Historical anchored (Type A) tags were associated with negative effects on North Atlantic right whale survival and reproduction

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ABSTRACT

Tagging data can provide critical information to support the conservation of marine mammal species, but these benefits must be balanced against any potential adverse effects on the health and vital rates of tagged individuals, particularly in endangered populations. Data from historical tag deployments can be used to evaluate these effects. Here, we expand a model for the Population Consequences of Multiple Stressors to investigate the effects of invasive tags deployed from the late 1980s through 2001 on the health, survival and reproduction of critically endangered North Atlantic right whales (*Eubalaena glacialis*). Historical tags deployed on this species include anchored (Type A) tags and consolidated (Type C) tags. The effects of these deployments were explored alongside the effects of other stressors included in the model (entanglements, vessel strikes and prey abundance). Our results indicate that historical anchored (Type A) tags had a negative effect on the health of tagged individuals, which is linked in the model with their survival and calving probabilities. We found limited evidence in additional exploratory analyses that confounding factors may have affected our findings. In contrast, we did not detect any effect of historical consolidated (Type C) tags. This study demonstrates the utility of our modelling approach for assessing the effects of invasive tagging on the survival and reproduction of tagged individuals. The model could be used to explore the effects of future deployments on this critically endangered species, contributing to improve tag design and inform future permitting decisions.

KEYWORDS: EUBALAENA GLACIALIS; HEALTH; MONITORING; SATELLITE TAGGING; SURVIVAL; REPRODUCTION; TELEMETRY

INTRODUCTION

Biologgers that record and transmit data on animal location (hereafter ‘tags’) have been deployed on various species of baleen whales to track their movements and habitat use (Andrews *et al.*, 2019; Hays *et al.*, 2019). The attachment of tags to the body of whales has been achieved using different designs over the years. While non-invasive suction-cap tags can be used to measure whale behaviour for a few hours (e.g., Johnson & Tyack, 2003), tracking individuals for longer periods involves the use of invasive instruments that require implantation in the dermal/hypodermal tissue, or penetration and anchoring at or below the blubber-muscle interface (Andrews *et al.*, 2019), with potential consequences for the health and vital rates of tagged animals (Weller, 2008). Collecting sufficient follow-up data on individuals in these wide-ranging and long-lived species is challenging, which has resulted in only a limited number of studies investigating the occurrence of any adverse effects of tagging (Weller, 2008; Andrews *et al.*, 2019; Gulland *et al.*, 2024). Reported effects on large whales include short-term behavioural responses to the tagging procedure (Mate *et al.*, 2007) and variable tissue responses (e.g., a divot or some swelling)

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around the tag site (Kraus *et al*., 2000; Mate *et al.*, 2007). When tagged individuals could be resighted over subsequent years, there was no indication of long-term effects on their health (Mate *et al.*, 2007), survival (Kraus *et al.*, 2000; Mizroch *et al.*, 2011) or reproductive rate (Best *et al.*, 2015; cf., Gendron *et al.*, 2015). Gulland *et al.* (2024) used long-term photographic monitoring of humpback whales (*Megaptera novaeangliae*) to describe a series of local tissue responses to tagging, which were mostly related to tag design, breakage and position of insertion. However, they observed progressive skin healing and scar contraction, highlighting minimal detectable long-term effects at tag sites. Early reports from this monitoring program also did not find any changes in resighting rates or apparent reproductive rates for tagged individuals (Robbins *et al*., 2013).

North Atlantic right whales (NARW; *Eubalaena glacialis*) are critically endangered (Pettis *et al.*, 2023; Runge *et al.*, 2023) as a result of a combination of multiple stressors that have lethal and sublethal effects on individuals (e.g., Knowlton *et al.*, 2012; van der Hoop *et al.*, 2017; Davies & Brillant, 2019; Sharp *et al.*, 2019; Meyer-Gutbrod *et al.*, 2021; Moore *et al.*, 2021; Stewart *et al.*, 2021; Pirotta *et al.*, 2023, 2024; Reed *et al.*, 2024). Satellite telemetry tags have been used to monitor the long-term movements of NARW between the late 1980s and the early 2000s (Mate *et al.*, 1997; Kraus *et al.*, 2000), but knowledge gaps on their migratory behaviour, seasonal distribution, habitat use and exposure to anthropogenic threats remain. In September 2023, there was a workshop hosted by the Marine Mammal Commission, the National Oceanic and Atmospheric Administration (NOAA) and the Office of Naval Research in the US, in coordination with Fisheries and Oceans Canada, to inform planning and permitting decisions regarding potential future tagging of NARW (Marine Mammal Commission, 2024), where the participants identified the assessment of the effects of historical tag deployments as an important next step for research on this topic.

The Population Consequences of Multiple Stressors (PCoMS) model provides a conceptual framework to link the exposure of individuals to stressors and the long-term effects on the population via changes in behaviour and physiology and their cascading effects on individual health and vital rates (National Academies, 2017; Tyack *et al.*, 2022). This framework was formalised for NARW as a Bayesian state-space model, which can be used to retrospectively quantify the effects of entanglements, vessel strikes and prey abundance on the health, survival and reproduction of individual whales (Pirotta *et al.*, 2023, 2024). The model can be readily expanded to include the deployment of an invasive tag as one of the stressors potentially affecting an individual. The objective of this study was therefore to use the existing PCoMS model for NARW to evaluate the occurrence and magnitude of any effects of invasive tags with historical designs (no longer in use) that were previously deployed on individuals in this critically endangered population.

