Climate and the Conservation Biology of North Atlantic Right Whales: The Right Whale at the Wrong Time?

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Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time?

Charles H Greene and Andrew J Pershing

With the end of commercial whaling, it was thought that populations of the highly endangered North Atlantic right whale (*Eubalaena glacialis*) would gradually recover. However, recent modeling studies have shown that the population's growth rate increased gradually during the 1980s, but began declining in the early 1990s, when female mortality rates increased substantially. Demographic projections predict that, assuming birth and mortality rates remain comparable to those observed in the early 1990s, the population will become extinct in less than 200 years. Further extrapolations suggest that reducing mortality rates by a few female deaths per year through conservation efforts would be sufficient to support a slow recovery of the population. However, the effects of climate variability and change on calving rates may make the North Atlantic right whale even more vulnerable than previous projections have suggested. Failure to incorporate the effects of climate in demographic projections may lead us to underestimate the conservation efforts required to ensure recovery of this whale population.

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We can conserve endangered species most effectively when we have adequate knowledge of the ecological and environmental requirements necessary for sustained population growth. The conservation efforts for many endangered species, especially those that were once commercially harvested, often focus on anthropogenic factors that affect mortality rates, while those that influence birth and growth rates are frequently downplayed or overlooked. Since sustained population growth is determined by the age-weighted balance between birth and mortality rates, it is important that we consider both when assessing the viability and recovery prospects for a particular endangered population (Boyce 1992). Here we review the case of the North Atlantic right whale (*Eubalaena glacialis*) (Figure 1) and suggest that previous studies, by focusing attention almost exclusively on sources of mortality, may have underestimated the important role that climate could play in this species' recovery or extinction.

Prior to commercial exploitation, right whales were distributed widely throughout the subtropical to subpolar regions of the Atlantic Ocean, with separate species occurring in the northern and southern hemispheres (Best *et al.* 2001). In the northern hemisphere, right whales were distributed in both the western and eastern sectors of the North Atlantic basin (Reeves and Mitchell 1986). Right whales are rich in oil and baleen, slow swimming, and have a tendency to float after being harpooned. These traits led early whalers to give them their common name, as they were clearly the "right" whales to hunt.

In a nutshell:

- The role of climate variability and change in the conservation biology of North Atlantic right whales has traditionally been underestimated
- By affecting reproduction rates, climate variability may make this species more vulnerable to extinction than previously thought
- This factor should be taken into account when formulating management plans that ensure the species' recovery

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The harvesting of North Atlantic right whales began nearly a millennium ago and steadily intensified, first driving the eastern North Atlantic population to near extinction and subsequently reducing the western population to a fraction of its former size (Reeves and Mitchell 1986; Aguilar 1986). In addition to reducing whale abundance, commercial harvesting also strongly impacted the distribution of right whales within the western sector. Basque whalers took thousands of right whales near Newfoundland and Labrador during the 16th and 17th centuries (Aguilar 1986), and the population has shown no substantive reoccupation of those former feeding grounds. By the latter part of the 19th century, the North Atlantic right whale population was so depleted that it no longer figured prominently in commercial harvests by the whaling industry (Allen 1908). In 1935, right whales were among the first cetaceans to receive international protection, and their protected status has been overseen by the International Whaling Commission since 1946 (Best *et al.* 2001).

Today, the small remnant population of right whales in the western North Atlantic ranges from the warm subtropical shelf waters of the southeastern United States to

Courtesy of Cornell Bioacoustics Research Program

Figure 1.*Female North Atlantic right whale* (Eubalaena glacialis) *and calf.*

the cold subpolar shelf waters of eastern Canada, with individuals rarely sighted outside of this range (Winn *et al.* 1986; Kraus *et al.* 1988; Knowlton *et al.* 1992). As is typical of most large cetaceans, these whales tend to calve in warm subtropical waters during winter, and migrate to feed in the highly productive cold temperate and subpolar waters in spring and summer. At present, the western North Atlantic population of right whales relies largely on feeding grounds in the Gulf of Maine/Western Scotian Shelf region (Winn *et al.* 1986). These present-day feeding grounds represent only the southern margin of the prewhaling feeding grounds that occupied much of the Northwest Atlantic sector. Kenney *et al.* (2001) have suggested that variability in prey abundance, through its effects on reproductive success, may have limited the recovery of right whales in this sector since the end of commercial whaling in the 20th century.

