NOAA Technical Memorandum NMFS-NE-324

Population size estimation of North Atlantic right whales from 1990-2023

US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole, Massachusetts
October 2024

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Citation: Linden D. 2024. Population size estimation of North Atlantic right whales from 1990-2023. US Dept Commer Northeast Fish Sci Cent Tech Memo 324. 15 p.

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SUMMARY

This report serves to update the population size estimate of North Atlantic right whales (*Eubalaena glacialis*; hereafter, right whales) for the most recent year of available sightings data. Using an established capture-recapture framework (Pace et al. 2017) and a new birth-integration approach (Linden 2024), the estimated median population size at the start of 2023 was 372 whales, with a 95% credible interval (CI) ranging from 360 to 383. The sharp decrease observed from 2015-2020 appears to have slowed, though the right whale population continues to experience annual mortalities above recovery thresholds. The updated right whale population estimate will be provided to the Atlantic Scientific Review Group for consideration in the 2025 Atlantic Stock Assessment Review process.

METHODS

I used a Bayesian version of a multistate Jolly-Seber capture-recapture model fit to sightings records of right whales to estimate population parameters including annual abundance and survival. The general approach has been described in detail elsewhere (Pace et al. 2017, 2021), including a new modification to integrate known births (Linden 2024). Here, I document the updated data and clarify modeling decisions to improve reproducibility.

Data

The New England Aquarium (NEAq), as data stewards of the North Atlantic Right Whale Consortium (NARWC), provided updated records on September 13, 2024, that included >81,500 sightings of 660 whales observed from 1990-2023. Individuals are identified primarily by natural markings (Hamilton et al. 2007) with additional information from genetic sampling (Frasier et al. 2007). The sightings were aggregated by individual into survey years (December 1-November 30) to align with the calving season and the seasonal distribution of survey effort (Pace et al. 2017). Annual capture histories ($y_{i,t}$) contained a binary observation (1 = seen or 2 = not seen) indicating whether an individual (i) was sighted in the given survey year (t), across a total of 34 years.

The capture histories corresponded to a matrix of true states ($z_{i,t}$) with the following definitions: 1 = not yet entered the population; 2 = alive; and 3 = dead. Individuals seen during a survey year were assigned a known alive state ($z_{i,t} = 2$), while those discovered dead were assigned a known dead state ($z_{i,t} = 3$) for the following survey year. Known alive states were also assigned for all survey years between the first and last years with sightings, including for individuals first seen prior to 1990. Additionally, 4 whales seen during the 2024 calving season and not seen in 2023 were assigned a known alive state for 2023. Along with sightings of live and dead individuals, those with known birth years were assigned a known state of $z_{i,t} = 1$ for all survey years prior to birth. Any years that were missing evidence of the known state for an individual were assigned as unknown ($z_{i,t} = \text{NA}$). For the terminal estimation year in 2023, there were 11 calves included as potential recruits to the population.

Age and sex were known for 63% and 93% of individuals, respectively. Given a known birth year, individuals were classified each year into 1 of 6 age classes (0, 1, 2, 3, 4, 5+) to accommodate modeling variation in survival for younger animals. While several options exist to handle unknown ages (Pace 2021), including explicit modeling of age 0 entry (Hostetter et al.

2021), here I assigned the age at entry to be 5+ (adult age class) for individuals with an unknown birth year, consistent with the original approach (Pace et al. 2017).

Model fitting

The multistate Jolly-Seber capture-recapture model uses a hierarchical formulation to describe probabilities of observations conditional on true states and transitions between states over time (Kéry and Schaub 2012; Royle and Dorazio 2012). I used Markov chain Monte Carlo (MCMC) methods for model fitting and directly estimated the partially latent true states across time. By having at least 3 true states, the processes of recruitment and survival could be estimated, in addition to population size. Our state transition matrix was specified as follows:

$$\boldsymbol{\Omega} = \begin{array}{c c} & z_{i,t+1} \\ z_{i,t} & \begin{bmatrix} 1-\gamma_t & \gamma_t & 0 \\ 0 & \phi_{i,t} & 1-\phi_{i,t} \\ 0 & 0 & 1 \end{bmatrix} \end{array}$$