MATERIALS & METHODS

Invasive tagging of North Atlantic right whales

Seventy-five invasive tags were deployed on 70 individual NARW between 1988 and 2001. Deployed tags were of two types: anchored (Type A) tags and consolidated (Type C) tags. As per definitions in Andrews *et al.* (2019), the electronics package in anchored tags is 'external to the skin, attached by one or more anchors that puncture and terminate below the skin'. In contrast, in consolidated tags, the 'electronics and retention elements are consolidated into a single implanted anchor. The electronics are typically inside a metal case, usually a cylinder, designed to be partially implanted in the body, with only a small part of the top of the tag and antenna and/or sensors projecting above the skin. Retention barbs, or petals, are connected directly to the implanted package.' The two tag types deployed on NARW correspond to a range of historical tag designs, described in detail in Mate *et al.* (1997, 2007) and Kraus *et al.* (2000). Briefly, tags of Type A with design BM-SAT-A, BM-SAT-B or BM-SAT-C rested externally along the whale's back and were anchored using curved stainless-steel tines or shafts. In contrast, tags of Type C with design NEA-SAT and NEA-RAD consisted of a stainless-steel cylinder with a variable number of cutting edges in the nose cone and folding retention toggles between the blades. JG-RAD and JG-SAT tags included Type A and Type C tags, with various designs (e.g., projectile-shaped tags, cylindrical aluminium housing with a stainless-steel anchor and partially implantable tags with external tag housing). Telonics transmitters were mounted into various designs, including Type A tags (ST-3 and ST-6) that had an external cylinder, and Type C tags (ST-15) that could be fully implanted beneath the whale's skin.

Thirty-three of the deployments on NARW were Type A tags and 42 were Type C tags. Of the 70 tagged individuals, 41 were females and 28 were males, while the sex was unknown for one. Of the 75 total deployments, 38 tags were deployed on adults, 23 on juveniles, two on calves and 12 on individuals of unknown class (but treated as juveniles when selecting matching controls in our analysis). In some cases, an individual's age class changed between different deployments.

Data on tag deployments and tag type were compiled and provided by Dr. Amy Knowlton at the New England Aquarium, using information derived from the NARW Consortium Database. Details of the tag type and design for each deployment included in this work are reported in Table S1.

Statistical analysis

The existing PCoMS model for NARW (Pirotta *et al.*, 2023) is a Bayesian state-space model for the survival and calving probability of individual whales as a function of their health status at a three-month time scale. A set of intrinsic (lactation and juvenile status) and extrinsic (occurrence of vessel strike or entanglement and a proxy for prey abundance) variables are modelled to affect underlying health. The model is informed using 1970–2019 data provided by the NARW Consortium[2], comprising individual sightings, health scores from a visual health assessment, known deaths, information on sex, age class and calving and records of anthropogenic traumas. Recently, the model was extended to include a component for individual length, informed by photogrammetric length measurements from drones and estimated to affect female calving probability (Pirotta *et al.*, 2024).

Here, we modelled the effect of tag deployment on underlying health of individual *i* at the time of implantation *t* ($h_{i,t}$), in addition to the other stressors already included in the model (model v1):

$$h_{i,t} \sim \mathrm{Normal}\left(h_{i,t-1} + \sum_{j=1}^{2} \alpha_j \, Z_{j,i,t} + \sum_{k=1}^{9} \beta_k \, W_{k,i,t} + \beta_{10} Y_{i,t}, \sigma \right) \tag{1}$$

where α_j and β_k indicate the effects of the two time-varying intrinsic ($Z_{j,i,t}$, with j = 1, 2) and nine time-varying extrinsic ($W_{k,i,t}$, with k = 1, 2,..., 9) stressors, respectively, and σ is the process standard deviation (Pirotta *et al.*, 2023). Here we include the effect β_{10} of tag deployment in time step *t* ($Y_{i,t}$, a binary variable). We then investigated whether this effect depended on tag type, because of the differences in tag design and potential impact between the two types (model v2). In practice, we estimated a separate coefficient for the effect of deployment for each tag type. Eq. 1 was therefore extended to include two terms, $\beta_{10}\ Y^A_{i,t}$ and $\beta_{11}\ Y^C_{i,t}$, where $Y^A_{i,t}$ and $Y^C_{i,t}$ are binary variables indicating the deployment of a tag of Type A or Type C, respectively.

There is some uncertainty as to the duration of tag attachment because satellite transmission can stop before the tag detaches from the body of the animal. Therefore, we only modelled the effect of tagging on the individual's health state in the time step where deployment occurred. However, the coarse temporal resolution of the model (three months) implies that any effect could be protracted over that time window. Moreover, underlying health is autocorrelated over time, i.e., health in one time step depends on health in the previous time step. As a result, an individual may take multiple time steps to recover from a decline in its health. Finally, if the tag had a continued, detectable effect on health throughout the duration of the deployment, this would be reflected in a stronger estimated effect at deployment (as evidenced by previous analysis of the effects of entanglements and vessel strikes (Pirotta *et al*., 2023)).

