Received: 2 July 2020 | Revised: 5 November 2020 | Accepted: 19 November 2020
DOI: 10.1111/csp2.346

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
WILEY

# Cryptic mortality of North Atlantic right whales

**Richard M. Pace III**[1] | **Rob Williams**[2] | **Scott D. Kraus**[3] | **Amy R. Knowlton**[3] | **Heather M. Pettis**[3]

[1]Northeast Fisheries Science Center, Woods Hole, Massachusetts
[2]Oceans Initiative, Seattle, Washington
[3]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, Massachusetts

**Correspondence**
Richard M. Pace III, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543.
Email: richard.pace@noaa.gov

**Funding information**
National Marine Fisheries Service and The New England Aquarium

**Abstract**
Evaluations of the conservation status of the endangered North Atlantic right whale as well as many other wildlife species often rely extensively on counts and cause-of-death determinations of carcasses found accidentally or during dedicated surveys. Even when survey effort dedicated to a population is extensive, many deaths may go unseen. We used an abundance estimation model to derive estimates of cryptic mortality for North Atlantic right whales and found that observed carcasses accounted for only 36% of all estimated death during 1990–2017. We found strong evidence that total mortality varied over time, and that observed carcass counts were poor predictors of estimated annual numbers of whales dying. Importantly, there were substantial differences between fractions of deaths determined to be entanglement related during necropsy (49%) and the fraction of cryptic deaths suffering serious injuries related to entanglement (87%). Although we concluded that a single year's observations produced poor estimates of carcass detection rates due to the volatility of ratios of small counts, ratio estimates of data pooled over periods of consistent survey may offer better information on detection rates. Additionally, it appears unwise to consider cause of death determinations from detected carcasses as representative of cause-specific mortality rates in right whales given the large number of seriously injured whales from entanglement that are likely part of the unseen mortality.

**KEYWORDS**
carcass detection, cryptic mortality, detection bias, right whale, total mortality

## 1 | INTRODUCTION

The North Atlantic right whale, *Eubalaena glacialis*, is among the world's most endangered large whale populations (Reynolds, Marsh, & Ragen, 2009). The population at its recent peak numbered ∼500 individuals in 2010 (Pace, Corkeron, & Kraus, 2017) but has been declining since and at the start of 2018 numbers ∼400 (Pettis, Pace III, & Hamilton, 2020). The deaths of at least 17 individuals in 2017 (Davies & Brillant, 2019) and 10 more in 2019 has renewed concerns about recovery potential of this population (Kraus et al., 2016). Between 2003 and 2018, conclusions drawn from 38 of 44 (88%) necropsies conducted on right whales attributed death to human causes, namely collisions with vessels and entanglement in

Richard M. Pace III and Rob Williams should be considered joint first author.

fishing gear (Moore, et al. 2004; Sharp, McLellan, Rotstein, et al., 2019).

The known deaths suggest that recovery of North Atlantic right whales is in serious jeopardy (Corkeron et al., 2018) unless substantial mitigation measures that reduce mortality and serious injury from human activities are instituted immediately (Kenney, 2018; Moore, 2014). But, these known deaths represent only a fraction of the true death toll, because counts of carcasses do not agree with the numbers of whales that disappear from long term sighting records. In the fisheries management literature, postrelease mortality of fish has been termed "cryptic mortality" (Coggins Jr, Catalano, Allen, Pine III, & Walters, 2007), and this term has been applied to human activities that kill marine mammals without resulting in an observed carcass. Several reference points have been developed that estimate the number of animals that can be removed from a marine mammal population each year while still achieving conservation objectives (e.g., Chilvers, 2008; Hammill & Stenson, 2007; Wade, 1998; Williams, Thomas, Ashe, Clark, & Hammond, 2016), but these all rely on unbiased calculations of mortality rates. For many smaller cetacean species, a bycatch mortality rate can be estimated from observers placed on a representative sample of fishing boats to document takes, which can then be scaled up to the fleet as a whole (Wade, 1998). The kinds of human activity resulting in major sources of mortality for many larger cetaceans do not lend themselves to estimation from dedicated observer coverage. Examples include bycatch in fixed gear and unattended fisheries, such as lobster or crab pots (Johnson et al., 2005), oil spills, or collisions with ships (Laist et al., 2001) Although these causes are readily detected in recovered carcasses, no sampling frameworks exist to infer their incidence rates.

