IMPACT OF CLIMATE VARIABILITY ON THE RECOVERY OF ENDANGERED NORTH ATLANTIC RIGHT WHALES

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Key words: *climate, demography, endangered species, North Atlantic Oscillation, physical-biological coupling, right whales*

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Abstract. **The demographic responses of long-lived endangered species to climate variability can be complex. Nonlinearities in physical and biological processes can obscure relationships between changes in climate and corresponding demographic responses. Efforts to conserve such species will require an understanding of the multi-tiered mechanisms linking climate variability to ecosystem processes and population dynamics. Here, we describe the physical-biological coupling of oceanographic processes linking climate variability to the reproduction of North Atlantic right whales. These findings suggest that future climate change, through its regional effects in the Northwest Atlantic, may emerge as a significant factor influencing recovery of this highly endangered species.**

The North Atlantic right whale is a critically endangered species, with a population in the western North Atlantic estimated at approximately 300 individuals (Caswell et al., 1999). Recent studies have shown that the population growth rate has shifted from gradually increasing in the 1980's to gradually declining in the 1990's (Caswell et al., 1999; Fujiwara and Caswell, 2001). Projections from demographic models suggest that, if mortality and reproductive rates remain comparable to those observed during the 1990's, the population will go extinct in less than 200 years (Caswell et al., 1999; Fujiwara and Caswell, 2001). Extrapolations from these models further suggest that the prevention of one or two female deaths per year would be sufficient to support the slow recovery of this species (Fujiwara and Caswell, 2001). While such demographic projections are instructive, it is important that they be interpreted in the context of climate-driven oceanographic variability in the Northwest Atlantic.

Historically, right whales were distributed broadly on both sides of the North Atlantic basin, with spring and summer feeding grounds in the northwest and northeast sectors (Reeves and Mitchell, 1986). Intense harvesting pressure, beginning nearly a millennium ago, first drove the eastern North Atlantic population to near extinction and subsequently reduced 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 strongly impacted the distribution of right whales. 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. Today, the small, remnant population of right whales in the western North Atlantic relies almost exclusively on feeding grounds in the Gulf of Maine/Western Scotian Shelf (GOM/WSS) 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 intensive whaling during the 20th century.

The GOM/WSS region presents right whales with a highly variable feeding environment. The region lies within an oceanographic transition zone, located between cold subpolar waters influenced by fluctuations in the Labrador Current to the northeast and warm temperate waters influenced by fluctuations in the Gulf Stream to the south (MERCINA, 2001). The transitions that occur within this zone are not only physical, as reflected by hydrographic changes, but also biological, as reflected by changes in the composition and relative abundance of plankton (Greene and Pershing, 2000; MERCINA, 2001). The shifting nature of this transition zone makes the

GOM/WSS region especially vulnerable to climate-driven changes in North Atlantic circulation patterns.

The physical responses of the GOM/WSS region to changes in ocean circulation are often mediated by the NW Atlantic's coupled slope water system (CSWS) (MERCINA, 2001). Two characteristic modes have been identified for the CSWS (Fig. 1). The minimum mode corresponds to a state in which Labrador Current transport around the Tail of the Grand Banks is intensified, and the frontal boundary of relatively cool, fresh Labrador Subarctic Slope Water (LSSW) advances further downstream than usual along the continental margin, displacing warmer, saltier Atlantic Temperate Slope Water (ATSW) offshore (Fig. 1A). The maximum mode of the CSWS corresponds to a state in which Labrador Current transport around the Tail of the Grand Banks is reduced, and the frontal boundary of LSSW retreats upstream along the continental margin, allowing ATSW to move onshore towards the shelf (Fig. 1B).

Recently, it has been shown that modal shifts in the CSWS are often associated with phase changes in the North Atlantic Oscillation (NAO) (MERCINA, 2001). From the early 1970's to the present, the NAO Index has been predominantly positive (Hurrell et al., 2001; 2003), and the CSWS usually has exhibited conditions characteristic of its maximum modal state (Fig. 2A, B) (MERCINA, 2001). However, five times during these three decades (1977, 1979, 1985, 1987, 1996), the NAO Index has dropped to negative values for a single year. In each case, the CSWS appears to have responded to a drop in the NAO Index by shifting toward its minimum modal state after a one- to two-year time lag (1978, 1981, 1987, 1989, 1998). While the first two responses of the CSWS, in 1978 and 1981, were relatively small, the latter responses were more substantial. The response to the 1985 and 1987 drops in the NAO Index involved a multi-year modal shift lasting from 1987 to 1990. The response to the 1996 drop in the NAO Index was both dramatic and the best documented modal shift to date.