In the model, survival probability $\vartheta_{i,t}$ emerges from a direct transformation of health (Pirotta *et al.*, 2023), via a complementary log-log link function:

$$\mathrm{c}\log\log(\vartheta_{i,t}) = h_{i,t} \tag{2}$$

$$s_{i,t} \sim \mathrm{Bernoulli}(\vartheta_{i,t}\ s_{i,t-1}) \tag{3}$$

where survival $s_{i,t}$ = 1 when the individual is alive and 0 when it is dead. Survival status is 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 is unknown and estimated for intervals between the last sighting and an observed death, or for two years

[2] *www.narwc.org/narwc-databases.html*

after the last sighting. Any effect on health is converted into the corresponding change in survival probability at a three-month scale.

Calving is considered to occur in the Dec–Jan interval of years when females are available to calve (i.e., alive, sexually mature, not in a pregnancy year and not resting in a year after calving). Calving probability in a year *y* when a female *i* is available to reproduce, $\varphi_{i,y}$, depends in the model on the female's health in the Sep–Nov time step, *t*(*y*), prior to *y* ($h_{i,t(y)}$):

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

where $m_{i,y}$ is the asymptote of the sigmoid relationship representing the maximum calving probability for individual *i* in year *y* (see below), δ is 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 a female is reproductive (i.e., has already calved or may do so in the future). We do not include any temporal dependency, because we only model calving probability in years when a female is available to reproduce, given the species' reproductive cycle. Calving probability is related to observations of calving events:

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

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 is unknown otherwise (and imputed in the Bayesian model).

However, Pirotta *et al.* (2023) showed that only approximately 20% of the variation in calving probability is explained by the health metric in the model, while Pirotta *et al.* (2024) demonstrated that the majority of its variation can be captured by including an effect of body length on calving probability. Therefore, we also tested whether tagging had a direct effect on calving probability that was not mediated by a change in the health metric. First, we assessed the effect of any tagging prior to a potential calving opportunity on the asymptote of the sigmoid relationship between a female's health and her calving probability $m_{i,y}$ (i.e., the effect of tagging on her maximum calving probability; model v3):

$$\text{logit}(m_{i,y}) = M_i + \zeta_1\ L^3_{i,t(y)} + \zeta_2 \tilde{Y}_{i,y} \tag{6}$$

where $M_i \sim$ Normal(λ, χ) is a normally distributed, individual-specific intercept, ζ_1 is the effect of body length $L_{i,t(y)}$ cubed and ζ_2 is the effect of having been tagged at any point prior to *y* ($\tilde{Y}_{i,y}$, a binary variable).

Next, we investigated whether having been tagged in the year immediately prior to a potential calving opportunity, $Y_{i,y-1}$, had any effect on the probability of calving in that year (model v4). These two analyses were also repeated by tag type (model v5 and v6). Standard model diagnostics were used to ensure that the models mixed and converged appropriately (please refer to details in Pirotta *et al.*, 2023).

Analyses of observational data, such as those used here, are subject to potential confounding factors. For example, if there was a general decline in health during the time the tags were deployed, this could be incorrectly interpreted as a tag effect. Moreover, there could have been a bias in selecting the individuals that were tagged. To assess the potential for confounding factors, we undertook a set of exploratory analyses using three simulated counterfactual datasets, where tagging events were allocated to alternative individuals in the population that matched the characteristics of tagged animals.

For each tagged individual, we selected three separate control individuals of the same sex and age class (adult, juvenile or calf) and allocated a simulated tagging event within ±2 years of the real tag deployment (constrained between 1988 and 2001, i.e., the first and last year of tagging). The three resulting datasets were completely independent, i.e., no control individual was shared among them. We also made sure that the number of individuals tagged multiple times was the same as in the real dataset. In these simulated datasets, true tagged individuals were considered non-tagged. With each of these three simulated datasets, we repeated the analysis investigating the effect of tagging on health (models v1 and v2). If an effect is detected on the real dataset but not on the simulated datasets, this means the effect is unlikely to be due to confounding factors.

We also compared the tagged cases with the matched controls in terms of time between tagging event and last sighting (which is a proxy for survival), time to next calving event after tagging and number of calves born between the tagging event and the last sighting. If these metrics are, on average, worse for tagged animals than controls, this supports that any detected effect is not due to confounding.

All parameter estimates reported below are posterior medians followed by 95% equal-tailed credible intervals (CI) in square brackets. Where 95% CIs of the estimated effect of tagging on health include 0, we interpret this as lack of evidence for an effect, given the data and model used.

RESULTS

A total of 728 individual NARW were included in the analysis, of which 437 were estimated to be alive at some point during the period 1988 to 2001 and 70 were instrumented with an invasive tag.