■ Current trends and future implications

With a western North Atlantic population currently estimated at approximately 300 individuals, the North Atlantic right whale is one of the most highly endangered of all cetacean species (Best *et al.* 2001). Recent modelling studies have shown that the population's growth rate, which increased gradually during the 1980s, slowly began to decline again during the early 1990s (Caswell *et al.* 1999; Fujiwara and Caswell 2001). Projections from demographic models suggest that if birth and mortality rates remain comparable to those observed during the early 1990s, extinction of the population will occur in less than 200 years (Caswell *et al.* 1999; Fujiwara and Caswell 2001). Extrapolations from these models further suggest that if mortality rates could be reduced by a few female deaths per year, this would be sufficient to support a slow recovery in numbers (Fujiwara and Caswell 2001). While such projections are useful for demonstrating the highly endangered status of this particular population, they may not adequately reflect the complexity of future threats to the species' survival. In fact, this population may be more vulnerable and facing a far more uncertain future than Fujiwara and Caswell's (2001) projections would suggest.

The major source of uncertainty is the limited demographic dataset upon which these population projections were based. While the North Atlantic right whale demographic dataset maintained at the New England Aquarium is remarkably good, it only goes back to 1980 (Kraus *et al.* 1986; SD Kraus pers comm). The period analyzed by Fujiwara and Caswell (2001), from 1980 to 1995, occurred during an unusual climate regime in the North Atlantic, characterized by predominantly positive values of the North Atlantic Oscillation (NAO) Index (Hurrell *et al.* 2001, 2003). Population projections are only valid for assessing the performance and viability of populations over time periods in which the demographic processes can be assumed to be stationary. Given the decadal-scale climate variability reported for the NAO (Hurrell *et al.* 2003), and its dramatic effects on the marine environment of right whales (Drinkwater *et al.* 2003; MERCINA 2001, 2003), population projections many decades into the future must be evaluated with considerable caution.

According to Fujiwara and Caswell (2001) the projected decline of the North Atlantic right whale population is driven primarily by the recent trend towards a higher female mortality rate. Although the principal factors behind this increasing rate are not known with certainty, collisions with ships and entanglement in fishing gear are considered to be likely causes (Knowlton and Kraus 2001). If we can attribute this increasing mortality rate largely to anthropogenic activities, such as commercial shipping and fishing, then the conservation policy issues become clearer. Only by implementing policies that regulate shipping and fishing in the regions frequented by right whales can we protect the population from further decline.

The problem, of course, is that shipping and fishing are of considerable economic importance to the regions frequented by right whales. This means that whatever policies are implemented must balance the conservation requirements of right whales with the economic interests of stakeholders engaged in commercial shipping and fishing. Given the potential for conflict in such a balancing act, it would be advantageous to find a simple conservation goal that could be agreed upon by both conservation advocates and representatives of those engaged in maritime commerce. It is tempting, therefore, to take the results of Fujiwara and Caswell (2001) and suggest that conservation policies leading to a modest reduction in female mortality rates would be enough to ensure the population's gradual recovery. Kareiva (2001), for example, concludes that "saving just two to three female whales each year could set this species on the road to recovery".

Unfortunately, complex problems rarely lend themselves to simple solutions. The demographic data analyzed by Fujiwara and Caswell (2001) were collected when the North Atlantic right whale population was experiencing not only increasing female mortality rates, but also, paradoxically, environmental conditions that were generally favorable for nutrition and reproduction (Greene *et al.* 2003). From 1980 to 1990, the NAO Index was predominantly positive, and, relative to climatological mean conditions for the past quarter century, right whale feeding grounds in the Gulf of Maine/Western Scotian Shelf region typically exhibited warmer ocean temperatures, higher standing stocks of phytoplankton, and higher abundances of the copepod species *Calanus finmarchicus* (Greene and Pershing 2000, 2003; MERCINA 2001, 2003; Pershing *et al.* in press; Figures 2 and 3).