where γ_t is the probability of entry and $\phi_{i,t}$ is the probability of survival. The matrix makes clear which transitions are allowed (e.g., $z_{i,t+1} = 2$ after $z_{i,t} = 1$) and which are not allowed (e.g., $z_{i,t+1} = 2$ after $z_{i,t} = 3$). The observation matrix was defined as follows:

$$\boldsymbol{\Theta} = \begin{array}{c c} & y_{i,t} \\ z_{i,t} & \begin{bmatrix} 0 & 1 \\ p_{i,t} & 1-p_{i,t} \\ 0 & 1 \end{bmatrix} \end{array}$$

where $p_{i,t}$ is the probability of sighting individual i in year t, given the true state $z_{i,t}$.

In this formulation, entry is a removal process given that only available individuals (those not yet entered) can transition into the population (Kéry and Schaub 2012). The entry probability is typically a nuisance parameter and not directly related to per capita recruitment, though the realized counts of recruits can be derived from the posterior distributions of true states. Here, I used a birth-integrated Jolly-Seber model (Linden 2024) to improve the population estimation process and increase accuracy of the terminal year estimate. Annual calf counts were used to define the expected number of entries for all years $t > 1$, and the γ_t entry probabilities adjusted accordingly. Calf mortality probability (κ), representing the probability that calves that may have survived the winter calving season but did not recruit to the population, was assumed constant.

I used parameter-expanded data augmentation as part of the MCMC approach to model fitting (Royle and Dorazio, 2012), where the capture history matrix of observed individuals is augmented with a number of additional all-zero capture histories representing potential individuals that were never sighted. Here, I added 300 additional capture histories, resulting in $M = 1{,}063$ total individuals in the $y_{i,t}$ data.

The likelihoods of the true states and the observations conditional on true states were then specified as follows:

$$z_{i,t+1}|z_{i,t} \sim \text{categorical}\left(\Omega_{z_{i,t},1:3}\right)$$

$$y_{i,t}|z_{i,t} \sim \text{categorical}\left(\Theta_{z_{i,t},1:2}\right)$$

To facilitate convenient model fitting, I added a dummy occasion before year 1 where $\Pr\left(z_{i,t} = 1\right) = 1$ for all individuals (Kéry and Schaub, 2012), allowing γ_1 to represent the proportion of M individuals either born in 1990 or already in the population before 1990.

I accommodated individual and temporal variation in survival and sighting probabilities using logit-linear models. For survival probability:

$$\text{logit}\left(\phi_{i,t}\right) = \beta_0 + \beta_{\text{age}} \times \text{Age}_{i,t} + \beta_{\text{female}} \times \text{Sex}_i \times \text{Adult}_{i,t} + \beta_{\text{regime}}\text{I}(\text{year}_t > 2010) + \epsilon_t^{\phi}$$

Here, β_0 is the average survival probability for $\text{Age}_{i,t}$ = 0 individuals (0.5 year olds); β_{age} is the coefficient for linear change in survival with ages from 1-5; β_{female} is the coefficient of difference in survival for adult females; β_{regime} is the coefficient of difference in survival for years after 2010, representing a climate regime shift; and ϵ_t^{ϕ} is the random effect of year. For sighting probability:

$$\text{logit}\left(p_{i,t}\right) = \alpha_0 + \alpha_{\text{female}} \times \text{Sex}_i + \epsilon_t^p + \epsilon_i^p$$

Here, α_0 is the average sighting probability for males; α_{female} is the coefficient of difference in sighting for females; ϵ_t^p is the random effect of year; and ϵ_i^p is the random effect of individual.

I used vague priors for most parameters including Uniform(0,1) for intercept probabilities, Uniform(-5,5) for regression coefficients, and Uniform(0,10) for random effect standard deviations. To assign a value for individuals with unknown sex, I estimated a general sex ratio according to Bernoulli(π_{female}) with an informed prior of Beta(5,5). Known states were provided as data during model fitting, and unknown states were initialized as $z_{i,t} = 1$ for all years prior to first sighting and $z_{i,t} = 3$ for all years following the last sighting. Augmented individuals were initialized at $z_{i,t} = 1$ for all years.