The estimated effect of tag deployment on health (irrespective of tag type; model v1) was centred on a negative value and the 95% CI showed a small overlap with 0 (–0.071 [–0.146, 0.004]). However, the analysis by tag type (model v2) highlighted that only Type A tags had an estimated effect with a 95% CI that did not overlap 0 (–0.138 [–0.257, –0.023] for Type A, vs. –0.028 [–0.127, 0.069] for Type C). The estimated decrease in health in the time step of deployments of Type A tags (Fig. 1) corresponded to a median hazard ratio (i.e., the ratio of the rates of three-month survival in tagged vs. non-tagged animals) of 0.87. In practice, for an individual in good health (e.g., with three-month survival probability of 0.995), being tagged with a Type A tag corresponded to a decrease in three-month survival probability to 0.990 [0.983, 0.994], whereas, for an individual in poor health (e.g., with three-month survival probability of 0.900), being tagged with a Type A tag corresponded to a decrease in three-month survival probability to 0.865 [0.831, 0.895]. In terms of annual survival probability, this corresponded to a decrease from 0.980 to 0.961 [0.935, 0.978] and from 0.656 to 0.561 [0.478, 0.640], respectively.

The 95% CI of the estimated effect of tag deployment on the asymptote of calving probability (irrespective of tag type) overlapped 0, both when considering tag deployment at any point prior to a calving opportunity (model v3; –0.193 [–0.593, 0.228]) and when considering tag deployment at the year prior to a calving opportunity (model v4; 0.130 [–1.262, 1.506]). The 95% CI of the estimated effects also overlapped 0 when conditioning by tag type (model v5: Type A –0.478 [–0.996, 0.038] and Type C 0.136 [–0.371, 0.679]; model v6: Type A 0.384 [–1.197, 2.040] and Type C –0.212 [–1.827, 1.353]). However, we note that the effect of being tagged with a Type A tag in model v5 has a probability of 0.97 of being negative. The median effect would correspond to a decrease in maximum calving probability for the average female in a year when she is available to reproduce from 0.3 to 0.21.

Rerunning models v1 and v2 using the first and third simulated sets of controls (i.e., alternative individuals of the same sex and age class, assumed to have been tagged in the same period as the true tagged individuals) resulted in an estimated effect of tagging that was centred on a positive value and/or largely overlapped 0, both when ignoring tag type and when modelling a separate effect for tags of Type A and C (Table 1). Using the second simulated set of controls, the effect of any tag deployment on health was negative, with a 95% CI that did not overlap 0, while the effects by type were both centred on a negative value and showed some small overlap with 0 (Table 1). We investigated this set of controls and found that four of the randomly selected matched controls

Table 1

Results of the test models run on the simulated datasets, where tag deployments were assigned to a set of control animals.

Test dataset	Model version	Estimated effect(s) on health
1	v1	0.053 [–0.047, 0.149]
1	v2	type A: –0.049 [–0.207, 0.107] type C: 0.116 [–0.01, 0.243]
2	v1	–0.116 [–0.218, –0.017]
2	v2	type A: –0.115 [–0.271, 0.044] type C: –0.114 [–0.249, 0.021]
3	v1	0.044 [–0.052, 0.139]
3	v2	type A: 0.021 [–0.163, 0.209] type C: 0.053 [–0.058, 0.165]