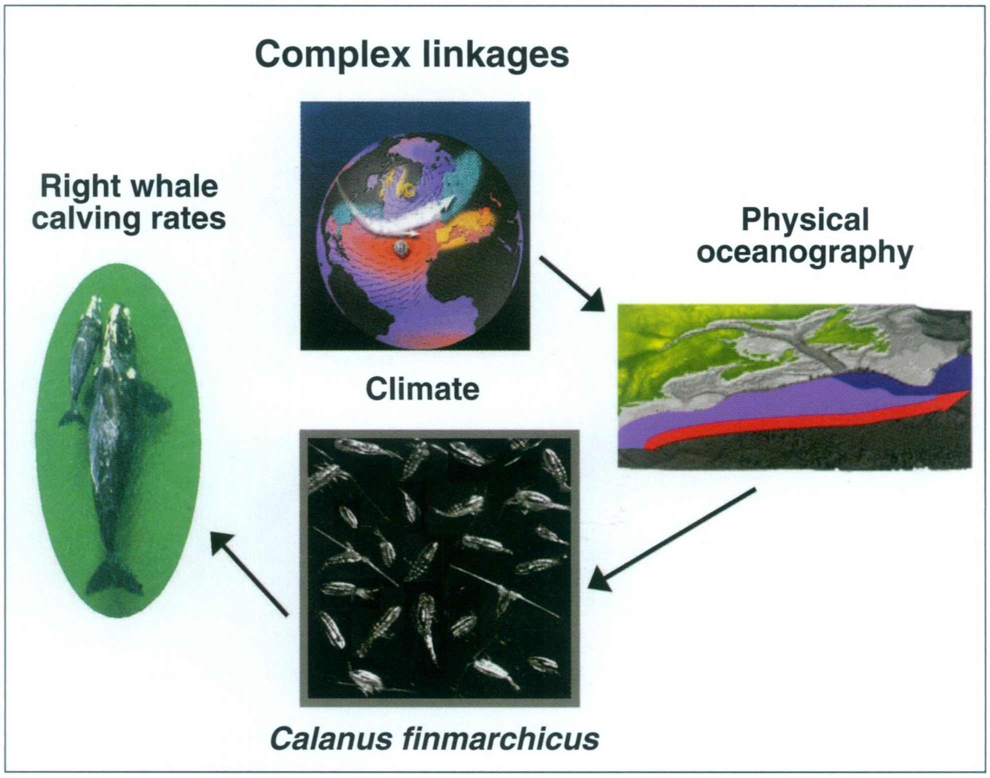

Figure 2. *Complex linkages among climate, physical oceanography,* Calanus finmarchicus *abundance, and right whale calving rates. The NAO is the principal mode of climate variability in the North Atlantic (Hurrell* et al. *2003). Physical oceanographic responses to phase changes in the NAO include changes in the modal state of the Northwest Atlantic's coupled slope water system (MERCINA 2001). The abundance of* Calanus finmarchicus *in the Gulf of Maine/Western Scotian Shelf region is linked to these modal shifts in the coupled slope water system (MERCINA 2001, 2003). Right whale calving rates are highly dependent on the regional abundance of* Calanus finmarchicus *(Greene* et al. *2003), serving as the final link in the chain between climate and right whale reproduction.*

As the principal source of nutrition for right whales, *Calanus* plays a key role in determining when environmental conditions are favorable for right whale reproduction. Modeling studies have shown that the stable calving rates of right whales observed during the 1980s can be attributed to the relatively high abundance of *Calanus* (Greene *et al.* 2003; Figure 4). After 1989, *Calanus* numbers began to decline, perhaps due to brief NAO-induced changes in the marine environment during the latter half of the 1980s (MERCINA 2001, 2003). *Calanus* abundance remained below the climatological mean until 1995, and right whale calving rates responded by dropping slightly below their climatological mean from 1993 to 1995. These observed calving rate patterns from the early 1980s to the mid-1990s are consistent with the model-predicted patterns reported by Greene *et al.* (2003) (Figure 4).