I fit the model in R (R Core Team 2022) using MCMC with NIMBLE (de Valpine et al. 2017, 2022). The MCMC algorithm was run for 25,000 iterations over 3 chains after a burn-in of 5,000 iterations. Convergence was assessed by examining trace plots and the potential scale reduction factor (R-hat; Brooks and Gelman 1998), the latter indicating a value of <1.1 for all parameters.

RESULTS

The birth-integrated Jolly-Seber model achieved convergence and exhibited expected patterns of variation regarding sex, age, and temporal characteristics of survival and sighting probabilities (Table 1). There was moderate evidence that females had a lower average sighting probability (α_{female} = –0.261 [–0.522, 0.011]) than males (Figure 1). There was strong evidence of reduced survival for adult females (β_{female} = –0.341 [–0.572, –0.114]) and younger whales (β_{age} = 0.213 [0.138, 0.284]) and for all individuals after 2010 (β_{regime} = –0.743 [–1.129, –0.346]).

While post-2010 survival probability was lower on average, annual fluctuations suggest there were recent increases in survival between 2020 and 2022 from the lower rates of survival in 2017 and 2019 (Figure 2). Calf mortality probability (κ) was 0.031 [0.002, 0.090].

The most recent estimate of total population size in 2023 was 372 whales, with a 95% CI ranging from 360 to 383. While the population continues to be in decline since 2011 (Table 2; Figure 3), the short-term trend is positive. While some negative bias in the terminal year abundance estimate might be expected (Pace 2021), this bias should be greatly reduced with the birth-integrated model (Linden 2024); the original model formulation suggested a 2023 estimate of 363 [95% CI: 352, 370]. Given the lower survival for adult females, patterns in sex-specific abundance continue to diverge across time series (Figure 4), as originally noted by Pace et al. (2017). The 2023 estimate included 157 [95% CI: 149, 164] females and 215 [95% CI: 206, 224] males; known reproductive females (with previous evidence of calving) was 70 [95% CI: 67, 73]. The predicted number of deaths continued to be lower from 2020-2022 compared to the highs from 2015-2019 (Table 3; Figure 5), though these annual mortalities are still above the Potential Biological Removal rate identified for right whales (0.7 deaths per year; Hayes et al. 2022).

ACKNOWLEDGEMENTS

I am grateful to the NARWC and NEAq for their work in updating and maintaining the Catalog and for access to the sightings data. The capacity to develop precise estimates of North Atlantic right whale demographic parameters is due to the thousands of photographic captures of whales contributed by hundreds of collaborators working through the NARWC for nearly 40 years. Special thanks to Philip Hamilton for coordinating data availability and Richard Pace for general guidance on all things right whale-related.

TABLES

Table 1. Posterior summaries of main parameters from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*) from 1990-2023. Parameters include: logit-linear coefficients for sighting probability, including the intercept (α_0) and the effect of individuals being female (α_{female}); logit-linear coefficients for survival probability, including the intercept (β_0), the linear effect of age from 0-5 (β_{age}), the effect of being an adult female (β_{female}), and the regime effect for years after 2010 (β_{regime}); the probability of a whale being female (π_{female}); the inclusion probability for population membership (ψ); the standard deviation of individual variation in sighting probability ($\sigma^{p(i)}$); the standard deviation of temporal variation in sighting probability ($\sigma^{p(t)}$); and the standard deviation of temporal variation in survival probability ($\sigma^{\phi(t)}$).

	mean	sd	2.5%	50%	97.5%	Rhat	n.eff
α_{female}	-0.260	0.136	-0.522	-0.261	0.011	1.00	2138
α_0	2.206	0.093	2.029	2.206	2.390	1.00	1711
β_{age}	0.212	0.037	0.138	0.213	0.284	1.00	10577
β_{female}	-0.341	0.118	-0.572	-0.341	-0.114	1.00	11705
β_{regime}	-0.743	0.200	-1.129	-0.743	-0.346	1.00	2465
β_0	3.099	0.182	2.758	3.097	3.469	1.00	6057
π_{female}	0.965	0.024	0.910	0.969	0.998	1.00	6598
ψ	0.460	0.019	0.424	0.460	0.497	1.00	11861
$\sigma^{p(i)}$	1.390	0.059	1.281	1.388	1.510	1.00	1519
$\sigma^{p(t)}$	1.032	0.139	0.798	1.018	1.342	1.00	7543
$\sigma^{\phi(t)}$	0.442	0.095	0.281	0.433	0.652	1.00	2053

Table 2. Posterior summaries of estimated population sizes from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*), including an integration of known calf counts, from 1990-2023.