Several factors interact to cause undercounting of human-caused mortalities of cetaceans. Generally speaking, in order for anthropogenic mortality to be detected, a whale carcass must float or strand, be detected by human observers before decomposition or scavenging occurs, be subject to an evaluation by a qualified veterinary pathologist to determine cause of death, and then have that result reported in the primary literature or in publicly accessible databases (Faerber & Baird, 2010). At any point along the time line from death to disintegration, information about the cause of mortality can be lost including even its occurrence. Herein, we distinguish between carcass "detection" (i.e., identifying an observed carcass to be a right whale and therefore a known death in the population regardless of whether it can be identified as a known individual), and carcass "recovery" (a term often used in studies of known individuals implying that the carcass has been identified to the list of known population members). Unless otherwise noted, we focus on carcass detection rates in this study.

Some studies have attempted to estimate carcass detection rates in a number of cetacean populations, and these studies reveal that the potential for underestimation of human-caused mortality is considerable. Two populations of resident, fish-eating killer whales (*Orcinus orca*) are found in the coastal waters of British Columbia (Canada) and Washington State (USA). The population is studied through an annual census. Between 1974 and 2008, only 3 and 20%, respectively, of the presumed deaths of northern and southern resident killer whales resulted in detected carcasses (Barbieri et al., 2013). In a relatively closed area, Wells et al. (2015) estimated dolphin carcass recovery rates as 33% in Sarasota Bay, FL. In a retrospective analysis inspired by the Deepwater Horizon oil spill, historic carcass detection rates in the northern Gulf of Mexico averaged 2% among 14 cetacean species (Williams, Gero, Bejder, et al., 2011). Some rare species had a carcass detection rate of 0%, and the sperm whale (*Physeter macrocephalus*, the largest whale in the study) had a detection rate of 3.4% (Williams et al., 2011).

A particularly data-rich study on a coastal population of bottlenose dolphins (*Tursiops truncatus*) revealed a carcass detection rate of 25% (95% CI = 20, 33%), and made the argument that observed (minimum) numbers of anthropogenic mortality of dolphins derived from strandings should be corrected to account for unobserved mortality (Carretta et al., 2016). This careful analysis led to a policy change for management of human activities affecting US Pacific coast dolphins. Now, US marine mammal stock assessment reports[1] for coastal bottlenose dolphins in California that report anthropogenic mortalities detected from beach-cast carcasses are multiplied by a factor of 4 to account explicitly for cryptic mortality.

A management focus merely on the number of detected carcasses will underestimate the severity of anthropogenic mortality, and consequently, the management response will fail to take into account the severity of the threats. Methods are needed to scale up the known mortality to estimate the total amount of human-caused mortality that must be mitigated to save endangered whales. An initial assessment of natural and human-caused mortality in North Atlantic right whales for the period 1980–1999 suggested a 17% carcass detection rate (Kraus, Brown, Caswell, et al., 2005), but increased search effort and stranding response funding in recent years would suggest a higher rate may apply now. Because the sighting rates of live right whales has varied over time (Pace et al., 2017), it stands to reason that carcass detection rate varies over time. Additionally, detectability of carcasses could be influenced by cause of death. For example, healthy whales struck by vessels likely float for longer periods and therefore may be detected at higher rates than chronically entangled animals that burn their fat stores for months as they slowly starve to death (Moore, Mitchell, Rowles, & Early, 2020). Additional analyses are needed to generate a robust multiplier that can be used in management (e.g., Carretta et al., 2016). Without a statistically robust multiplier, correction factors to account for imperfect carcass detection can result in estimates of mortality that exceed the size of the entire population (Parrish & Boersma, 1995).