The more troubling observations have occurred since 1995, when environmental conditions and right whale calving rates have become much more variable. In 1996, the NAO Index exhibited its largest single-year drop of the 20th century, attaining a negative value not seen since the 1960s (Figure 3). This drop had striking effects on the North Atlantic's physical and biological oceanography, but its effects in the Gulf of Maine/Scotian Shelf region were not observed until late 1997 and 1998 (MERCINA 2001; Drinkwater 2003). It should be noted that such a 1- to 2-year time lag is characteristic of this region's oceanographic responses to NAO forcing (MERCINA 2001; Greene and Pershing 2003). In one of nature's ironic twists, even as the dramatic 1996 NAO phase change was setting the stage for subsequent declines, the *Calanus* population exhibited a short-term recovery, and right whale calving rates responded positively with a sharp upward spike during 1996 and 1997. The amplitude of this response may seem somewhat surprising given the relatively modest increase in *Calanus* abundance. However, right whale calving rate is a function of food availability, as well as the number of females available to reproduce (Figure 4). Since fewer females reproduced during the poor feeding conditions of the

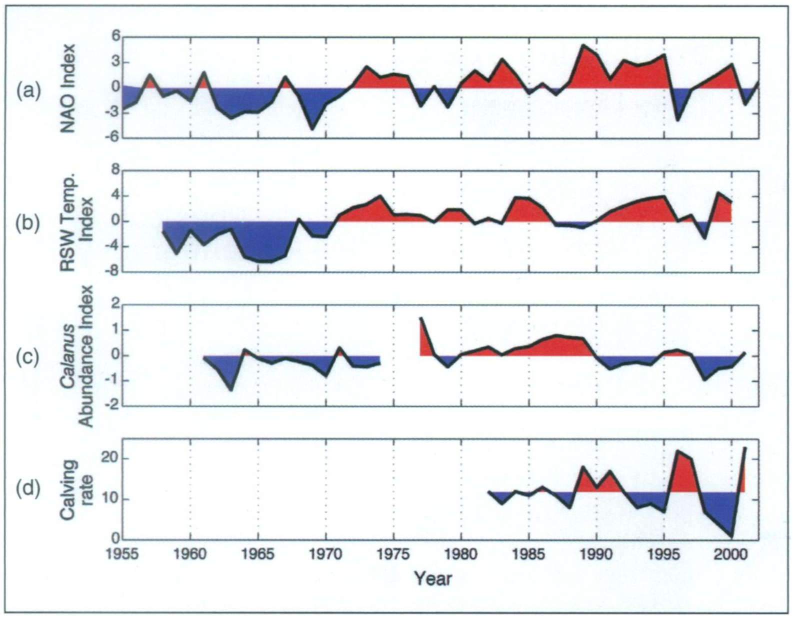

***Figure 3.** Time series from the North Atlantic. (a) Winter NAO Index, the mean atmospheric pressure difference between the North Atlantic's subtropical high-pressure system, measured in Lisbon, Portugal, and the subpolar low pressure system, measured in Stykkisholmer, Iceland (Hurrell 1995). (b) Regional Slope Water Temperature Index, an indicator of the modal state of the Northwest Atlantic's coupled slope water system, with positive (negative) values corresponding to warmer maximum (cooler minimum) modal state conditions (MERCINA 2001). It is the dominant mode derived from a principal components analysis of eight slope water temperature anomaly time series from the GOM/WSS region. (c)* Calanus finmarchicus *Abundance Index, the mean abundance anomaly for this species, calculated each year as the mean difference between log-transformed observed abundances and log-transformed expected abundances (MERCINA 2001). Data derived from Continuous Plankton Recorder (CPR) surveys conducted in the GOM/WSS region since 1961. (d) Right whale calving rate, the number of individually identified females accompanied by calves observed during a year beginning in December of the preceding calendar year. Data through 2001 provided by SD Kraus, New England Aquarium.*

early 1990s, more were available to calve when feeding conditions improved during the mid-1990s. The interaction between its feeding history and 3-year reproductive cycle is one of the more interesting nonlinear aspects of the right whale's numerical response to prey abundance (Greene *et al.* 2003).