	Year	mean	sd	2.5%	50%	97.5%
N[1]	1990	287.53	3.18	281	288	294
N[2]	1991	296.07	3.41	290	296	303
N[3]	1992	303.66	3.15	297	304	310
N[4]	1993	297.62	3.11	292	298	304
N[5]	1994	302.53	2.68	298	302	308
N[6]	1995	303.69	2.55	299	304	309
N[7]	1996	318.55	2.70	314	318	324
N[8]	1997	328.15	2.72	323	328	334
N[9]	1998	327.80	2.55	323	328	333
N[10]	1999	326.42	2.23	322	326	331
N[11]	2000	318.20	1.88	315	318	322
N[12]	2001	346.30	1.76	343	346	350
N[13]	2002	354.44	1.49	352	354	358
N[14]	2003	363.92	1.54	361	364	367
N[15]	2004	371.83	1.54	369	372	375
N[16]	2005	396.99	1.28	395	397	400
N[17]	2006	404.20	1.40	402	404	407
N[18]	2007	413.32	1.09	412	413	416
N[19]	2008	431.56	1.15	430	431	434
N[20]	2009	466.61	1.23	465	466	469
N[21]	2010	476.86	1.74	474	477	480
N[22]	2011	483.58	1.81	480	483	487
N[23]	2012	474.20	2.48	470	474	479
N[24]	2013	479.09	3.08	473	479	485
N[25]	2014	476.02	2.98	470	476	482
N[26]	2015	470.39	4.38	462	470	479
N[27]	2016	456.13	3.58	450	456	464
N[28]	2017	431.63	2.45	427	431	437
N[29]	2018	388.70	1.59	386	389	392
N[30]	2019	378.91	1.34	377	379	382
N[31]	2020	358.13	1.64	355	358	362
N[32]	2021	369.28	1.45	367	369	372
N[33]	2022	366.96	2.07	363	367	371
N[34]	2023	371.91	5.76	360	372	383

Table 3. Posterior summaries of estimated deaths from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*) from 1990-2023. Note: these deaths do not include early calf losses (< 6 months).

	Year range	mean	sd	2.5%	50%	97.5%
Nd[2]	1990-1991	6.11	1.58	3	6	9
Nd[3]	1991-1992	3.51	1.50	1	3	7
Nd[4]	1992-1993	12.49	2.12	8	12	17
Nd[5]	1993-1994	5.15	1.67	2	5	9
Nd[6]	1994-1995	4.25	1.28	2	4	7
Nd[7]	1995-1996	6.65	1.54	4	7	10
Nd[8]	1996-1997	9.24	1.73	6	9	13
Nd[9]	1997-1998	4.84	1.52	2	5	8
Nd[10]	1998-1999	9.79	1.90	6	10	14
Nd[11]	1999-2000	8.97	1.70	6	9	13
Nd[12]	2000-2001	5.91	1.19	4	6	9
Nd[13]	2001-2002	10.87	1.22	8	11	13
Nd[14]	2002-2003	10.49	1.48	8	10	13
Nd[15]	2003-2004	7.75	1.49	5	8	11
Nd[16]	2004-2005	4.51	1.25	2	4	7
Nd[17]	2005-2006	12.54	1.44	10	13	15
Nd[18]	2006-2007	12.02	1.33	10	12	15
Nd[19]	2007-2008	5.63	1.10	4	6	8
Nd[20]	2008-2009	5.11	1.04	3	5	7
Nd[21]	2009-2010	9.83	1.61	7	10	13
Nd[22]	2010-2011	14.10	1.62	11	14	17
Nd[23]	2011-2012	16.52	2.34	12	17	21
Nd[24]	2012-2013	11.27	2.70	6	11	17
Nd[25]	2013-2014	11.30	2.76	6	11	17
Nd[26]	2014-2015	18.45	4.07	11	18	26
Nd[27]	2015-2016	28.43	4.56	20	28	38
Nd[28]	2016-2017	29.64	3.64	23	29	37
Nd[29]	2017-2018	42.92	2.63	38	43	48
Nd[30]	2018-2019	16.85	1.64	14	17	20
Nd[31]	2019-2020	31.00	1.70	28	31	34
Nd[32]	2020-2021	7.88	1.28	6	8	11
Nd[33]	2021-2022	12.61	1.68	9	13	16
Nd[34]	2022-2023	5.60	4.17	0	5	15