Our study had three main objectives:

1. To estimate average carcass detection rates of North Atlantic right whales, and explore how this may have changed over time. Estimating this parameter will not affect our understanding of population dynamics, because detected and undetected mortality are already subsumed within the survival estimates (Pace et al., 2017). However, understanding the extent to which anthropogenic mortality is undercounted may alter our perspective of the potential scope for population recovery if precautionary mitigation measures were implemented broadly. We briefly explore two alternative estimators for detection rate over a specified time interval.
2. Explore the hypothesis that carcass detection may vary with cause of death. Evidence for differential carcass detection rates could change our understanding of the relative importance of the two main risk factors (i.e., collision with vessels and entanglement), and more accurate information could change the emphasis placed on various mitigation measures.
3. Our long-term objective is to stimulate a discussion at the science-policy interface on the need to improve the way that cryptic mortality is handled in management. Using the extremely data-rich case study of the North Atlantic right whale, we advocate developing multipliers to better account for cryptic mortality when assessing conservation status of marine mammal stocks (Carretta et al., 2016).

## 2 | METHODS

Three lines of inquiry were used to explore factors influencing carcass detection rates in North Atlantic right whales.

### 2.1 | The ratio of observed to estimated mortalities

Observed mortalities of right whales exist in two categories: (1) a discovered carcass that can be identified as a whale known to the North Atlantic Right Whale Catalog (Hamilton, Knowlton, & Marx, 2007) and (2) a discovered carcass that is not identifiable to individual either by photograph (position of carcass obscuring matching features or state of decomposition) or genetic fingerprint (no sample gathered or no match found).

Annual estimates of the total number of right whale deaths from 1990 to 2017 were generated from a previously published hierarchical state-space model of right whale abundance (Pace et al., 2017). The model to estimate abundance is parameterized to yield posterior distributions of $\mathrm{N}_t$ and $\mathrm{B}_t$, which are respectively, the abundance and numbers of new entrants (Births) to the population in year $t$. For each of 20,000 realizations in the Markov chain Monte Carlo run after initial burn-in, we calculated the estimated number of deaths according to the following formula:

$$\mathrm{D}_t = \mathrm{N}_t - \mathrm{N}_{t+1} + \mathrm{B}_t$$

where $\mathrm{D}_t$ is the number of deaths occurring in the interval $[t,\ t+1]$. We assumed that the derived values represented a posterior distribution for each $\mathrm{D}_t$ and calculated 95% highly credible regions for each estimate. We further assume that the population is closed to permanent emigration, which seems well supported by the long study period and the lack of evidence of right whale being resident in other parts of the North Atlantic. We calculated an additional total mortality estimate from abundance estimates from the aforementioned model and detected calf counts according to:

$$\mathrm{D}_{\mathrm{total}} = \mathrm{N}_{1990} - \mathrm{N}_{2018} + \mathrm{C}_{\Sigma(1990-2017)}$$

where $\mathrm{C}_{\Sigma(1990-2017)} = 407$ was the total calf count during 1990–2017.

We fitted generalized linear models (GLMs) to examine whether or not the observed number of carcasses were predictive of estimated median number of deaths each year. Candidate models included: constant estimated death rate over time; a linear predictive relationship between annual carcass counts and annual estimated death count; a simple periodic variation in the estimated death count over three “eras” (1990–1991; 1992–2009; and 2010–2017); and a model with both era effect and observed carcass counts as predictors. The choice of eras was based on time frames of significant changes in search effort patterns and/or animal distributions, where the predictive value of carcass counts might vary with these changes. In particular, we believed that variable periods evident in the recapture rates of individuals was indicative of three eras that might have differing carcass detection rates. We estimated the relative effective detection effort as the mean adult female capture probability for the era.