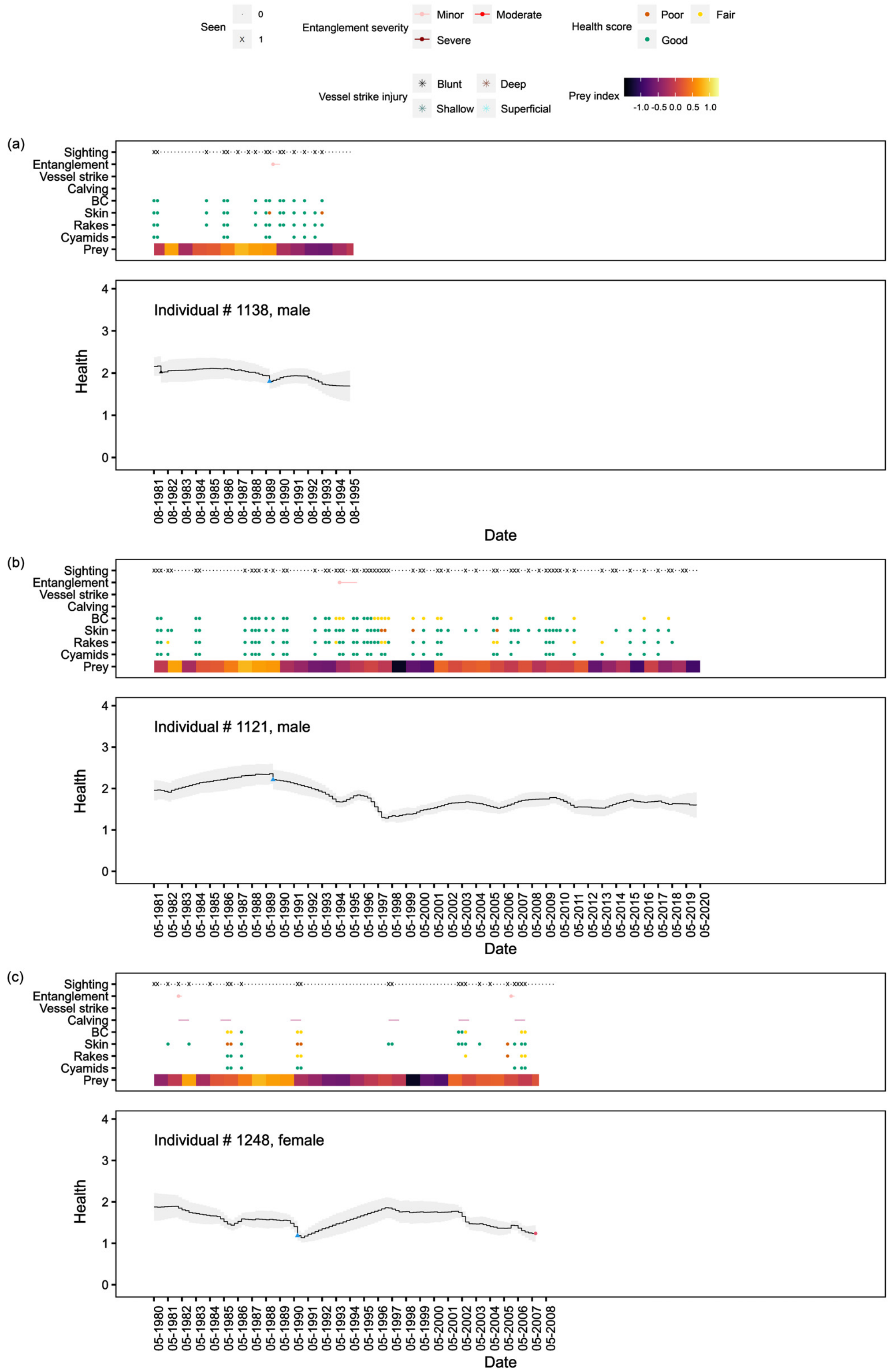

Figure 1. Time series of data streams (top panel) and estimated health (black line and grey ribbon in bottom panel, reporting the posterior mean and standard deviation, respectively) for three NARW individuals that were tagged with a Type A tag at the times shown by the blue triangle on the health trajectory. Health is the complementary log-log 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 estimate of most likely 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[3] and the sex.

[3] *http://rwcatalog.neaq.org*

for Type A tags (vs. three in the real data) and five of the matched controls for Type C tags (vs. three in the real data) were last seen in the time step of simulated deployment, which likely contributed to the estimated effect of these pseudo-deployments.

Comparisons between tagged individuals and matched controls are reported as medians, followed by the range in square brackets. Because only Type A tags had an estimated effect with a 95% CI that did not overlap 0 in the analysis described above, comparisons were limited to individuals instrumented with tags of this type and their matched controls. The comparison of the time between tag deployment and last sighting (as a proxy for survival) indicated that, on average, control individuals tended to be seen for longer after the tagging time step, but with large variation among individuals (18.0 [0, 30.2] years for tagged individuals vs. 21.8 [0, 30.2] years for controls; Fig. 2). In particular, 73% of tagged individuals were known to be alive five years after the tagging date, as opposed to 85% of control individuals, which corresponded approximately to an additional four possible deaths over that time period. Moreover, of the tagged individuals, three were not sighted after the three-month interval in which they were tagged (corresponding to 9% of individuals, vs. 8% of individuals not seen after the three-month interval in which tag deployment was simulated in the matched controls).

The time to the next calving event was also longer on average in tagged females than for controls, but again the variability was large (5.0 [0, 11.2] years for tagged individuals vs. 3.0 [0.2, 20] years for controls; Fig. 3). As a result of the differences in apparent survival and, to a lesser extent, reproduction, the number of calves observed between the tagging event and the last sighting of a female was also higher in control individuals (Fig. 4). Note: because the number of calves is a discrete quantity, the median is the same (3 [1, 7] for tagged individuals and 3 [1, 19] for controls) but the mean is higher (3.2 for tagged individuals vs. 4.4 for controls).