FIGURES

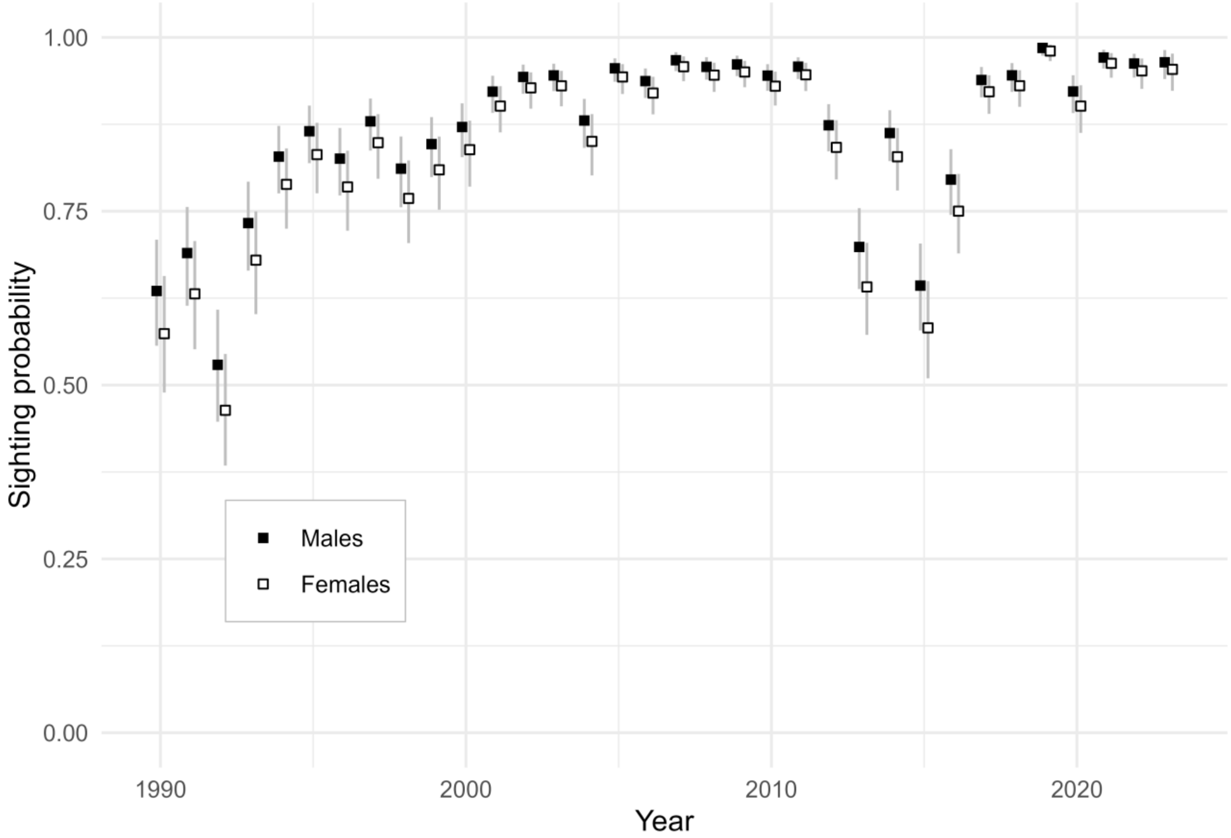

Figure 1. Sighting probabilities for North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2023.

