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NOTE

How compromised is reproductive performance in the endangered North Atlantic right whale?

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ABSTRACT: The endangered North Atlantic right whale *Eubalaena glacialis* showed limited recovery from the cessation of industrial whaling until 2011, and has since been in decline. Research is therefore focused on identifying what factors are limiting recovery and what conservation actions will be most effective. A compromised reproductive rate is one of the reasons for this lack of recovery, yet there is no consensus on how to quantify reproductive performance. As one potential solution, we propose a relatively simple approach where we calculate the theoretical maximum number of calves each year. Comparing this expected number to those observed (which is thought to be an accurate representation of those births that actually occurred) provides a means to quantify the degree to which reproduction is compromised annually and trends thereof over time. Implementing this approach shows that, between 1990 and 2017, the number of calves born never came close to the theoretical maximum, resulting in overall reproductive performance of only about 27% of that expected. In addition to quantifying the degree to which reproduction is compromised, this approach should also be useful for quantifying the role of reduced reproductive performance in limiting species recovery, and for aiding research programs focused on identifying what factors are compromising reproduction.

KEY WORDS: Reproduction · Right whale · Conservation · Endangered · Recovery potential

1. INTRODUCTION

There is increasing concern regarding the viability of the North Atlantic right whale *Eubalaena glacialis*, which is currently listed as endangered in both the USA and Canada, and is currently represented by <400 individuals (Pettis & Hamilton 2024). This species was once the target of intensive whaling, but has not recovered despite the cessation of that directed persecution: there were only subtle signs of recovery for decades (at a rate of ~2.5% yr^{-1}; Pace et al. 2017), but the situation has since worsened and the species has been in decline since 2011 (Pettis & Hamilton 2024).

This lack of recovery has been attributed to 2 major factors: a high rate of anthropogenic mortality from vessel strikes and entanglement in fishing gear (Knowlton et al. 2012, Pace et al. 2021), and a reproductive rate that is markedly lower than the species' known potential (Kraus et al. 2001, 2007). While many conservation efforts have been directed at lowering rates of anthropogenic mortality (e.g. Vanderlaan et al. 2008, van der Hoop et al. 2015), the factors compromising reproductive performance are not yet well-understood and are likely multifaceted (e.g. Kraus et al. 2007, Stewart et al. 2022).

For North Atlantic right whales, high quality measurements exist for observed reproductive rates, but

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there are currently no clear benchmarks of expected reproductive potential. Our goal was to develop a simple and clear method with which to gauge observed reproductive output against a theoretical benchmark based on the reproductive cycle and age structure of the population. Such quantification will be helpful in quantifying the degree to which reproduction is compromised and the subsequent implications for species recovery. By quantifying the magnitude and trends of the problem itself, it will also aid research focused on identifying what factors are limiting reproductive performance.

2. MATERIALS AND METHODS

2.1. Data

Analyses were based on reproductive histories of females from 1990 to 2017. Individual North Atlantic right whales can be identified based on callosity patterns on their heads, and also on variation in skin pigmentation and scarring (Kraus et al. 1986a). Dedicated field studies began in 1980, and fieldwork now takes place almost year-round and throughout the range of the species (Brown et al. 2007). The ability to recognize individuals across space and time has provided a wealth of individual-based information (Hamilton et al. 2007). Moreover, one identified calving area has been intensively surveyed since the early 1990s. The extensive nature of these surveys, combined with the coastal distribution of mother—calf pairs and the fact that few calves are seen later in the year that were not first seen on the calving ground, suggest that the vast majority of calving events are documented (Kraus et al. 2007). The observed reproductive histories for females are therefore thought to be highly accurate (Kraus et al. 1986b, Brown et al. 2007). Data on female age and reproductive histories were obtained from the North Atlantic Right Whale Consortium (www.narwc.org).

2.2. Characterization of reproductive performance

Two major components of poor reproductive performance have been identified: (1) those associated with inter-birth intervals; and (2) females that delay their first reproduction until much later in life than average, or that are completely nulliparous.