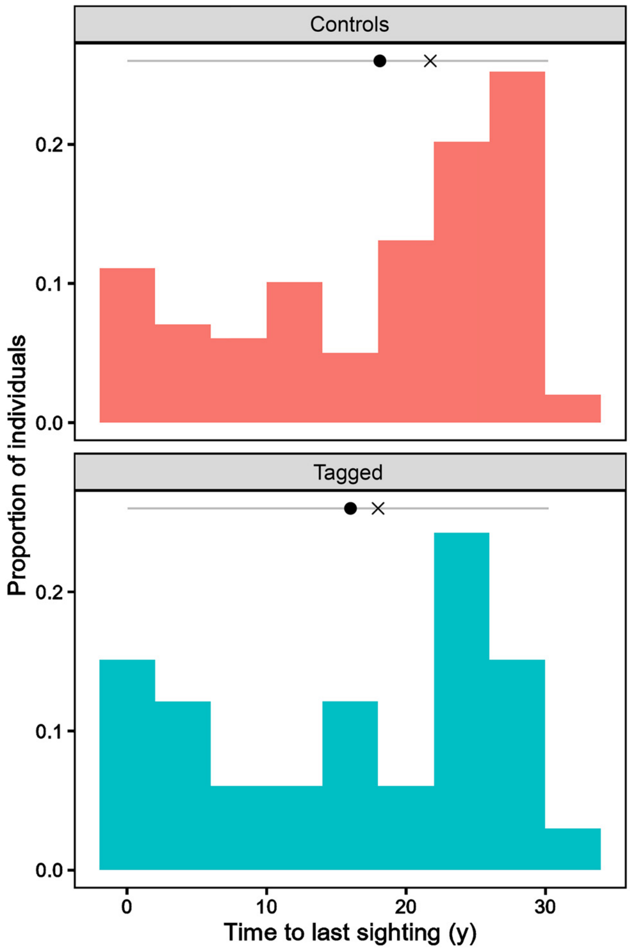

Figure 2. Distribution of time between deployment of a Type A tag (either real or simulated) and the last sighting of an individual, for control and tagged individuals. At the top of each panel, the dot, the cross and the grey bar indicate the posterior mean, median and range, respectively.

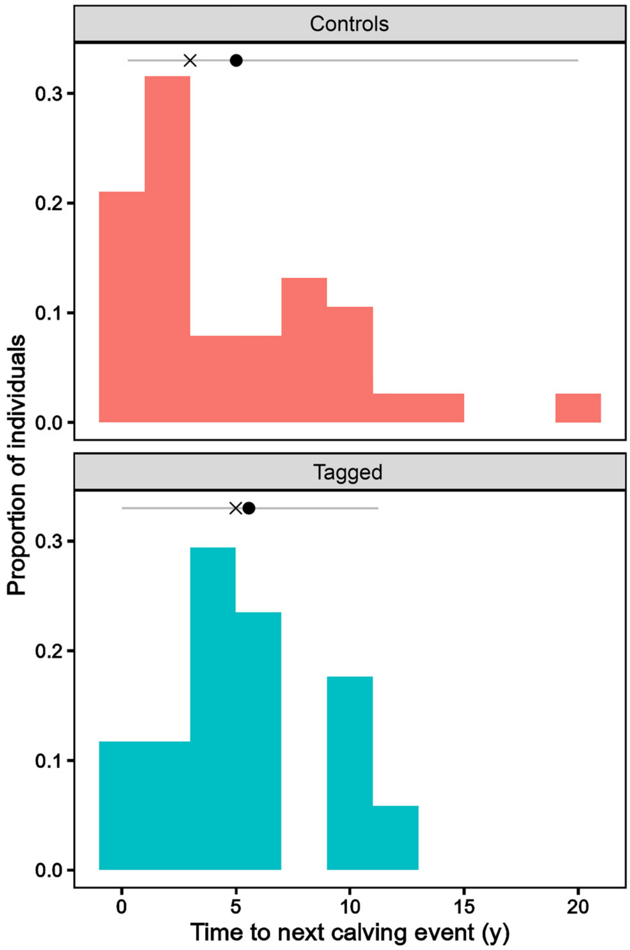

Figure 3. Distribution of time between deployment of a Type A tag (either real or simulated) and the first subsequent calving event, for control and tagged individuals. At the top of each panel, the dot, the cross and the grey bar indicate the posterior mean, median and range, respectively.

DISCUSSION

In this study, we assessed the effects of the historical deployment of invasive tags on the health, survival and reproduction of NARW using a state-space model for the population consequences of multiple stressors (Pirotta *et al.*, 2023, 2024). We detected an effect of historical Type A tags on the health of subject individuals, which corresponded to a decrease in their survival and, to a lesser extent, calving probability. For comparison, the effect of the deployment of a Type A tag on health was estimated to be about 0.6 times the effect of a vessel strike resulting in a shallow wound (which was –0.217 [–0.405, –0.033]) and about 0.3 times the effect of a severe entanglement (which was –0.486 [–0.550, –0.423]) (see Pirotta *et al.* (2023) for definitions of these events). Type A tags are characterised by the electronics package being external to the skin, with anchors that terminate in the dermal or hypodermal tissue along the dorsum (Andrews *et al.*, 2019). Previous work has discussed the design issues (e.g., tag breakage) and physiological impact (e.g., local or regional swelling around tag sites) of early tags of this type (Kraus *et al.*, 2000; Mate *et al.*, 2007). It should be noted that these early designs differ substantially from other anchored tags that are currently used on cetaceans (e.g., Low Impact Minimally Percutaneous Electronic Transmitters, or LIMPETs; Wildlife Computers Inc.). Therefore, the results presented here do not imply that the use of current Type A tags will have the same effect as the historical ones.