## 2.2 | Cause of serious injuries and cause of death

Additionally, mortalities can be inferred for whales seen alive but declared seriously injured by the National Marine Fisheries Service (NMFS; Henry et al., 2017). These injured whales are often in poor health condition or suffering from complex entanglements that will interfere with foraging. Many are eventually presumed to have died as they commonly disappear from the sighting records within 1–2 years following their injury. We only counted whales as seriously injured the first year of their determined status and removed from the counts two whales that were determined to be seriously injured but appeared to recover. From first principles, it seems plausible that whales that become entangled and lose fat during the months it takes them to die may be less likely to be detected as carcasses if they sink soon after death, although Moore et al. (2020) show that carcasses that sink in shallower water are more likely to bloat and refloat. Conversely, healthy whales killed immediately by ship strikes would be more likely to float. It is impossible to test directly for differences in detection rate based on cause of death, precisely because one never sees the unobserved mortality. We explored the plausibility of this scenario using a subset of whales that were observed with serious injuries just prior to their disappearance (Henry et al., 2017; Knowlton, Hamilton, Marx, Pettis, & Kraus, 2012). Using data from New England Aquarium (NEAQ) and NMFS, we examined the fate of animals last seen with serious injuries arising from either fisheries gear entanglement or "other" (i.e., mostly consistent with blunt force trauma or fresh propeller wounds). We compared the frequency of occurrence of serious injuries from entanglement and other anthropogenic sources with sources of mortality determined from examined carcasses of noncalf animals. Causes of mortality for examined carcasses have been documented in Moore, Knowlton, Krauss, McLellan, and Bonde (2004) and Sharp et al. (2019). We note that a few animals may have been observed as serious injuries and later found dead but no link clearly establishing that it was the same individual. Because we are comparing the distributions of death causes, double counting in this instance would only act to reduce differences in distributions.

## 2.3 | Body condition and subsequent carcass recovery of known individuals

Each individual in the North Atlantic right whale catalog has a suite of health records over its sighting history, each of which includes a visual estimate of body fat stores (Pettis et al., 2004). For 159 whales that were known (28) or presumed (131) to have died and had an assessment of body condition within 6 months of its last sighting, we modeled the probability that a carcass would be recovered as a function of visual body condition. The rationale was that whales observed to be skinny just before death could act as a proxy for entangled whales that took several months to die (Pettis et al., 2017), whereas whales with healthy fat stores just before their death could act as a proxy for whales that were struck by a ship and died immediately with fat reserves intact (Moore et al., 2020).

We fitted a binomial GLM to the fate of each individual whale, whose carcass was either recovered (1) or not recovered (0), using body fat condition as a candidate covariate. Statistical support for including the covariate was estimated by comparing AIC of this model to an intercept-only model.

# 3 | RESULTS

## 3.1 | Magnitude of cryptic mortality

When compared with the derived estimates of total mortality from the abundance model (Pace et al., 2017) extended to produce estimates for 1990–2017, counts of carcasses seriously underrepresented total right whale mortality (Figure 1). During this period, the number of deaths derived from the abundance model was 2.8 times the carcass count.

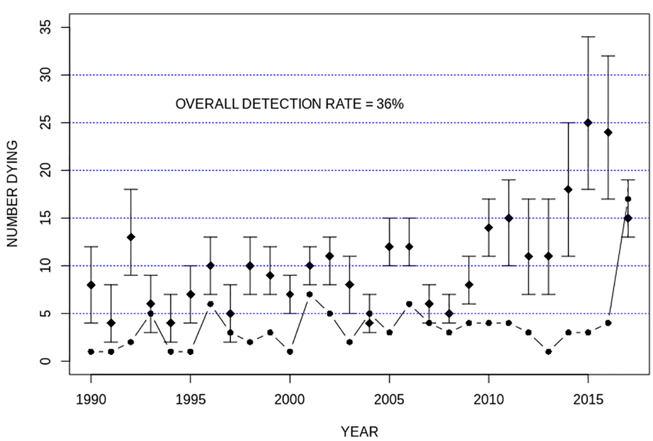


**FIGURE 1** Counts (black dots) of right whale carcasses and total number of right whale deaths estimated from an abundance model (diamonds) together with their 95% credible intervals. Overall detection rate was the sum of carcass counts across the entire time frame divided by the sum of estimated deaths

**TABLE 1** Information criteria generated from GLMs fit to estimated annual mortality of North Atlantic right whales

| Model | Parameters count | AICc | Delta_AICc | AICcWt |
|---|---|---|---|---|
| Era | 3 | 151.0 | 0 | 0.79 |
| Era + Carcass count | 4 | 154.5 | 2.7 | 0.21 |
| Carcass count | 2 | 184.6 | 32.8 | 0 |
| Constant | 1 | 185.8 | 34.1 | 0 |

*Note:* Prior choice of models included (1) constant death count over time, (2) linear correspondence between observed carcasses estimates, (3) varying by different eras of survey effort or whale distribution a model, and (4) an additive model including 2 and 3. Models assumed data were Poisson and the three Eras were 1990–1991, 1992–2009, and 2010–2017.