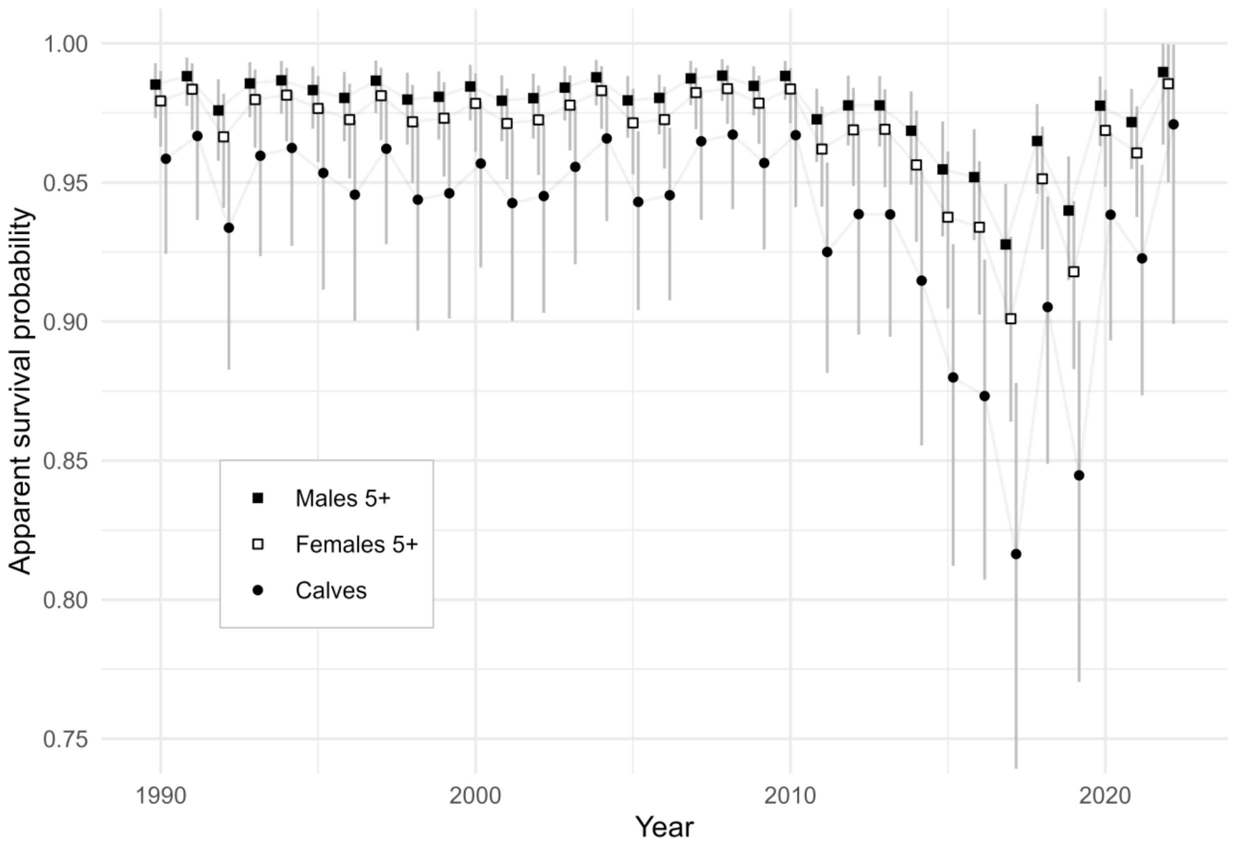

Figure 2. Apparent survival probabilities for North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2023.