It is likely that not all individuals were affected by Type A tag deployment to the same extent. The trajectories of the estimated health of different tagged individuals illustrate this variability: in some cases, tagging was associated with a negative change in the visual health assessment variables that are used to inform the underlying

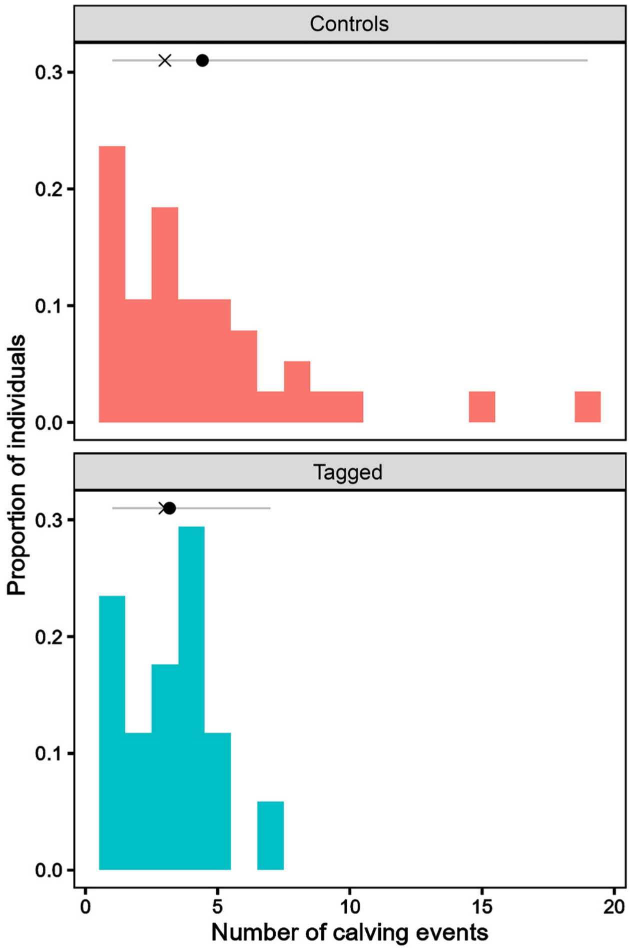

Figure 4. Number of calving events after deployment of a Type A tag (either real or simulated), for control and tagged individuals. At the top of each panel, the dot, the cross and the grey bar indicate the posterior mean, median and range, respectively.

health metric (e.g., Fig. 1a); in others, no change in visual health assessment variables was noted (e.g., Fig. 1b); finally, in some cases, tag deployment coincided with exposure to other extrinsic or intrinsic stressors that may have confounded its effect (e.g., a calving event; Fig. 1c). The estimated effect of tagging on health is averaged across all tagging events and over this variation. Factors that could have contributed to a differential impact include attachment duration (e.g., days vs. weeks), the tag breaking after deployment, variable implantation angle and depth, or simply different physiological reactions between animals. Some of this deployment-specific information is available in the NARW Consortium Database and could be used in further qualitative analyses of each tagging event.

In contrast, we did not detect any effect of historical Type C tags. Our findings do not prove that these tag deployments had no effect on NARW; they only indicate that any putative effect could not be conclusively detected at the spatio-temporal scale at which our model operates and given the sample size of deployments and the nature of the data on individual health that informed the analysis (Pirotta *et al.*, 2023). However, we note that the sample size for Type C tags was larger (n = 42, vs. 33 Type A tag deployments). Therefore, any effect of historical tags of this type was likely smaller than the detected effect of historical Type A tags.

We investigated whether model results could have emerged from other confounding factors operating concurrently with the tagging by simulating three sets of control individuals of the same sex and age class, assumed to have been tagged in the same period as the true tagged individuals. Overall, the results of this exercise indicated that the estimated effect of tagging with historical Type A tags was unlikely to be the result of some other factor affecting health and survival during the tagging period. However, in one of the simulated sets of controls, the effect of tag deployment was estimated to be negative. Further exploration suggested that individuals that were last seen shortly after tag deployment could have affected the results, even if the tag was not necessarily the primary cause of their putative death. There was not a sufficient number of potential control individuals to support additional replication of the case-control exercise and quantify the false positive rate, but this result highlights the issues associated with a small sample size (Andrews *et al.*, 2019). In addition to running the model on the simulated sets of control individuals, we compared the life history performance of tagged individuals (i.e., their apparent survival and reproduction) to their associated controls. We found no evidence in this exploratory data analysis that other confounding factors may have affected our findings.

The current model cannot be used to evaluate the interactive effects of multiple stressors on health or vital rates. Therefore, the present analysis only assessed the occurrence of any effect of tagging in addition to other stressors, but it could not be used to explicitly test interactive effects. Moreover, this analysis was by nature retrospective, i.e., it investigated the occurrence of any effects of past deployments (using the tags available at that time) but cannot provide predictions of the effects of future deployments using different tags. Tag design and deployment practices have substantially evolved since NARW were first tagged in the late 1980 to early 1990s (Mate *et al.*, 2007; Andrews *et al.*, 2019). The NARW PCoMS model could be used to explore the effects of recent tag designs if newer tags are deployed in the future and suitable follow-up data are collected on tagged individuals.

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Supplementary material

Table S1

Details of tag deployments on North Atlantic right whales in 1988–2001. Whale IDs correspond to the individual numbers from the North Atlantic Right Whale Catalog (*http://rwcatalog.neaq.org*). When the exact age was unknown, an individual was marked as either an adult (A) or an individual of unknown class (U). Uncertain tag designs are indicated with a question mark ('?'). Data compiled by Dr Amy Knowlton at the New England Aquarium. Tag designs are described in Mate *et al.* (1997; 2007) and Kraus *et al.* (2000).

