CLIMATE AND THE CONSERVATION BIOLOGY OF NORTH ATLANTIC RIGHT WHALES: BEING A RIGHT WHALE AT THE WRONG TIME?

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Abstract. Centuries of commercial whaling decimated the population of North Atlantic right whales. With the cessation of commercial whaling, it was expected that the population of this highly endangered species would recover gradually. Recent modeling studies by Fujiwara and Caswell (2001) have shown that the population's growth rate was increasing gradually during the 1980's but began declining during the early 1990's when female mortality rates increased significantly. Demographic projections indicate that, assuming birth and mortality rates remain comparable to those observed during the early 1990's, the population will become extinct in less than 200 years. Further extrapolations from these models suggest that if conservation efforts could reduce mortality rates by a few female deaths per year, then this improvement would be sufficient to support a slow recovery of the population. Here, we suggest that climate variability and change, through their effects on calving rates, may make the North Atlantic right whale population even more vulnerable than Fujiwara and Caswell's (2001) population projections would suggest. Failure to incorporate the effects of climate in demographic projections may lead us to underestimate the conservation efforts required to ensure recovery of the North Atlantic right whale population.

In a nutshell:

- By focusing attention almost exclusively on anthropogenic sources of mortality, previous studies have underestimated the important role that climate can play in the conservation biology of North Atlantic right whales.
- Climate variability and change, through their effects on calving rates, may make this species more vulnerable to extinction than previous population projections would suggest.
- A precautionary approach to managing this species' recovery should take into account the effects of climate variability and change.

- Failure to account for these effects of climate may lead us to underestimate the conservation efforts required to ensure this species' recovery.

The conservation of endangered species can best be achieved when there is adequate knowledge of the ecological and environmental requirements necessary for sustained population growth. In the conservation efforts for many populations of endangered species, especially those that were once commercially harvested, there is often a tendency to focus attention on anthropogenic factors affecting mortality rates, while those factors affecting 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 both be considered 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 can play in this species' road to recovery or extinction.

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. 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).

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 small 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 off 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 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 right whales tend to breed and ~~calf~~ calve in warm subtropical waters during winter and migrate to feed in the highly productive, cold temperate and subpolar waters during 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 pre-whaling feeding grounds that occupied much of the Northwest Atlantic sector. Kenney et al. (2001) have suggested that variability in prey abundance, via its effects on reproductive success, may have limited the recovery of right whales in this sector since the end of commercial whaling during the 20th century.

Current Trends and their Implications for the Future

With a population in the western North Atlantic 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 modeling studies have shown that the population's growth rate has gone from gradually increasing during the 1980's to gradually declining during the early 1990's (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 1990's, 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, then this improvement would be sufficient to support a slow recovery of the population (Fujiwara and Caswell 2001). While such projections are useful for demonstrating the highly endangered status of the North Atlantic right whale population, they may not adequately reflect the complexity of future threats to the species' survival. In fact, we argue here that this population may be more vulnerable and facing a far more uncertain future than Fujiwara and Caswell's (2001) population projections would suggest.

The major source of uncertainty is the limited demographic data set upon which these population projections were based. While the North Atlantic right whale demographic data set maintained at the New England Aquarium is remarkably good, it only goes back to 1980 (Kraus et al. 1986, Kraus personal communication). 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 periods of time when the demographic processes can be assumed as stationary. Given the interdecadal-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 interpreted with a considerable degree of caution.

In discussing the projected decline of the North Atlantic right whale population, Fujiwara and Caswell (2001) demonstrate that it is driven primarily by the recent trend towards a higher female mortality rate. Although the principal factors behind this increasing female mortality rate are not known with certainty, collisions with ships and entanglement in fishing gear are considered to be likely candidates (Kraus 1990, Knowlton and Kraus 2001). If the increasing female mortality rate can be attributed 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 the population be protected 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 conservation advocates as well as advocates representing 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 sufficient to ensure the population's gradual recovery. Karieva (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 during a period of time 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) (Figure 2, 3). 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 decade of the 1980's can be attributed to the relatively high abundances of *Calanus* (Greene et al., 2003) (Figure 4). After 1989, *Calanus* began to decline in abundance, perhaps due to brief NAO-induced changes in the marine environment during the latter half of the 1980's (MERCINA 2001, 2003). Abundances of *Calanus* remained below their 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 1980's to the mid-1990's are consistent with the model-predicted patterns reported by Greene et al. (2003) (Figure 4).