For inter-birth intervals, North Atlantic right whale females are capable of giving birth once every 3 yr (Knowlton et al. 1994, Kraus et al. 2001, 2007). This represents approximately 1 yr of lactation, 1 yr of 'resting' to replenish tissue and energy stores, and then 1 yr of gestation. However, there is a great deal of variation around this 3 yr interval at temporal and individual scales. Temporally, the average inter-birth interval fluctuates over time, and has increased during periods where the species appeared to be nutritionally stressed (Kraus et al. 2001, Miller et al. 2011, Moore et al. 2021). Second, there is a high degree of variability across different females, where some females have reproduced fairly regularly at 3 or 4 yr intervals, whereas other females have much longer average intervals.

The second major component of reduced reproductive performance involves increased age of primiparity and adult females that are nulliparous. It was previously estimated that about 12% of adult female North Atlantic right whales are nulliparous (Kraus et al. 2007). Moreover, although the estimated average or modal age of first parturition has historically ranged between 8 and 10 yr (Knowlton et al. 1994, Kraus et al. 2001), recent evidence suggests that this age has been increasing due to a range of factors that may be delaying reproduction, such as nutritional stress and non-lethal entanglements (Moore et al. 2021, Reed et al. 2022). We used 9 yr in our analyses because most healthy females reproduce by this age, and the goal is to identify reproductive rates expected under 'ideal' conditions (i.e. if reproduction was not being compromised by such factors).

To assess the relative contribution of both components on reproductive patterns, we characterized the observed reproductive histories of adult females in each year. This involved identifying how many adult females were 'presumed alive' in each year (the majority of mortalities are not detected (Pace et al. 2021), and therefore individuals are 'presumed alive' until their 6th year without being sighted (Knowlton et al. 1994, Hamilton et al. 2007)), and what their reproductive histories were up to and including that year: (1) those that had not yet reproduced; (2) those that had produced 1 calf; and (3) those that had reproduced 2 or more times, and were therefore available for analyses of inter-birth intervals. This resulted in a reproductive cross-section of the adult females in each year, with respect to these categories.

2.3. Quantifying reproductive performance

Our approach is based on calculating the expected number of calves born in each year, and using that as a metric against which the actual number of calves born is compared. We argue that the expected number of calves born can be calculated as the number of living adult females minus those that gave birth in the previous 2 yr. The rationale is that if reproduction was not being compromised then we would expect each adult female to give birth approximately once every 3 yr. This approach captures both manifestations of the reproductive problem. First, females and/or time periods with longer inter-birth intervals will result in fewer calves born than expected because fewer females will be reproducing on the expected 3 yr schedule. Second, non-reproducing females will also cause the observed number of calves to be lower than expected because they are not producing calves.

This approach is justified as follows. First, we know that North Atlantic right whale females can reproduce once every 3 yr because many of them have done so before (Knowlton et al. 1994, Kraus et al. 2001, Pettis & Hamilton 2024). Indeed, the average inter-birth interval from 1980 through 1992 was 3.67 yr (median = 3, SD = 1.04) (Knowlton et al. 1994). Thus, it is physiologically possible for them to do so under favorable conditions. Second, the average inter-birth interval for females in many populations of the closely related southern right whale (*Eubalaena australis*) is approximately 3 yr (e.g. South Africa, 3.12 yr; Best et al. 2001). Lastly, data from other baleen whale populations indicate that the proportion of reproducing females is closely aligned with known calving intervals. For example, the average inter-birth interval for female humpback whales *Megaptera novaeangliae* in the North Atlantic is ~2.4 yr, and the estimated percentage of adult females that are pregnant each year closely matches this at 41% (Clapham & Mayo 1988). Many studies of other large mammals also show a close relationship between inter-birth intervals and pregnancy rates (e.g. Festa-Bianchet et al. 1998, Clutton-Brock et al. 2003), indicating that, in a healthy population, the vast majority of females reproduce at their maximum physiological rate (at least for species that do not live in social groups where the reproductive success of some females is controlled by others). Moreover, the North Atlantic right whale population is very small and therefore should be growing at their maximum intrinsic rate of increase, uninhibited by density-dependent factors (e.g. Caughley & Birch 1971).