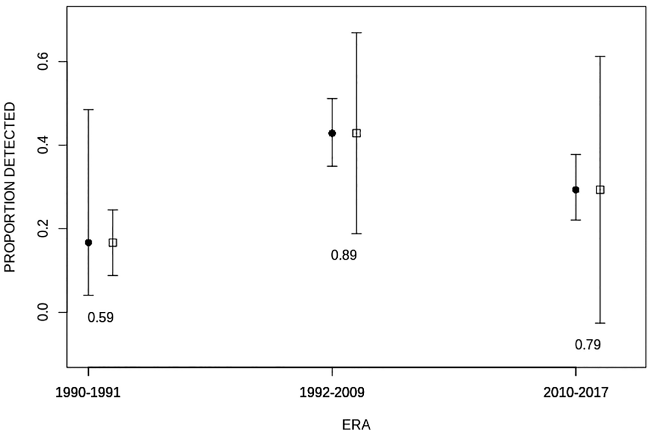


**FIGURE 2** Variability in carcass detection rate in three periods that appear to correspond to changes in NARW distribution and search effort. Solid circles represent the retransformed predictions from the binomial GLM with Era as a categorical predictor accompanied by approximate 95% confidence bounds. Open squares are calculated as ratio estimates for each Era where Proportion detected = Sum of observed/(Sum estimated total mortality for the period) mathematically equivalent to the GLM predicted values. Error bars are 1 standard error of each ratio estimates demonstrate the large variance among calculated annual detection ratios. Values below intervals are the Era-specific means of estimated capture probability of adult females from the abundance model used to calculate total number of deaths

## 3.2 | The predictive ability of observed carcass counts

Comparison of four models used to evaluate the predictive value of annual carcass counts revealed that very little information about the number of right whales dying in a given year could be derived from carcass counts (Table 1). The model with the most support validated the higher undetected death tolls during 2010–2017 shown in Figure 1.

The overall estimate of carcass detection rate was 36%. Our GLM produced little support that annual counts of carcasses were predictive of annual mortality estimates (Table 1). However, when we pooled data from eras of more similar survey effort and whale distribution, a pattern of detection emerged that fit with our prior suspicions (Figure 2). When survey effort was lower for important whale use areas during 1990–1991, the ratio of detected carcasses was only 17% (2 s.e. = 5.5%). Detection increased significantly to 43% (2 s.e. = 0.6%) during a lengthy period of high whale recapture rate (1992–2009) and declined to 29% (2 s.e. = 2.8%) from 2010 to 2017 as whales changed their area use patterns and recapture rates declined.

**TABLE 2** Likely cause of death distribution for noncalf North Atlantic right whales during 1990–2017 (excluding undetermined, $n = 3$) from examined carcasses versus live animals declared as seriously injured by NMFS

| Data source | Entanglement | Vessel collision |
|---|---|---|
| Carcass | 20 (49%) | 21 (51%) |
| Serious injury | 54 (87%) | 8 (13%) |

*Note:* Chi-sq. test for similar distributions between data sources $X^2 = 16.1$, $p < .001$.

## 3.3 | Cause of serious injuries and cause of death

From 1990 to 2017, a total of 62 North Atlantic right whales were reported by NMFS as having "serious injuries" that were defined as life-threatening, and subsequently disappeared. Entanglement accounted for the vast majority (54 of 62, or 87%) of serious injuries (Table 2). Because these whales were never seen again, one would also expect to see 87% of deaths to be caused by entanglement. Among 41 examined carcasses, only 49% of deaths were determined to be entanglement related. Assuming all of the "other" sources of serious injury or mortality of noncalf whales can be attributed to vessel collisions, there is a large disparity between the sets of observations ($X^2 = 16$, $p < .001$). This disparity suggests that it may be unreasonable to use the distribution of causes of death from examined carcasses to characterize the cryptic deaths.