The more troubling observations have occurred since 1995, with environmental conditions and right whale calving rates becoming much more variable. In 1996, the NAO Index exhibited its largest single-year drop of the twentieth century, attaining a negative value not seen since the 1960's (Figure 3). This large drop in the NAO Index had striking effects on the North Atlantic's physical and biological oceanography, but effects in the Gulf of Maine/Scotian Shelf region were not observed until 1997/1998 (MERCINA 2001, Drinkwater 2003). It should be noted that such a one to two-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 1996's dramatic phase change in the NAO 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 early 1990's, more were available to reproduce when feeding conditions improved during the mid-1990's. The interaction between its feeding history and three-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* abundance did arrive in 1998, it led to a drop in right whale calving rates from 1998 to 2000 that was even more impressive than the previous upward spike. With poor feeding conditions and fewer females available to reproduce after the 1996/1997 burst in reproduction, calving rates plummeted to their historical lows in 1999 and 2000. When *C. finmarchicus* abundance again increased in 2000, many females in the right whale population had not given birth in recent years and were available for reproduction. With the combination of many females available to reproduce and good feeding conditions, the calving rate reached an historical high in 2001.

Uncertain Prospects for the Future

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 increasing 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 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 such a scenario, 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, the IPCC has concluded that it is likely that continually rising greenhouse gas concentrations will lead to an increase in climate variability (IPCC 2001). During the late 1990's, 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 rising greenhouse gas concentrations may have been responsible for this unusual behavior (Hurrell et al. 2001, 2003). In this context, one must ask whether the extreme drop of 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 1990's, and the strongly negative NAO conditions observed in winter 2003 may have similar consequences during the coming years. It is important that the effects of increased climate variability on right whale calving rates be incorporated 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, we raise the possibility of what might be considered the worst-case climate scenario for right whale conservation biology – what if 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 such conditions in the not-too-distant future (Wood et al. 1999, Hillaire-Marcel et al. 2001). If right whale calving rates were depressed to low levels for a considerable period of time, then the projected time to extinction would occur much sooner than that predicted by Fujiwara and Caswell (2001). Under such a climate scenario, even a large decline in the female fatalities associated with anthropogenic activities might not be sufficient to "set this species on the road to recovery." Instead, more active conservation measures might be necessary to help the species survive through particularly lean times.

Concluding Remarks

Prior to human exploitation, the North Atlantic right whale population was considerably larger and exhibited a much broader geographical distribution than 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 likely experienced periods of food-limited reproduction, comparable to those observed in recent times, as *Calanus* abundance fluctuated with climate. The consequences of these lean periods, however, would be much different for the large, unexploited population of the past and the small, highly endangered population of today.

Unimpacted by anthropogenic sources of mortality and exhibiting a reproductive period spanning decades, females from the unexploited stock could produce calves at a rate sufficient to insulate the population from wild swings in abundance during such lean periods. When commercial whaling disrupted the population's natural demographic balance, females could not produce calves at a rate sufficient to sustain the population even when food was abundant. Today, the right whale population is protected from commercial whaling; however, due to other anthropogenic impacts, its mortality rates are still elevated above those prior to human exploitation.

From Fujiwara and Caswell's (2001) results, it appears that today's demographic balance is a delicate one, sensitive to small fluctuations in the numbers of females dying each year. We suggest that under such conditions, the demographic balance also may be sensitive to fluctuations in the numbers of calves born to each female. While the reproductive longevity of right whale females 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 account for these effects may lead us to underestimate the conservation efforts required to ensure recovery of the North Atlantic right whale population.

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Figure Captions

Figure 1. Female North Atlantic right whale and calf.

Figure 2. Complex linkages among climate, physical oceanography, *C. finmarchicus* abundance, and right whale calving rates. The NAO is the principal mode of climate variability in the North Atlantic (Hurrell 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 *C. 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). Finally, right whale calving rates are highly dependent on the regional abundance of *C. finmarchicus* (Greene et al. 2003), thereby, completing the final link in the chain between climate and right whale reproduction.

