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Population size estimation of North Atlantic right whales from 1990-2022

**US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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Northeast Fisheries Science Center
Woods Hole, Massachusetts
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SUMMARY

This report serves to update the population size estimate of North Atlantic right whales (*Eubalaena glacialis*; hereafter, right whales) at the beginning of 2022 using the most recent year of available sightings data (collected through December 2022). Using an established capture-recapture framework (Pace et al. 2017), the estimated population size in 2022 was 356 whales, with a 95% credible interval ranging from 346 to 363. Given uncertainty in the accuracy of the terminal year estimate (Pace 2021), interpretations should focus on the multi-year population trend. 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 2024 Atlantic Stock Assessment Review process.

METHODS

We used a Bayesian version of a multistate Jolly-Seber capture-recapture model fit to sightings records of North Atlantic right whales to estimate population parameters including annual abundance and survival. The general approach has been described in detail elsewhere (Pace et al. 2017; Pace 2021). Here, we 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 22 September 2023 that included >78,000 sightings of 747 whales observed from 1990-2022. 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 (1 December-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 (seen or not seen) indicating whether an individual (i) was sighted in the given survey year (t) across a total of 33 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, 5 whales seen during the 2023 calving season and not seen in 2022 were assigned a known alive state for 2022. 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 ($z_{i,t} = \text{NA}$).

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 we 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). We 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:

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

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:

$$\mathbf{\Theta} = z_{i,t} \begin{matrix} & y_{i,t} \\ \begin{bmatrix} 0 & 1 \\ p_{i,t} & 1 - p_{i,t} \\ 0 & 1 \end{bmatrix} \end{matrix}$$

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 therefore 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. We 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, we added 300 additional capture histories, resulting in $M = 1047$ 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:

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

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

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

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

$$\text{logit}(\phi_{i,t}) = \beta_0 + \beta_{age} \times \text{Age}_{i,t} + \beta_{female} \times \text{Sex}_i \times \text{Adult}_{i,t} + \epsilon_t^\phi$$

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; and ϵ_t^ϕ is the random effect of year. For sighting probability:

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

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.

We 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, we 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.

We 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 20,000 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 multistate capture-recapture model achieved convergence and exhibited similar patterns to Pace (2021) 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 ($\alpha_{female} = -0.248$ [-0.534, 0.038]) than males (Figure 1). There was strong evidence of reduced survival for adult females ($\beta_{female} = -0.380$ [-0.618, -0.142]) and younger whales ($\beta_{age} = 0.206$ [0.130, 0.278]) and for all individuals after 2010 ($\beta_{regime} = -0.720$ [-1.120, -0.295]). While post-2010 survival probability was lower on average, annual fluctuations suggest recent increases in survival from the lows in 2017 and 2019 (Figure 2).

The most recent estimate of total population size in 2022 was 356 whales, with a 95% credible interval ranging from 346 to 363. The population continues to be in decline since 2011 (Table 2; Figure 3), though the short-term trend is equivocal due to the recent increase in survival. Given the lower average survival for adult females, patterns in sex-specific abundance continue to separate across time series (Figure 4), as originally noted by Pace et al. (2017). Predicted number of deaths continued to be lower from 2021–2022 compared to the highs from 2014–2020 (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

We are grateful to the NARWC and NEAq 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 AND FIGURES

Table 1. Posterior summaries of main parameters from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*) from 1990-2022. 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}	-0.248	0.145	-0.534	-0.248	0.038	1.00	2024
α_0	2.296	0.096	2.104	2.295	2.488	1.00	1674
β_{age}	0.206	0.038	0.130	0.206	0.278	1.00	11326
β_{female}	-0.381	0.121	-0.618	-0.380	-0.142	1.00	12000
β_{regime}	-0.718	0.207	-1.120	-0.720	-0.295	1.00	1892
β_0	3.060	0.180	2.718	3.058	3.410	1.00	5808
π_{female}	0.460	0.019	0.424	0.460	0.497	1.00	11971
ψ	0.737	0.014	0.711	0.738	0.764	1.00	6146
$\sigma^{p(i)}$	1.430	0.064	1.309	1.428	1.559	1.01	1509
$\sigma^{p(t)}$	0.989	0.137	0.764	0.975	1.299	1.00	7953
$\sigma^{\phi(t)}$	0.446	0.097	0.284	0.436	0.664	1.00	1848

Table 2. Posterior summaries of estimated population sizes ($N[t]$) from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*) from 1990-2022.