### 3.4 | Body condition and subsequent carcass recovery of known individuals

The model with the highest information content based on AIC was one not relying on body condition to predict the probability of detection (AIC = 150.0). Using body fat condition at the time of the last sighting had little support from the data (AIC = 151.9; ΔAIC = 1.9 over an intercept-only model).

## 4 | DISCUSSION

Recent results from a hierarchical state-space model of North Atlantic right whale population dynamics (Pace et al., 2017) were integrated with data on animal health, encounters, necropsies, and serious injuries held by the North Atlantic Right Whale Consortium at the New England Aquarium (Hamilton et al., 2007; Pettis et al., 2004) or published literature (Moore et al., 2004; Sharp et al., 2019) with the serious injury and mortality database held by NMFS (Henry et al., 2017). Taken together, these data suggest that 36% of right whale deaths resulted in a carcass detection. Experts who have led the data collection efforts believe that changes in whale distribution and search effort by agencies on both sides of the Canada-US border may have changed carcass detection rates over time. By pooling data across relatively homogeneous periods of survey effort and whale distribution, we found modest deviations in carcass detection rates over time. The period of much lower effective searching (lower capture rates of live whales) produced a low estimated detection rate consistent with that reported by Kraus et al. (2005) using different methods to estimate total mortality. They estimated that the carcass detection rate was 17% based on data from 1980 to 1999 (Kraus et al., 2005). There appears to have been a large increase in detection rate to 43% during a period coincident with the highest estimated recapture rates of live whales reported by Pace et al. (2017), but the estimated value is still below half. In the most recent era, carcass detection rates have fallen off as whales spend less time in previously well surveyed areas.

Our analysis allows us to caution strongly against relying on a single year's count of carcasses to infer differing amounts of total mortality. These counts are usually small (<10) and hence widely varying relative to their mean. Despite our own cautionary note, we found it of interest that during 2017, a year of an unusually high carcass count coupled with a dramatic increase in Canadian survey effort to find carcasses, the number of dead found may have accounted for nearly every whale estimated to have died that year. This finding is clearly not indicative of the recent past, given that the overall detection rate during 2010–2017 was only 29%.

There is a striking mismatch between the causes of serious injuries observed in living whales and the causes of mortality revealed in necropsies of dead whales. Entanglement accounted for the vast majority (54 of 62, or 87%) of serious injuries, but only 20 of 41 (49%) of mortality in examined carcasses. Collisions with vessels and "other" causes represent 8 of 62 (13%) of serious injury cases, but represent 21 of 42 (51%) of mortalities in examined carcasses. We caution, however, that blunt force trauma incurred by whales that are seriously injured by a vessel collision may be difficult to detect from photographs of free swimming whale that may ultimately die as a result of the collision. Despite the possibility of missing some vessel collisions that produced serious injuries, the disparity in observed rates of serious injury by cause suggests that cryptic deaths due to entanglements significantly outnumbers cryptic deaths from vessel collisions or other causes. Although this dissonance could not be explained by a model of carcass detection as a function of visual body condition, the topic warrants continued research. If attempts are made to expand detected causes of mortality to total counts, detection rates should be calculated over a rolling time block to reduce the influence of any 1 year's values. Alternatively, estimated mortality values should be calculated over periods of homogeneous live right whale capture probabilities. Regardless, entanglement-related mortality is widely underestimated, which has important implications for management actions to promote recovery.

## 5 | CONCLUSION

The amount of cryptic mortality occurring over longer time intervals seem to vary with effective survey effort to finding live whales. The evidence surrounding whales not recovered following their likely deaths, suggests that cryptic deaths are more likely entanglement related than the record of examined carcasses indicates. As monitoring and managing the conservation status of North Atlantic right whales requires robust quantitative data, this study showed that total mortality was 2.8 times the number of detected carcasses during 1990–2017. Annual counts of right whale carcasses do a poor job of indicating the total mortality for that year, and carcass detection rates seem to vary with effective survey effort. The incidence rates among causes of mortality differs significantly between those examined carcasses from which a cause of death was determined, and those animals whose likely death followed a serious injury. The evidence surrounding whales not recovered following their likely deaths, suggests that cryptic deaths are almost twice as likely to be due to entanglements than the records from examined carcasses whales indicate.