In 1996, the NAO Index exhibited its largest single-year drop of the 20th century, followed during the subsequent two years by a modal shift in the CSWS (Fig. 2A). During this modal shift, the flow of the Labrador Current around the Tail of the Grand Banks intensified, with LSSW steadily advancing along the shelf break, displacing ATSW offshore, and penetrating to the southwest as far as the Middle Atlantic Bight (Fig. 1A) (MERCINA, 2001). As it advanced along the shelf break, the LSSW also invaded the deep basins of the GOM/WSS region . The deep waters of these basins are derived from slope water incursions, and, from the early 1970's until 1997, these deep waters were relatively warm and salty, reflecting their ATSW origin. By early winter 1998, LSSW had replaced the deep waters of Emerald Basin on the WSS and began entering the GOM through Northeast Channel. By early autumn 1998, the hydrographic properties of the GOM deep basins reflected the advective replacement and mixing that had occurred between the invading LSSW and the resident deep waters derived largely from ATSW.

The observed hydrographic changes in the GOM/WSS region during 1998 were short-lived, however. The drop in the NAO Index during the winter of 1996 was a single-year event, with the Index returning to positive values for the remainder of the 1990's. Similarly, the CSWS shifted back to its maximum modal state, with the Labrador Current weakening and the frontal boundary of the LSSW retreating northeastward along the Scotian Shelf. As the supply of LSSW to the region decreased, ATSW returned to its previous position adjacent to the shelf break and began supplying warmer, saltier slope water to the deep basins on the shelf. By the end of 1999, the hydrographic conditions in the GOM/WSS deep basins resembled those prior to the modal shift in the CSWS triggered by the 1996 drop in the NAO Index.

The climate-driven changes in ocean circulation observed over the past 40 years have had a profound impact on the plankton ecology in the GOM. The abundance of *Calanus finmarchicus*, a copepod species that dominates the spring and summertime zooplankton biomass in the GOM, is tightly coupled to the modal state of the CSWS (Fig. 2B, C) (Greene and Pershing, 2000; MERCINA, 2001). During the decade of the 1960's, when the NAO Index was predominantly negative and the CSWS was in its minimum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively low. During the 1980's, when the NAO Index was predominantly positive and the CSWS was predominantly in its maximum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively high. During each of the maximum- to minimum-modal shifts in the CSWS after 1980, *C. finmarchicus* abundance declined in subsequent years. The modal shift during 1981-83 preceded a large, single-year decline in abundance during 1983. The modal shift during 1988-91 preceded a large decline in abundance that persisted throughout the early 1990's. Then, after *C. finmarchicus* abundance began building up again during the mid-1990's, the NAO Index underwent its aforementioned drop of the century in 1996. This event triggered the intense modal shift of the CSWS during 1997, which, in turn, led to very low abundances of *C. finmarchicus* during 1998 and early 1999.

The mechanisms underlying these climate-driven changes in *C. finmarchicus* abundance have not been fully resolved; however, they appear to be linked to the advective supply of this species into the GOM/WSS region from the slope waters (Greene and Pershing, 2000; MERCINA, 2001). Since *C. finmarchicus* is recognized as the principal source of nutrition for right whales in the region (Kenny et al., 2001), we hypothesize that right whale population responses to climate variability are mediated primarily by trophic interactions with this prey species. To explore this hypothesis, we examine right whale calving rate patterns since the early 1980's (Fig. 2D).

Since consistent data were first collected in 1982, major multi-year declines in right whale calving rates have tracked major multi-year declines in *C. finmarchicus* abundance (Fig. 2C, D). From 1982 to 1992, calving rates exhibited no multi-year declines and were relatively stable with a mean rate of 12.4 ± 0.9 (SE) calves per year. These findings are consistent with the relatively high abundance of *C. finmarchicus* observed during the 1980's. From 1993 to 2001, calving rates exhibited two major, multi-year declines, with the mean rate dropping and becoming much more variable at 11.2 ± 2.7 (SE) calves per year. These findings are consistent with the two precipitous drops in *C. finmarchicus* abundance observed during the early and late 1990's.

Although both major declines in right whale calving rates were associated with drops in *C. finmarchicus* abundance, the timing of responses varied during the two multi-year events. During the first event, calving rates dropped steeply two years after *C. finmarchicus* abundance had begun to fall. During the second event, calving rates dropped steeply the same year that *C. finmarchicus* abundance began to fall. We hypothesize that right whale reproductive physiology underlies these different responses.

Female right whales typically require at least three years between births – one year for lactation, one year to amass fat stores to support the next pregnancy, and one year during the pregnancy (Knowlton et al., 1994). Hence, feeding conditions over several years are likely integrated when determining if a given female will reproduce or not. Since the first multi-year decline in calving rates occurred two years after a period of relatively stable reproduction and good feeding conditions, the time-lagged response may have required two years of poor feeding conditions before taking effect. When *C. finmarchicus* abundance increased in the mid-1990's, many females in the right whale population had not given birth recently and were available for reproduction. Hence, when good feeding conditions returned, calving rates nearly doubled during 1996 and 1997. This burst of reproduction reduced the number of females available for subsequent reproduction, and, when combined with the poor feeding conditions during the late 1990's, calving rates plummeted from 1998 to 2000. When *C. finmarchicus* abundance increased again in 2000, many females in the right whale population had not given birth recently and were available for reproduction. With the combination of many females available for reproduction and good feeding conditions, the annual calving rate reached a high point in the two-decade record in 2001.