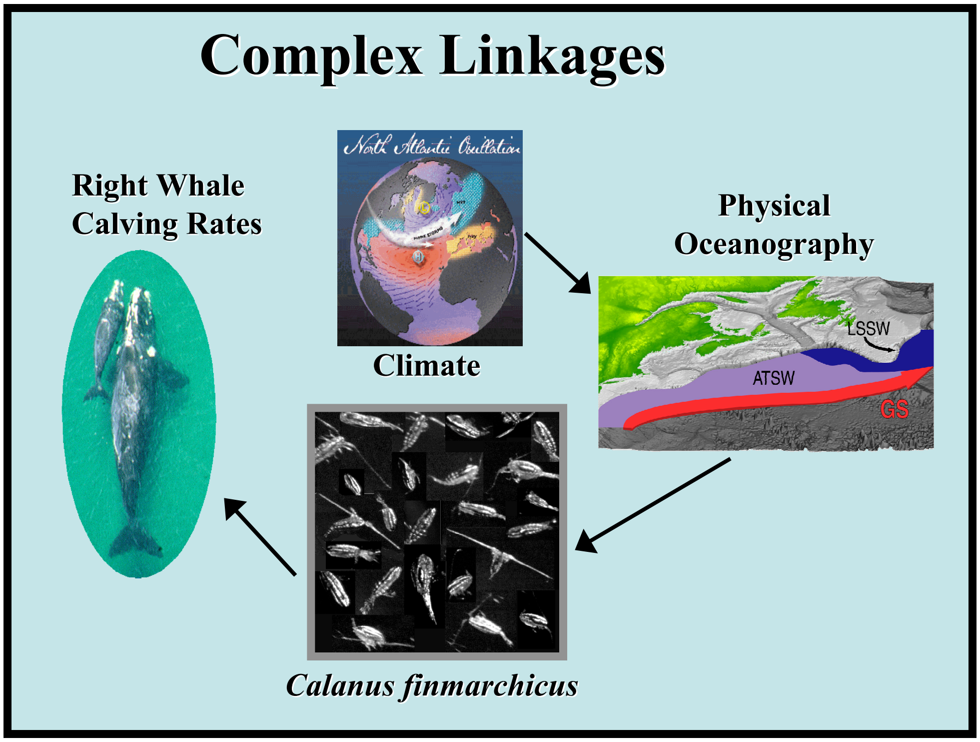
Figure 3. Time series from the North Atlantic. A. Annual values of the winter NAO Index. B. Annual values of the Regional Slope Water Temperature Index. C. Annual values of the *Calanus finmarchicus* Abundance Index. D. Annual values of right whale calving rate. The winter NAO Index is the mean atmospheric 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). The Regional Slope Water Temperature Index is 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. The *Calanus finmarchicus* Abundance Index is 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). Abundance data were derived from Continuous

Plankton Recorder (CPR) surveys conducted in the GOM/WSS region since 1961. Right whale calving rate is the number of individually identified females accompanied by calves observed during a year beginning in December of the preceding calendar year. Data, through 2001, were provided by S.D. Kraus, New England Aquarium.

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, pregnant, nursing, or recovering, will move to the next state with a probability determined by *Calanus finmarchicus* abundance in that year. If reproduction is unsuccessful, then the animal will move to the recovery state. B. The transitional probabilities are simple functions of *Calanus finmarchicus* abundance as described by two parameters, τ, the saturating food level, and p_{max}, the maximum transitional probability. Parameter values were selected using a genetic algorithm to yield the best agreement between predicted and observed calving rates. C. The *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).

Figure 1.

Figure 2.


Complex Linkages
North Atlantic Oscillation
Right Whale
Calving Rates
Physical
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LSSW
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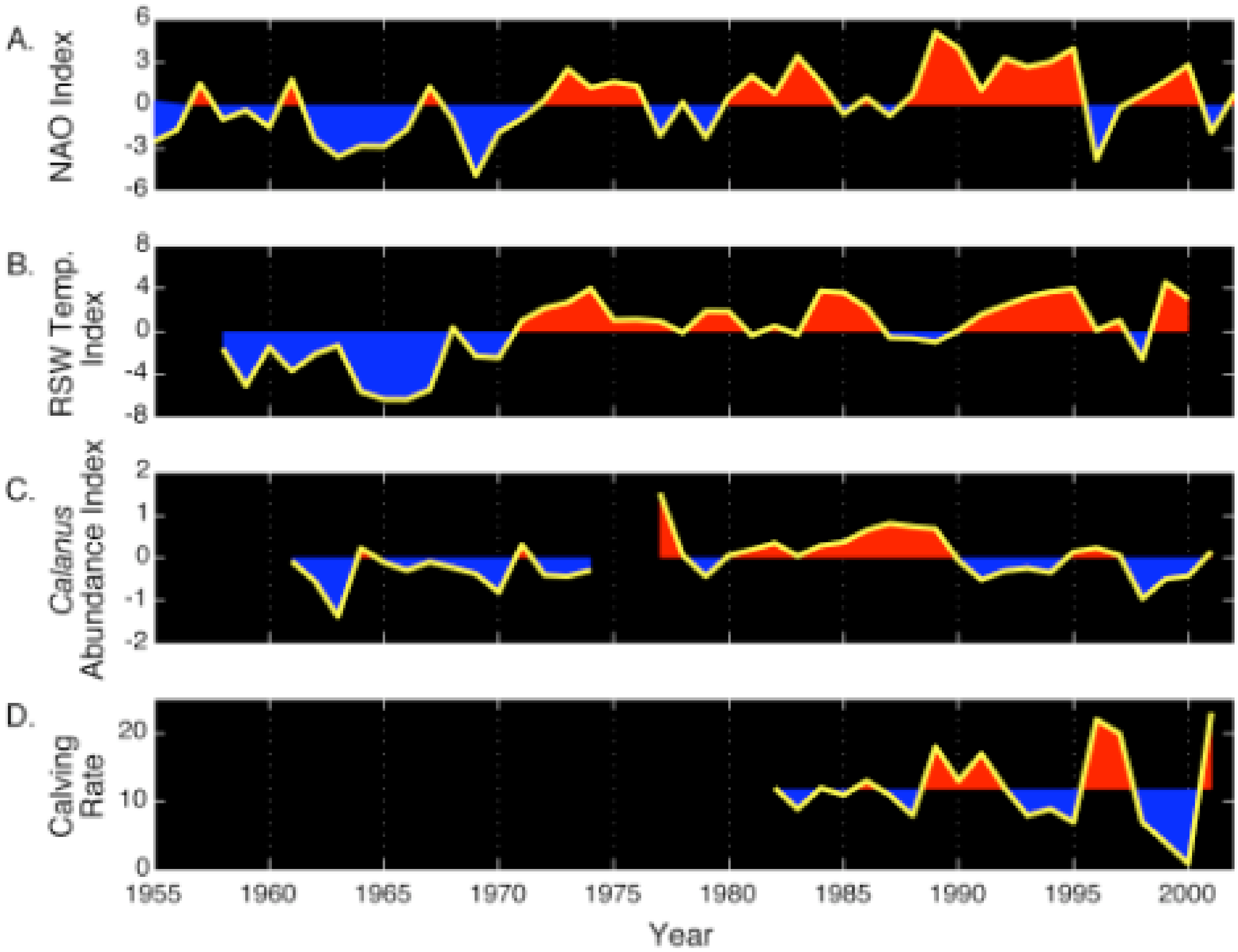
Calanus finmarchicus