## ACKNOWLEDGMENTS

The authors gratefully acknowledge support to New England Aquarium's right whale research program from the Volgenau Foundation, and to Oceans Initiative from Fisheries and Oceans Canada and Save Our Coasts Foundation. The authors also thank A. Henry for verifying accounting of right whale serious injury and mortality data from NEFSC archives. 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 North Atlantic Right Whale Consortium for over nearly 40 years.

## CONFLICT OF INTEREST

The authors have no conflicts of interests to declare.

## AUTHOR CONTRIBUTIONS

Richard M. Pace and Rob Williams contributed equally to the analysis and writing of this paper and should be regarded as joint first authors. Scott D. Kraus helped focus the content, provided extensive edits, and access to data. Amy R. Knowlton and Heather M. Pettis compiled and extracted data and provided text and edits.

## DATA AVAILABILITY STATEMENT

Data used to calculate total mortality and a table of known deaths by cause are available from RMP.

## ETHICS STATEMENT

Data used in this manuscript were all collected using guidelines and permits provided by federal (US and Canadian) agencies which govern the ethical treatment of animals.

## ORCID

*Richard M. Pace III* https://orcid.org/0000-0002-8506-1210

## ENDNOTE

[1] https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-stock-assessment-reports-species-stock

## REFERENCES

Barbieri, M. M., Raverty, S., Bradley Hanson, M., Venn-Watson, S., Ford, J. K. B., & Gaydos, J. K. (2013). Spatial and temporal analysis of killer whale (*Orcinus orca*) strandings in the North Pacific Ocean and the benefits of a coordinated stranding response protocol. *Marine Mammal Science*, *29*, E448–E462.

Carretta, J. V., Danil, K., Chivers, S. J., Weller, D. W., Janiger, D. S., Berman-Kowalewski, M., … Lambourn, D. M. (2016). Recovery rates of bottlenose dolphin (*Tursiops truncatus*) carcasses estimated from stranding and survival rate data. *Marine Mammal Science*, *32*, 349–362.

Chilvers, B. L. (2008). New Zealand sea lions *Phocarctos hookeri* and squid trawl fisheries: Bycatch problems and management options. *Endangered Species Research*, *5*, 193–204.

Coggins, L. G., Jr., Catalano, M. J., Allen, M. S., Pine Iii, W. E., & Walters, C. J. (2007). Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries*, *8*, 196–210.

Corkeron, P., Hamilton, P., Bannister, J., Best, P., Charlton, C., Groch, K. R., … Pace, R. M., III. (2018). The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. *Royal Society Open Science*, *5*, 180892.

Davies, K. T. A., & Brillant, S. W. (2019). Mass human-caused mortality spurs federal action to protect endangered North Atlantic right whales in Canada. *Marine Policy*, *104*, 157–162.

Faerber, M. M., & Baird, R. W. (2010). Does a lack of observed beaked whale strandings in military exercise areas mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and main Hawaiian Islands. *Marine Mammal Science*, *26*, 602–613.

Hamilton, P. K., Knowlton, A. R., & Marx, M. K. (2007). Right whales tell their own stories: The photo-identification catalog. In *The urban whale: North Atlantic right whales at the crossroads* (pp. 75–104). Cambridge, MA: Harvard University Press.

Hammill, M., & Stenson, G. (2007). Application of the precautionary approach and conservation reference points to management of Atlantic seals. *ICES Journal of Marine Science: Journal du Conseil*, *64*, 702–706.

Henry A., Cole T.V.N., Garron M., Ledwell W., Morin D.M., & Reid A. (2017). Mortality and serious injury determinations for baleen whale stocks along the Gulf of Mexico, United States, United States East Coast and Atlantic Canadian Provinces, 2011-2015. Northeast Fisheries Science Center Reference Document 17–19, 57 pp.

Johnson, A., Salvador, G., Kenney, J., Robbins, J., Kraus, S., Kraus, S., & Clapham, P. (2005). Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science*, *21*, 635–645.