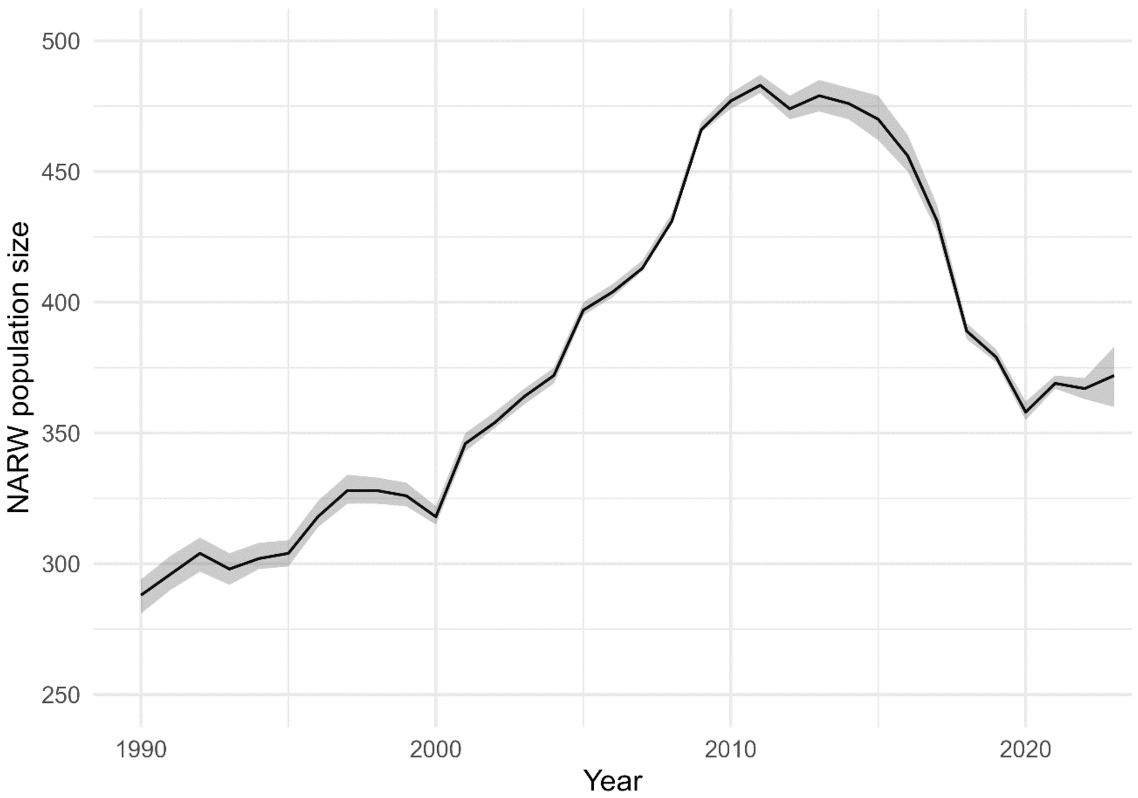

Figure 3. Population size of North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data, including an integration of known calf counts, from 1990-2023. Solid line indicates median of posterior distribution with shading for the 95% credible interval.