	Year	mean	sd	2.5%	50%	97.5%
N[1]	1990	261.658	1.658	259	261	265
N[2]	1991	269.033	2.041	266	269	274
N[3]	1992	279.514	1.974	276	279	284
N[4]	1993	276.115	1.858	273	276	280
N[5]	1994	286.040	1.415	284	286	289
N[6]	1995	291.836	1.291	290	292	295
N[7]	1996	303.216	1.626	300	303	307
N[8]	1997	313.498	1.574	311	313	317
N[9]	1998	312.783	1.590	310	313	316
N[10]	1999	311.642	1.592	309	311	315
N[11]	2000	308.505	1.207	307	308	311
N[12]	2001	332.979	0.950	332	333	335
N[13]	2002	345.205	1.051	344	345	348
N[14]	2003	359.663	1.222	358	360	362
N[15]	2004	367.825	1.257	366	368	371
N[16]	2005	391.527	1.087	390	391	394
N[17]	2006	402.121	1.328	400	402	405
N[18]	2007	412.247	1.065	411	412	415
N[19]	2008	430.587	1.140	429	430	433
N[20]	2009	462.580	1.199	461	462	465
N[21]	2010	476.174	1.745	473	476	480
N[22]	2011	481.101	1.703	478	481	485
N[23]	2012	472.016	2.492	467	472	477
N[24]	2013	478.235	3.220	472	478	485
N[25]	2014	473.876	3.176	468	474	480
N[26]	2015	469.367	4.433	461	469	479
N[27]	2016	453.425	3.715	447	453	461
N[28]	2017	430.786	2.665	426	431	436
N[29]	2018	388.806	1.858	386	389	393
N[30]	2019	378.568	1.743	376	378	382
N[31]	2020	355.838	2.107	352	356	360
N[32]	2021	363.789	2.239	360	364	369
N[33]	2022	355.327	4.465	346	356	363

Table 3. Posterior summaries of estimated deaths (Nd[t]) from multistate capture-recapture model of North Atlantic right whales (*Eubalaena glacialis*) from 1990-2022.

	Year range	mean	sd	2.5%	50%	97.5%
Nd[2]	1990-1991	7.772	1.906	4	8	11
Nd[3]	1991-1992	3.697	1.601	1	4	7
Nd[4]	1992-1993	13.469	2.186	9	13	18
Nd[5]	1993-1994	5.146	1.670	2	5	9
Nd[6]	1994-1995	4.257	1.237	2	4	7
Nd[7]	1995-1996	6.725	1.545	4	7	10
Nd[8]	1996-1997	9.805	1.697	7	10	13
Nd[9]	1997-1998	4.742	1.472	2	5	8
Nd[10]	1998-1999	10.188	1.744	7	10	14
Nd[11]	1999-2000	9.162	1.494	7	9	12
Nd[12]	2000-2001	5.616	1.042	4	5	8
Nd[13]	2001-2002	10.833	1.104	9	11	13
Nd[14]	2002-2003	10.606	1.352	8	11	13
Nd[15]	2003-2004	7.885	1.360	5	8	11
Nd[16]	2004-2005	4.360	1.208	2	4	7
Nd[17]	2005-2006	12.473	1.352	10	12	15
Nd[18]	2006-2007	11.921	1.302	10	12	15
Nd[19]	2007-2008	5.720	1.074	4	6	8
Nd[20]	2008-2009	5.125	1.020	3	5	7
Nd[21]	2009-2010	9.527	1.638	6	9	13
Nd[22]	2010-2011	14.206	1.645	11	14	18
Nd[23]	2011-2012	15.185	2.335	11	15	20
Nd[24]	2012-2013	12.180	2.893	7	12	18
Nd[25]	2013-2014	11.510	2.936	6	11	18
Nd[26]	2014-2015	18.985	4.096	11	19	27
Nd[27]	2015-2016	29.229	4.627	21	29	39
Nd[28]	2016-2017	29.729	3.704	23	30	37
Nd[29]	2017-2018	42.995	2.756	38	43	49
Nd[30]	2018-2019	17.286	1.796	14	17	21
Nd[31]	2019-2020	31.885	1.925	28	32	36
Nd[32]	2020-2021	7.419	1.469	5	7	10
Nd[33]	2021-2022	8.602	3.754	3	8	17