Kenney, R. D. (2018). What if there were no fishing? North Atlantic right whale population trajectories without entanglement mortality. *Endangered Species Research*, *37*, 233–237.

Knowlton, A. R., Hamilton, P. K., Marx, M. K., Pettis, H. M., & Kraus, S. D. (2012). Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: A 30 yr retrospective. *Marine Ecology Progress Series*, *466*, 293–302.

Kraus, S. D., Brown, M. W., Caswell, H., Clark, W. C., Fujiwara, M., Hamilton, P., & Kenney, R. (2005). North Atlantic right whales in crisis. *Science*, *309*, 561–562.

Kraus, S. D., Kenney, R. D., Mayo, C. A., McLellan, W. A., Moore, M. J., & Nowacek, D. P. (2016). Recent scientific publications cast doubt on North Atlantic right whale future. *Frontiers in Marine Science*, *3*, 137.

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A.S., & Podesta, M. (2001). Collisions between ships and whales. *Marine Mammal Science*, *17*, 35–75.

Moore, M. J. (2014). How we all kill whales. *ICES Journal of Marine Science: Journal du Conseil*, *71*, 760–763.

Moore, M. J., Knowlton, A. R., Krauss, S. D., McLellan, W. A., & Bonde, R. K. (2004). Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). *Journal Cetacean Research Management*, *6*, 199–214.

Moore, M. J., Mitchell, G. H., Rowles, T. K., & Early, G. (2020). Dead cetacean? Beach, bloat, float, sink. *Frontiers in Marine Science*, *7*, 333. https://doi.org/10.3389/fmars.2020.00333

Pace, R. M., Corkeron, P. J., & Kraus, S. D. (2017). State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution*, *7*, 8730–8741.

Parrish, J. K., & Boersma, P. D. (1995). Muddy waters. *American Scientist*, *83*, 112–116.

Pettis, H.M. Pace, R.M., III, & Hamilton, P.K. (2020). North Atlantic Right Whale Consortium 2019 Annual Report Card. Report to the North Atlantic Right Whale Consortium. Available from https://www.narwc.org/report-cards.html

Pettis, H. M., Rolland, R. M., Hamilton, P. K., Brault, S., Knowlton, A. R., & Kraus, S. D. (2004). Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. *Canadian Journal of Zoology*, *82*, 8–19.

Pettis, H. M., Rolland, R. M., Hamilton, P. K., Knowlton, A. R., Burgess, E. A., & Kraus, S. D. (2017). Body condition changes arising from natural factors and fishing gear entanglements in North Atlantic right whales *Eubalaena glacialis*. *Endangered Species Research*, *32*, 237–249.

Reynolds, J. E., Marsh, H., & Ragen, T. J. (2009). Marine mammal conservation. *Endangered Species Research*, *7*, 23–28.

Sharp, S. M., McLellan, W. A., Rotstein, D. S., Costidis, A. M., Barco, S. G., Durham, K., & Pitchford, T. D. (2019). Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. *Diseases of Aquatic Organisms*, *135*, 1–31.

Wade, P. R. (1998). Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, *14*, 1–37.

Wells, R. S., Allen, J. B., Lovewell, G., Gorzelany, J., Delynn, R. E., Fauquier, D. A., & Barros, N. B. (2015). Carcass-recovery rates for resident bottlenose dolphins in Sarasota Bay, Florida. *Marine Mammal Science*, *31*, 355–368.

Williams, R., Gero, S., Bejder, L., Calimbokidis, J., Kraus, S., Lusseau, D., & Read, A. J. (2011). Underestimating the damage: Interpreting cetacean carcass recoveries in the context of the Deepwater horizon/BP incident. *Conservation Letters*, *4*, 228–233.

Williams, R., Thomas, L., Ashe, E., Clark, C. W., & Hammond, P. S. (2016). Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: A case-study approach using two whale populations. *Marine Policy*, *70*, 58–64.

**How to cite this article:** Pace RM III, Williams R, Kraus SD, Knowlton AR, Pettis HM. Cryptic mortality of North Atlantic right whales. *Conservation Science and Practice*. 2021;3:e346. https://doi.org/10.1111/csp2.346