Whale ID	Deployment date	Sex	Age	Tag type	Tag design
1705	28/05/1988	F	1	C	JG-RAD
1202	29/05/1988	U	U	C	JG-RAD
1405	29/05/1988	F	4	C	JG-RAD
1624	29/05/1989	M	U	A	JG-RAD
1705	01/06/1989	F	2	A	JG-RAD
1163	03/06/1989	F	8	A	JG-RAD
1903	09/09/1989	M	0	A	JG-RAD
1422	13/09/1989	M	A	A	1989 ST-3?
1611	13/09/1989	F	3	A	1989 ST-3?
1138	21/09/1989	M	8	A	1989 ST-3, BM-SAT-B
1602	21/09/1989	F	3	A	1989 ST-3, BM-SAT-B
1027	12/10/1989	F	A	A	1989 ST-3, BM-SAT-A
1703	12/10/1989	F	2	A	1989 ST-3, BM-SAT-A
1121	15/10/1989	M	A	A	JG-RAD
1146	15/10/1989	M	A	A	1989 ST-3, BM-SAT-A
1428	15/10/1989	M	A	A	1989 ST-3, BM-SAT-B
1135	24/08/1990	F	A	A	1990 ST-6, BM-SAT-C
1140	24/08/1990	F	A	A	1990 ST-6, BM-SAT-C
1152	24/08/1990	M	A	A	1990 ST-6, BM-SAT-C
1248	24/08/1990	F	A	A	1990 ST-6, BM-SAT-C
1127	25/08/1990	F	A	A	1990 ST-6, BM-SAT-C
1981	25/08/1990	M	1	A	1990 ST-6, BM-SAT-C
1629	26/08/1990	F	U	A	1990 ST-6, BM-SAT-C
1941	26/08/1990	F	1	A	1990 ST-6, BM-SAT-C
1702	31/08/1990	M	3	A	JG-RAD
1421	12/09/1990	M	A	A	1990 ST-6, BM-SAT-C
1245	22/09/1990	F	8	A	JG-SAT
1243	27/09/1991	F	9	A	1990 ST-6, BM-SAT-C
1608	28/09/1991	F	5	A	1990 ST-6, BM-SAT-C
1406	05/10/1991	F	7	A	1990 ST-6, BM-SAT-C
2440	09/12/1994	M	0	A	NEA-RAD
1268	01/02/1995	F	A	C	NEA-RAD
1254	27/02/1995	F	A	C	NEA-RAD
1609	10/09/1995	M	9	A	JG-SAT
1802	11/09/1995	F	7	A	JG-SAT
1281	16/09/1995	F	A	A	JG-SAT
1503	16/09/1995	F	10	A	JG-SAT
2220	03/10/1995	M	U	A	JG-SAT
1026	08/10/1995	M	15	C	NEA-SAT-A
1813	08/10/1995	M	U	C	NEA-SAT-A
2250	08/10/1995	M	U	C	NEA-SAT-A
1334	07/02/1996	F	A	C	NEA-SAT-B
1705	08/02/1996	F	9	C	NEA-SAT-B
1812	21/02/1996	F	A	C	NEA-SAT-B
1308	06/09/1996	F	13	C	NEA-SAT-B
1408	16/09/1996	F	12	C	NEA-SAT-B
2610	01/10/1996	F	U	C	NEA-SAT-B
1509	20/01/1997	F	A	C	NEA-SAT-C
1243	22/01/1997	F	15	C	NEA-SAT-C
1405	28/01/1997	F	13	C	NEA-SAT-C
2135	23/04/1997	M	6	C	NEA-SAT-C
1153	18/08/1997	F	17	C	NEA-SAT-D
1125	25/08/1997	F	A	C	NEA-SAT-D
1136	27/08/1997	M	A	C	NEA-SAT-D
1327	29/08/1997	M	A	C	NEA-SAT-D
1122	11/09/1997	M	A	C	NEA-SAT-D
1048	26/09/1997	M	A	C	NEA-SAT-D
1303	04/10/1997	F	A	C	NEA-SAT-D
2223	25/03/1998	F	6	C	CCS RADTG
2710	01/09/1999	F	2	C	NEA-RADTG
2430	09/07/2000	F	U	C	1998 ST-15 D
2645	13/07/2000	F	4	C	1998 ST-15 D
1613	11/08/2000	M	14	C	1998 ST-15 D
2320	11/08/2000	F	U	C	1998 ST-15 D
2743	11/08/2000	M	3	C	1998 ST-15 D
2795	11/08/2000	M	U	C	1998 ST-15 D
1027	12/08/2000	F	A	C	1998 ST-15 D
1114	12/08/2000	F	A	C	1998 ST-15 D
2240	12/08/2000	F	A	C	1998 ST-15 D
2310	12/08/2000	M	U	C	1998 ST-15 D
2601	12/08/2000	F	4	C	1998 ST-15 D
2617	12/08/2000	F	4	C	1998 ST-15 D
3030	12/08/2000	M	U	C	1998 ST-15 D
2614	01/08/2001	F	5	C	1998 ST-15 D
2110	14/08/2001	M	10	C	1998 ST-15 D