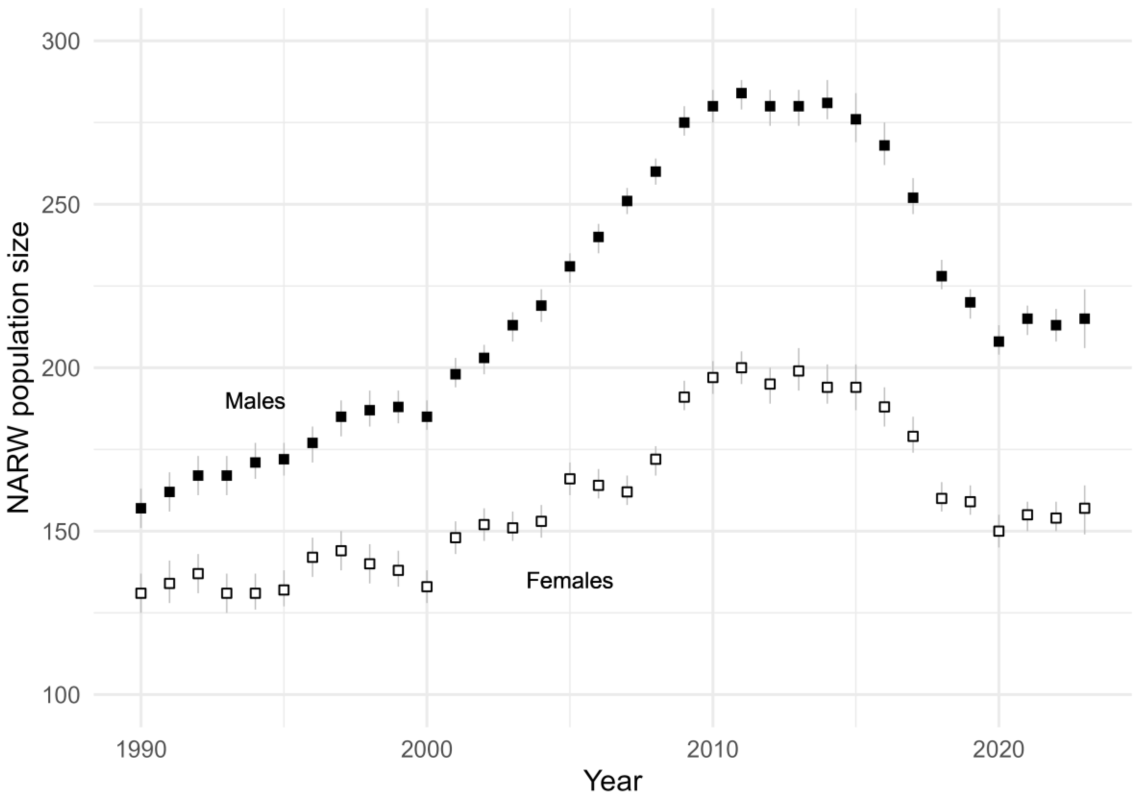

Figure 4. Median abundance (with 95% credible intervals) of female and male North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2023.

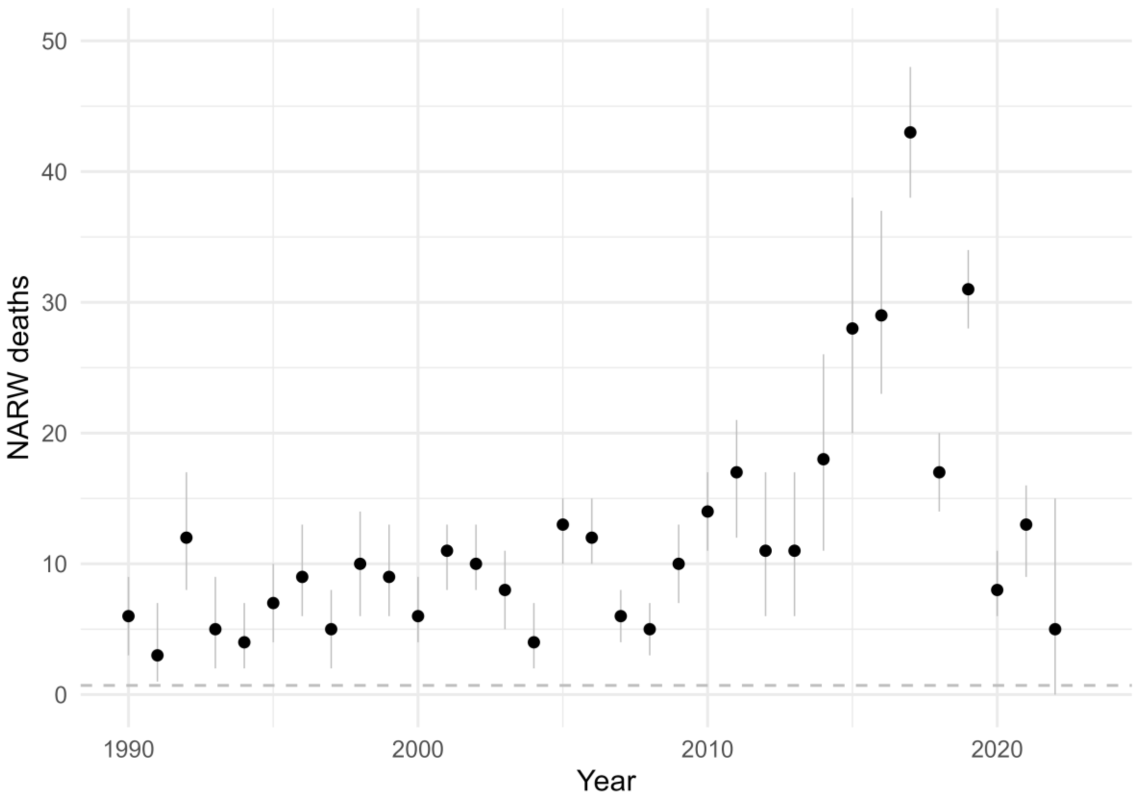

Figure 5. Median deaths (with 95% credible intervals) of North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2023. Note: These deaths do not include early calf losses (< 6 months).

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