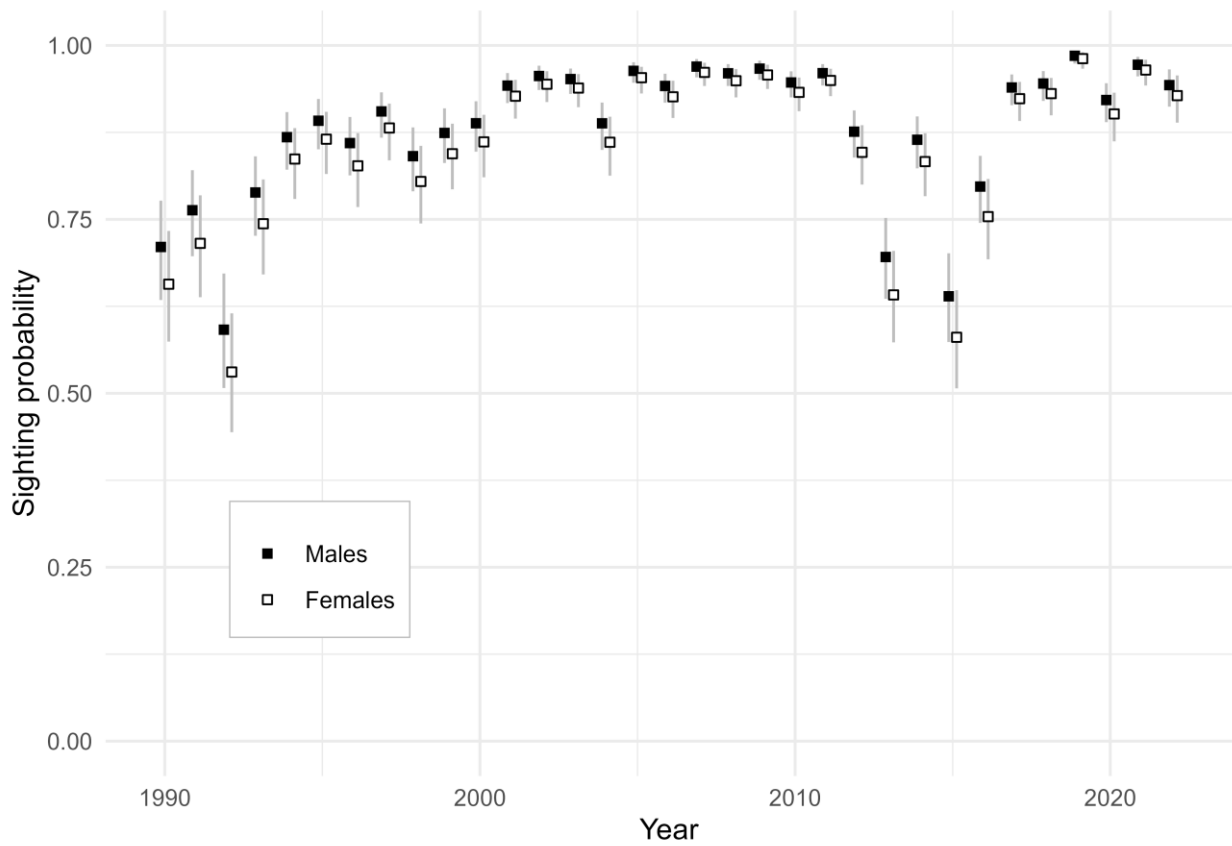


Figure 1. Sighting probabilities for North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2022.