Combined, these data suggest that if reproduction was not being compromised, it would be reasonable to expect North Atlantic right whale females to reproduce approximately once every 3 yr. Based on this logic, we used the mark–recapture abundance estimation model described in Pace et al. (2017) to estimate the expected number of calves born in each year as the median estimated number of adult females alive in each year minus the number of females that gave birth within the previous 2 yr.

3. RESULTS

The reproductive histories of adult females presumed alive in the years 1990–2017 are shown in Fig. 1A, and a cross-section of those females for the year 2017 is shown in Fig. 1B. The data show a clear decreasing trend in females that have reproduced multiple times, with a corresponding increase in the

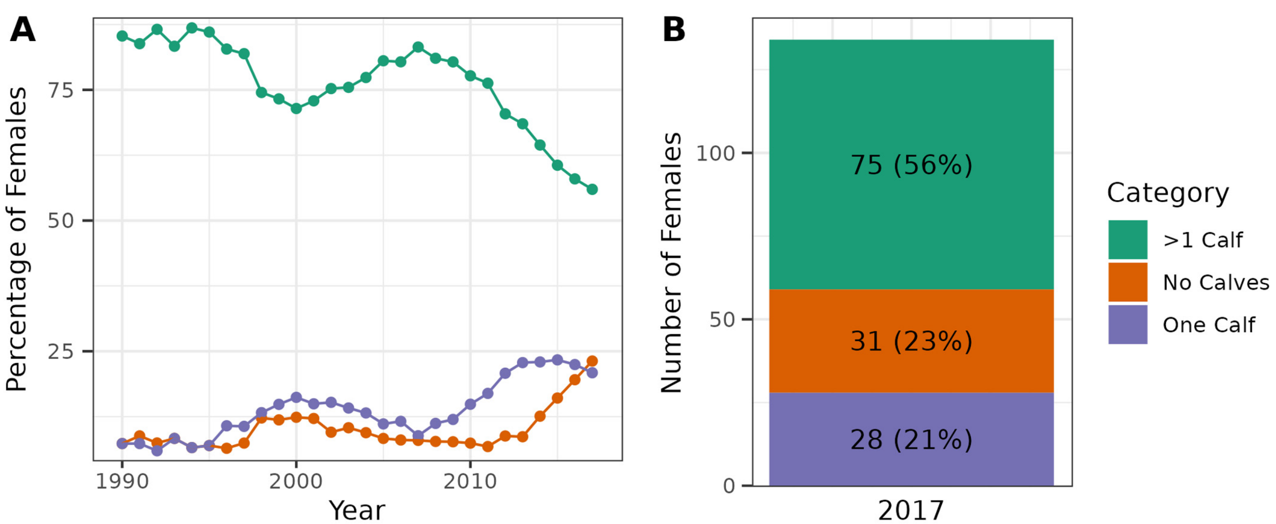

Fig. 1. Reproductive histories of adult females in the years 1990–2017. Females were binned in 1 of 3 categories: (1) no calves as of that year, (2) 1 calf as of that year, or (3) having given birth to >1 calf as of that year. (A) Percentage of adult females that were in each category across years. (B) Cross-section of the adult females alive in 2017

number of females that have not yet reproduced or have had just 1 calf. In 2017 there were 134 females presumed to be alive and adult. Of these 134 females, 75 (56%) had given birth to more than 1 calf and were therefore available for analyses of inter-birth intervals. Of these females, 28 (21%) had given birth to just 1 calf (as of 2017). The remaining 31 individuals (23%) had not yet given birth.

The expected number of calves born for the years 1990–2017 is shown in Fig. 2A. Also shown is the observed number of calves born in each year. Fig. 2B shows the same data in a different manner, where the observed number of calves is plotted as a percentage of those that were expected for each year. Although there is substantial annual variability, the average over time shows that the reproductive performance of this species is slightly less than a third (~27%) of that expected.

