort reduction to reduce entanglement risk to this species. For too long, the burden has been on the research community and management to provide evidence that a given fishery is the problem. Yet, it is clear that wherever NARWs range, if there is overlap with fixed-fishing gear that is not modified to protect whales, the risk remains.

These results also have negative implications for large whale species worldwide. Evidence is mounting that entanglements occur wherever fixed-gear fisheries and large whales overlap (Thomas et al., 2016). Although most large whale populations do not have the extensive data needed to analyze effects on individuals, entanglements are under-reported (Ramp et al., 2021) and their impacts are probably grossly underestimated. Entanglements not only threaten individual whales or species but also have broader ecological consequences in regions with diminishing whale populations. Whales are nutrient recyclers in marine ecosystems, supporting primary productivity (Roman et al., 2016), fisheries (Lavery et al., 2014), and mitigating climate change (Nicol et al., 2010; Pershing et al., 2010). Thus, if worldwide fisheries-related entanglements of large whales continue unabated, the resilience and productivity of marine ecosystems could be permanently altered (Thomas et al., 2016).

AUTHOR CONTRIBUTIONS

Amy R. Knowlton and Robert S. Schick designed the model framework. Robert S. Schick, with guidance from James S. Clark, carried out the programming and running of the model and conducted the analyses. Amy R. Knowlton and Robert S. Schick co-wrote the manuscript. All authors discussed the results and contributed to the final manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and analyses conducted for this study are available at https://github.com/robschick/tangled.

ORCID

Amy R. Knowlton https://orcid.org/0000-0001-9124-4315

James S. Clark https://orcid.org/0000-0002-5677-9733

Philip K. Hamilton https://orcid.org/0000-0002-0643-039X

Scott D. Kraus https://orcid.org/0000-0003-4367-6548

Heather M. Pettis https://orcid.org/0000-0003-2206-979X

Rosalind M. Rolland https://orcid.org/0000-0003-0910-5813

Robert S. Schick https://orcid.org/0000-0002-3780-004X

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