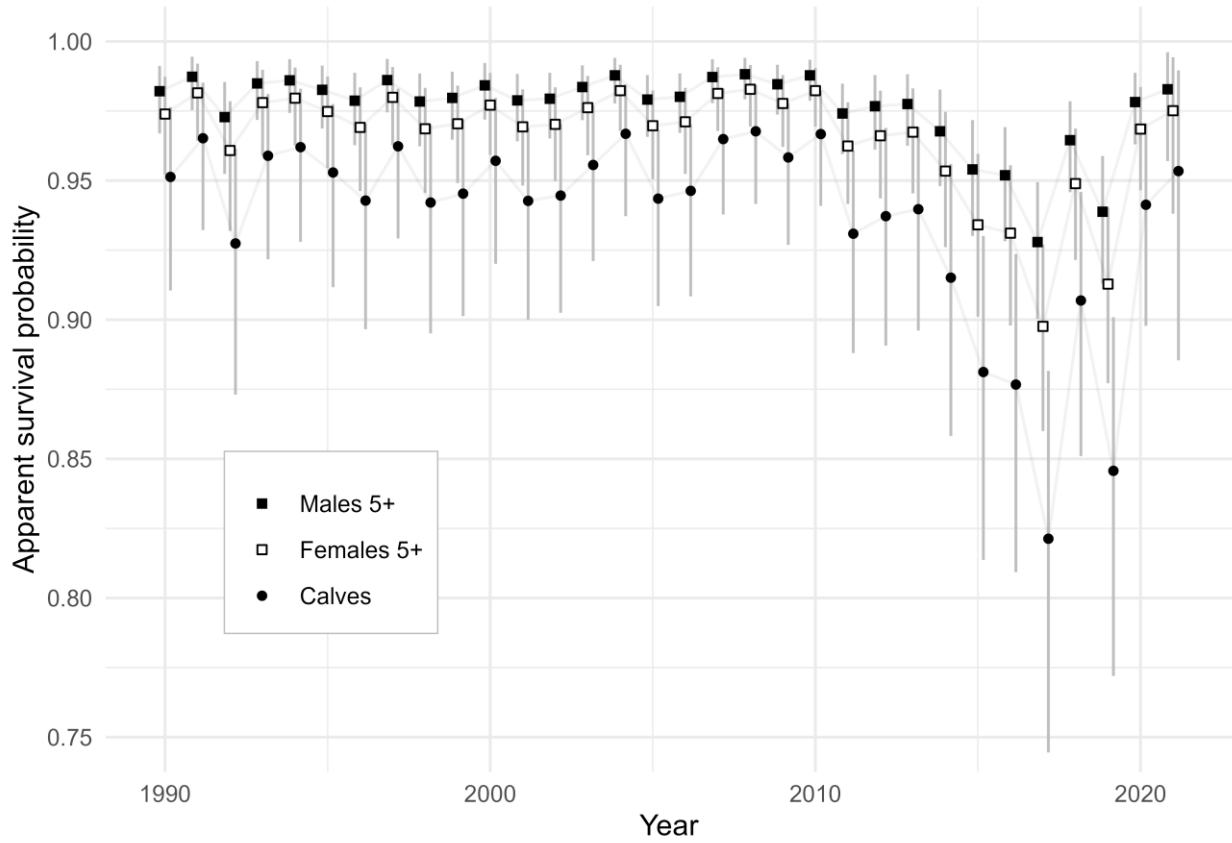


Figure 2. Apparent survival probabilities for North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2022.