Figure 3.


A.
NAO Index
6
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B.
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Calanus Abundance Index
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D.
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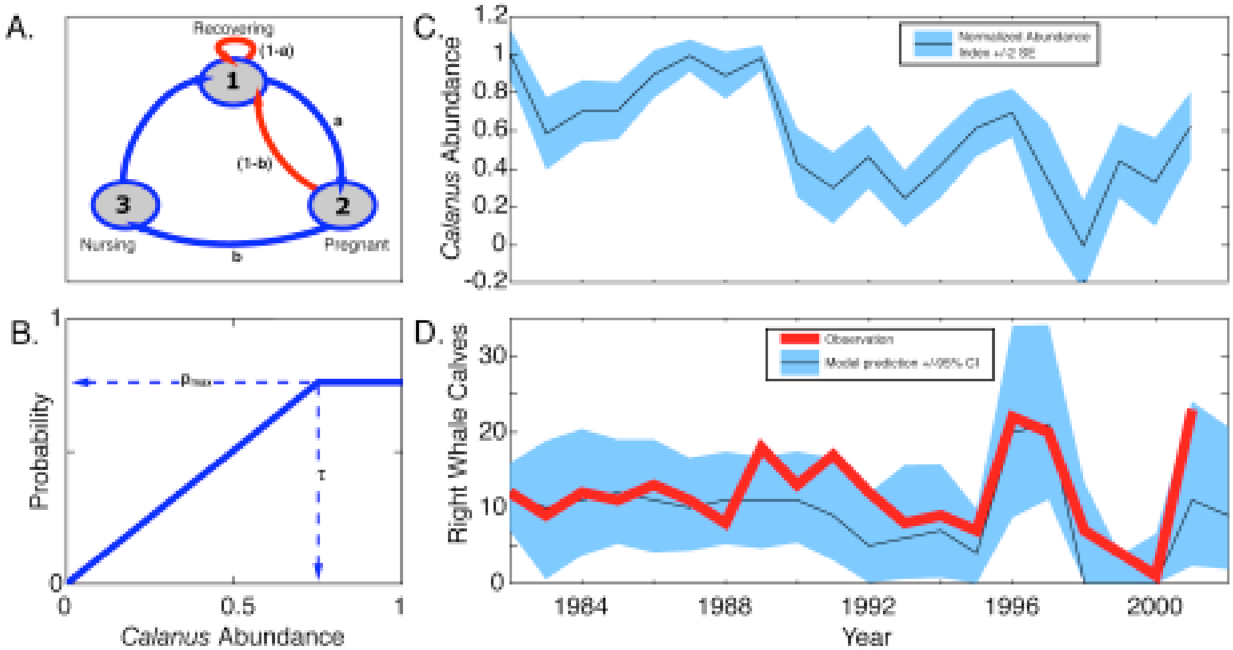
Figure 4.


A.
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D.
Right Whale Calves
Observation
Model prediction +/-95% CI
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