When the NAO-associated decline in *Calanus* numbers did occur in 1998, it led to a fall in right whale calving rates from 1998 to 2000 that was even more substantial than the previous upward spike. With poor feeding conditions and fewer females available to reproduce after the 1996/1997 surge in reproduction, calving rates plummeted to their historical lows in 1999 and 2000. When *Calanus* abundance again increased in 2000, many females in the population had not given birth in recent years and were available for reproduction. This, together with the good feeding conditions, resulted in the calving rate reaching a historical high in 2001.

■ Uncertain prospects

As the new millennium unfolds, there is considerable uncertainty about future climate change. While the Intergovernmental Panel on Climate Change (IPCC) has concluded that it is highly likely that anthropogenic forcing, due to rising greenhouse gas concentrations, will lead to an increase in global mean temperature, the regional effects are far more difficult to predict (IPCC 2001). In the North Atlantic, the NAO Index has been predominantly positive during the past quarter of a century, and a number of investigators have suggested that this may be associated with greenhouse forcing (Gillett *et al.* 2003; Hurrell *et al.* 2003). Given the generally favorable conditions for right whale nutrition and reproduction associated with positive phases of the NAO, one might view this as the best-case climate scenario for right whale conservation biology. Under these conditions, Fujiwara and Caswell's (2001) population projections should provide a solid foundation for setting appropriate right whale conservation goals.

Another IPCC conclusion is less encouraging, however. In addition to global warming, it is probable that continually rising greenhouse gas concentrations will lead to an increase in climate variability (IPCC 2001). During the late 1990s, the North Atlantic climate exhibited some unusual behaviors, including a northeastward shift in the subpolar low-pressure center towards the Greenland Sea (Ulbrich and Christoph 1999). Several investigators have suggested that higher levels of greenhouse gases may have been responsible for this unusual behavior (Hurrell *et al.* 2001, 2003). In this context, one must ask whether the extreme drop in the NAO Index in 1996 was an unusual event or a sign of the larger swings in climate that we might expect in a greenhouse future. The flip side of the NAO, when a large phase reversal from positive to negative NAO conditions occurs (Greene and Pershing 2003), appears to have had a highly detrimental effect on right whale calving rates during the late 1990s, and the strongly negative NAO conditions observed in early winter 2003 may have similar consequences in the coming years. It is important that we incorporate the effects of increased climate variability on right whale calving rates into future demographic modeling studies. By exploring a range of climate variability scenarios, it should be possible to determine how sensitive right whale population projections are to such variable climate forcings.

Finally, let us consider the worst-case climate scenario for right whale conservation biology. What if the North Atlantic climate were to enter a long period of negative

NAO-like conditions? While the evidence for such a turn of events is not compelling at present, paleoclimate records indicate that such conditions have occurred in the past (Cook 2003). Furthermore, some investigators have suggested that we might expect a return to these conditions in the near future (Wood *et al.* 1999; Hillaire-Marcel *et al.* 2001). If right whale calving rates were depressed to low levels for a considerable period, then the projected time to extinction would occur much sooner than that predicted by Fujiwara and Caswell (2001). In that case, even a large decrease in the number of female fatalities associated with anthropogenic activities might not be sufficient to "set this species on the road to recovery" (Kareiva 2001). Instead, more active conservation measures might be necessary to help the species survive through particularly lean times.