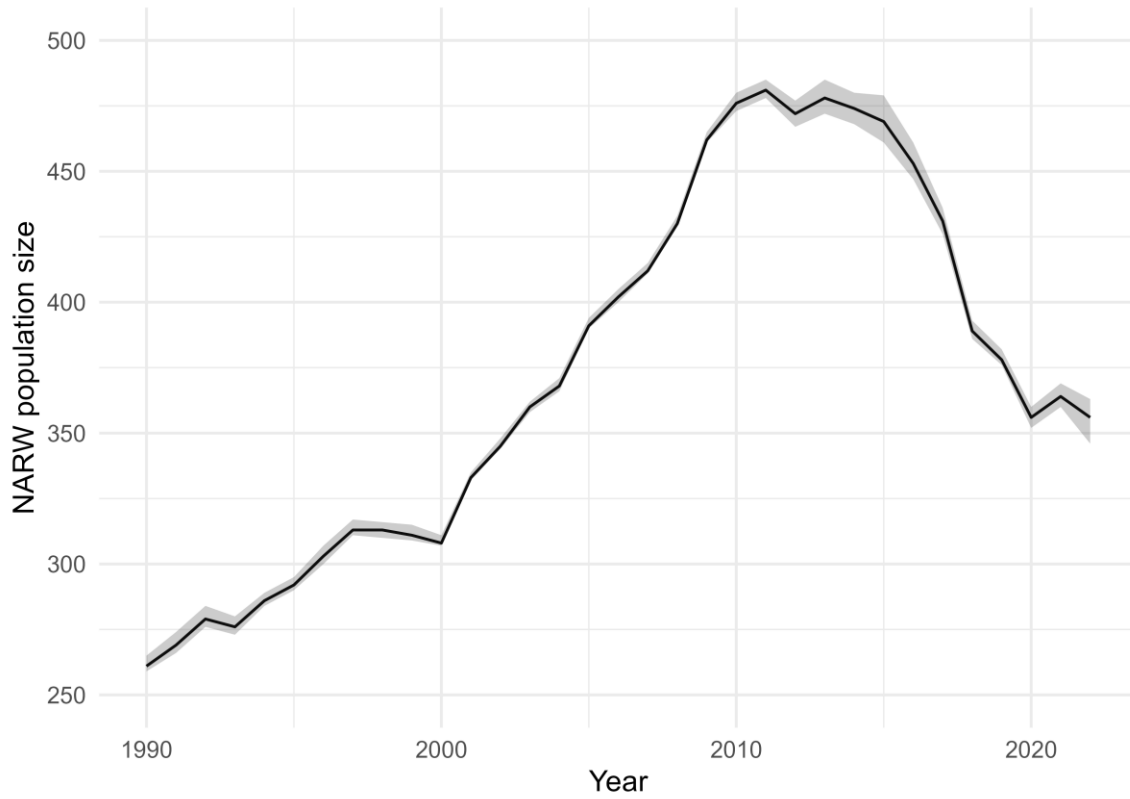


Figure 3. Population size of North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2022. Solid line indicates median of posterior distribution, with shading for the 95% credible interval.