4. DISCUSSION

The first major result from this work is the identification and quantification of the degree to which nulliparous females — and females who delay reproduction until much later than expected — are contributing to the decreased reproductive performance (Fig. 1). Indeed, by 2017 almost half (44%) of adult females had either not given birth or had just 1 calf, whereas just slightly over half (56%) had reproduced more than once and are therefore available for analyses of inter-birth intervals. These results show that non-reproductive females, and females who are delaying reproduction until later in life, represent a major component of the reproductive problem, and should be considered along with data on inter-birth intervals when quantifying reproductive performance (see also Reed et al. 2022).

Second, our approach provides clear targets for maximum reproduction each year, providing a scientific baseline against which actual reproductive performance can be compared (although we would expect natural variation around this theoretical maximum even if reproduction were not compromised). This approach shows that in none of the 28 yr considered were the number of calves close to those expected (Fig. 2). This result is alarming, and demonstrates the magnitude of the degree to which reproduction is compromised within this species.

Lastly, our approach provides a clear and scientific method to quantify and monitor reproductive performance over time. This approach indicates that, on average, the species is reproducing at only about 27% of its expected maximum rate, or put another way, the reproductive rate is about 73% lower than its known potential. Such information is critical for quantifying the relative degree to which reduced reproductive performance is limiting the recovery potential of the species. For example, future analyses could compare observed population trends with those expected if reproduction rates were not compromised, as well as those expected if anthropogenic mortalities were

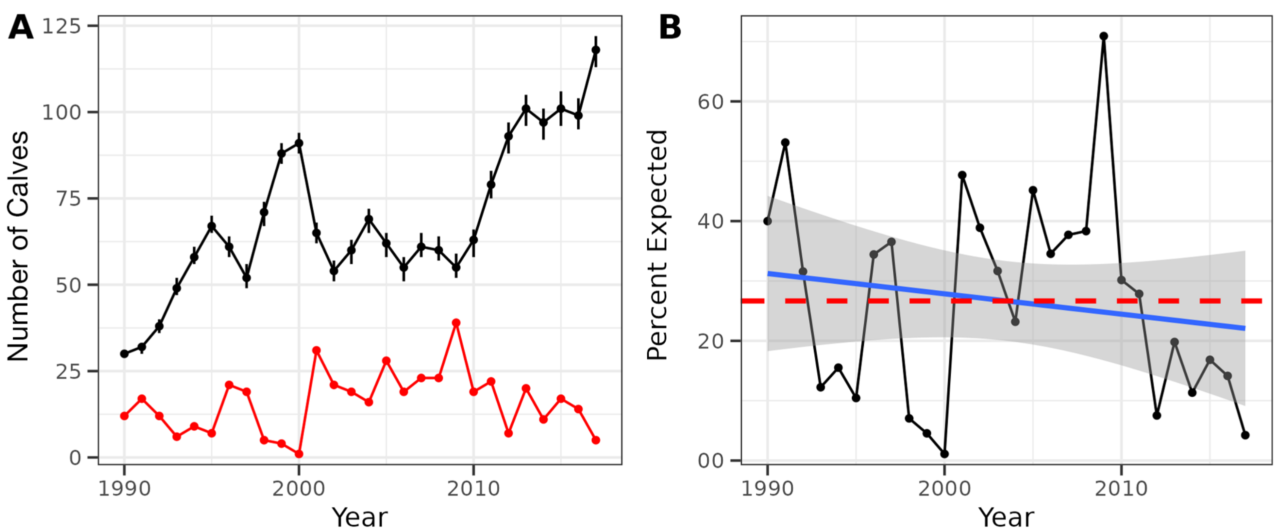

Fig. 2. Expected and observed number of calves born in each year from 1990 to 2017. (A) Expected number of calves born each year (black dots) and associated 95% highest density intervals (HDIs). The observed number of calves is shown in red. (B) Proportion of expected calves that were actually born. The values for each year are shown as black dots, and the average across all years (from 1990 to 2017, 27%) is shown as a red dashed line. A linear estimate of the trend over time is shown in blue, indicating a slight decrease over time (mean = −0.0034, SE = 0.0040)

reduced or non-existent, to quantify the relative contribution of anthropogenic mortality and compromised reproduction on species recovery. Additionally, this quantification of reproductive performance will aid research programs focused on identifying what factors are limiting reproduction, and to what degree.

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