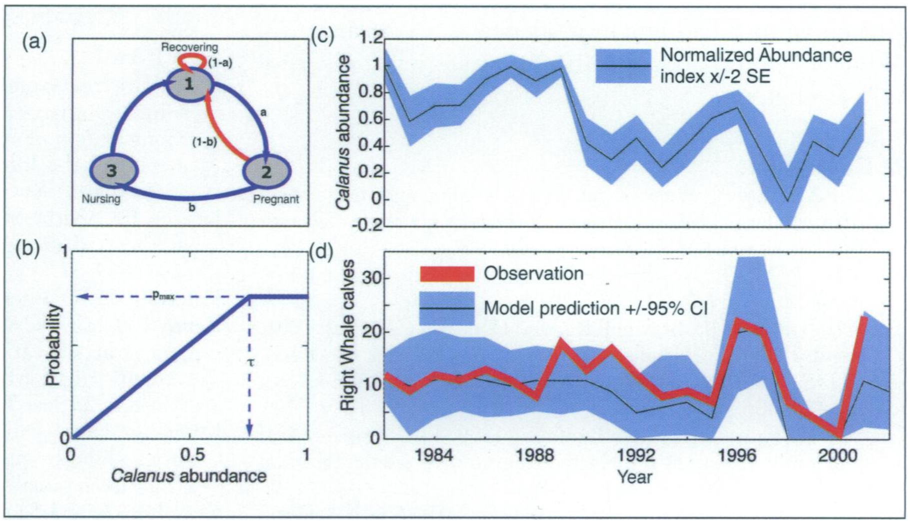

Figure 4. *Reproduction model for North Atlantic right whales. (a) Diagram of reproductive cycle, with transitional probabilities between states indicated. A whale in any of the three states will move to the next state with a probability determined by* finmarchicus *abundance in that year. If reproduction is unsuccessful, the animal will move to the recovery state. (b) Transitional probabilities are simple functions of* C finmarchicus *abundance as described by two parameters: the saturating food level* τ, *and the maximum transitional probability* p_{max}. *Parameter values were selected using a genetic algorithm to yield the best agreement between predicted and observed calving rates. (c)* Calanus finmarchicus *Abundance Index as determined from CPR surveys in the Western Gulf of Maine. (d) Number of right whale calves observed (red) and predicted by the model (blue). The blue region encompasses the 95% confidence interval surrounding the model predictions. For further details see* Greene et al. *(2003).*

■ Conclusions

Prior to human exploitation, the North Atlantic right whale population was considerably larger and exhibited a much broader geographical distribution than it does today. If recent estimates of pre-exploitation population abundances for other cetacean species in the North Atlantic are correct (Roman and Palumbi 2003), then it is conceivable that the right whale population was also much larger in the past than previously appreciated. Even under this shifting baseline scenario (Pauly 1995; Jackson *et al.* 2001), the right whale population prior to exploitation probably experienced periods of food-limited reproduction comparable to those observed in recent times, as *Calanus* abundance fluctuated with climate. However, the consequences of these lean periods would be very different for the large, unexploited population of the past as compared to the small, highly endangered numbers of today.

Females from the unexploited stock, free of anthropogenic sources of mortality and exhibiting a reproductive period spanning decades, could reproduce quickly enough to insulate the species from wild swings in numbers during the lean periods. When commercial whaling disrupted the natural demographic balance, females could not reproduce quickly enough to sustain the population, even when food was abundant. Today, right whales are protected from commercial whaling. However, due to other anthropogenic impacts, mortality rates are still higher than those that existed prior to human exploitation.

According to Fujiwara and Caswell's (2001) results, it appears that today's demographic balance is sensitive to small fluctuations in the numbers of females dying each year. It may also be sensitive to fluctuations in the numbers of calves born to each female. While the reproductive longevity of female right whales still insulates the population from short periods of food-limited reproduction, long periods of food limitation could put the population at greater risk than the demographic projections of Fujiwara and Caswell (2001) would suggest. A precautionary approach (United Nations 1992) to managing the recovery of this population should take the effects of climate variability and change into account. Failure to do so may lead us to underestimate the conservation efforts required to ensure recovery of the North Atlantic right whale population.

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