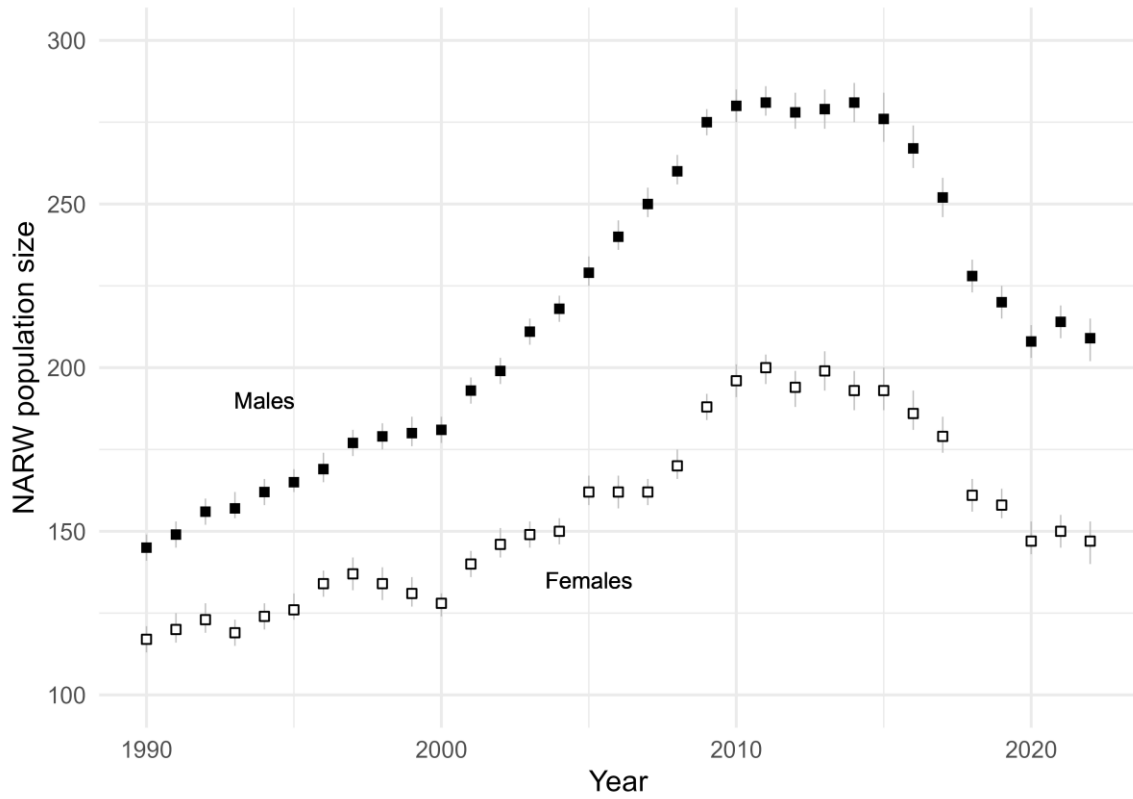


Figure 4. Median abundance (with 95% credible intervals) of female and male North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2022.

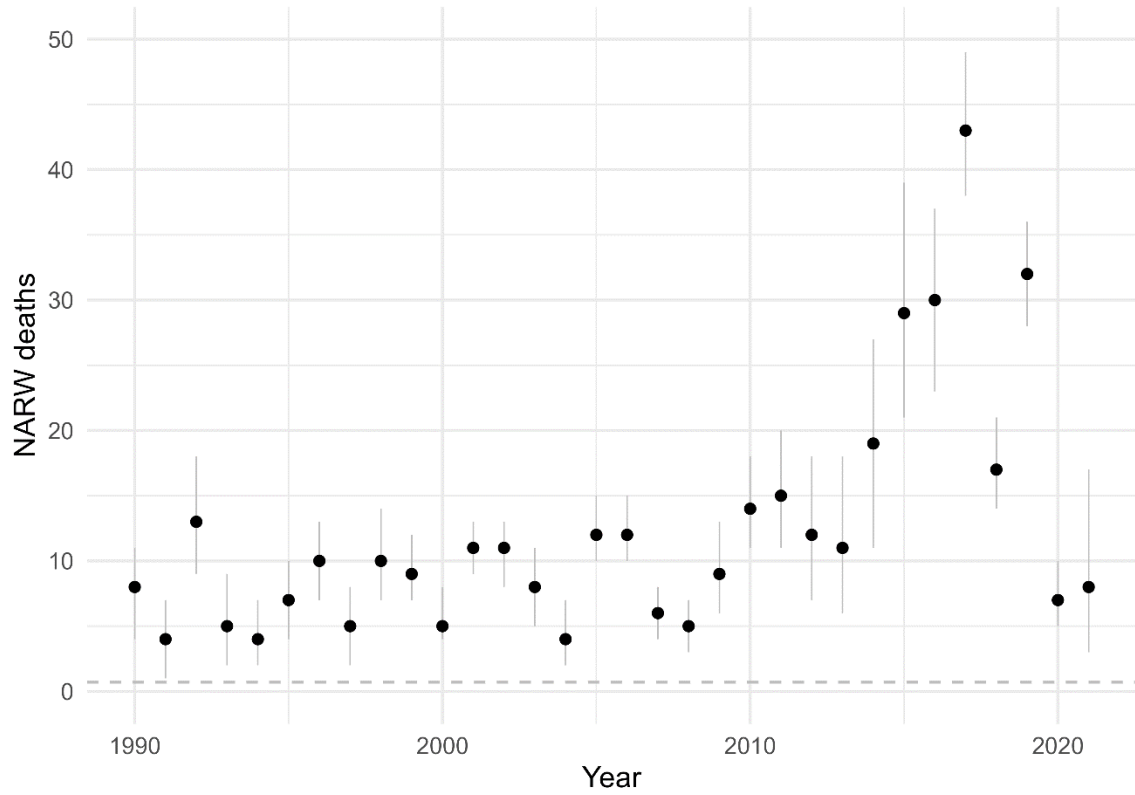


Figure 5. Median deaths (with 95% credible intervals) of North Atlantic right whales (*Eubalaena glacialis*) estimated from a Bayesian capture-recapture model of sightings data from 1990-2022. Gray dotted line indicates the Potential Biological Removal for right whales at 0.7 deaths a year.

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