To assess the feasibility of the above hypotheses quantitatively, we developed a simple model that captures the key features of the right whale reproductive cycle and links these to food availability (Fig. 3). The transitional probabilities among the three states of females in the model, pregnant, nursing, and recovering, are functions of food availability, as represented by *C. finmarchicus* annual abundances in the western Gulf of Maine (Fig. 3A, B, C).

Our model captures the overall calving rate patterns very well, especially the wild fluctuations of recent years (Figure 3D). Both multi-year declines observed during the early and late 1990's were reproduced by the model. In addition, our model accurately predicts the dramatic increase in right whale calves born during 2001. These results give us confidence in the utility of this simple model, not only to hindcast past events, but also to forecast right whale reproductive performance at least one year into the future.

While our findings support the hypothetical link between climate and the calving rates of North Atlantic right whales, predicting the effects of climate variability and change on this species' long-term recovery will require a broader perspective. The recovery rate of the right whale population is determined by its age-structured demography, i.e., the age-weighted balance between the population's birth rate and mortality rate. Historically, human activities have impacted the population primarily by affecting mortality rates. During the centuries of commercial whaling, humans were clearly the major source of right whale mortality. Since the cessation of commercial whaling, most attention has remained on human activities, such as shipping and fishing (Fujiwara and Caswell, 2001; Knowlton and Kraus, 2001), which directly affect mortality rates. Because right whale population recovery is more sensitive to mortality rates than to birth rates (Caswell et al., 1999), conservation efforts to reduce collisions with ships and entanglement with fishing gear are appropriate. In addition, however, we suggest that attention also should be focused on the effects of climate variability on right whale calving rates. Failure to account for these effects of climate may cause us to underestimate the conservation efforts required to ensure recovery of the North Atlantic right whale population (Greene and Pershing, submitted).

During the past quarter century, the NAO Index has been predominantly positive, and there is increasing evidence that this may be associated with greenhouse warming and the rise in ocean heat content, especially in the tropics (Hoerling et al., 2001; Hurrell, 2001; 2003). While we have presented evidence that the positive NAO conditions of the 1980's were favorable to right whale calving rates, the increased climate variability predicted by some models as a consequence of continually rising greenhouse gas concentrations (IPCC, 2001) is cause for concern. The NAO exhibited unusual behavior during the decade of the 1990's, including a northeastward shift in the subpolar low-pressure center towards the Greenland Sea . Several investigators have suggested that rising greenhouse gas concentrations may be responsible for this unusual behavior (Hurrell et al., 2001). 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 can expect in the future. This flip-side of the NAO (Greene and Pershing, 2003) clearly had detrimental effects on right whale calving rates during the late 1990's. This also raises the issue of what we might expect if the NAO were to enter a long, predominantly negative phase. Paleoclimate records indicate that such conditions have occurred in the past (Appenzeller et al., 1998; Jones et al., 2001), and 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). Ultimately, our ability to assess the long-term prospects for North Atlantic right whale recovery may only be as a good as our ability to predict regional climate variability and change in the Northwest Atlantic.

ACKNOWLEDGMENTS

We thank S. Kraus, for sharing data; H. Caswell and M. Fujiwara, for providing comments; and the large number of researchers and institutions collaborating through the North Atlantic Right Whale Consortium, for their long-term efforts to monitor the population biology of right whales. Supported by the NOAA Coastal Ocean Program, as part of the US GLOBEC NW Atlantic/Georges Bank Program, the Northeast Consortium's North Atlantic Right Whale Program, and the URI-NOAA Cooperative Marine Education and Research program. This paper was begun while CHG was in residence as a sabbatical fellow at the National Center for Ecological Analysis and Synthesis, University of California Santa Barbara and completed while he was in residence as a scholar at the Whitely Center, Friday Harbor Laboratories, University of Washington. Contribution ### from the US GLOBEC Northwest Atlantic/George Bank Program.

LITERATURE CITED

Aguilar, A. 1986. A review of old Basque whaling and its effect on right whales (*Eubalaena glacialis*) of the North Atlantic. Reports of the International Whaling Commission, Special Issue **10**: 191-199.

Appenzeller, C., T.F. Stocker, and M. Anklin. 1998. North Atlantic Oscillation dynamics recorded in Greenland ice cores. Science **282**: 446-449.

Caswell, H., M. Fujiwara, and S. Brault. 1999. Declining survival probability threatens the North Atlantic right whale. Proceedings of the National Academy of Science USA **96**: 3308-3313.

Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. Nature **414**: 537-541.

Greene, C.H., and A.J. Pershing. 2000. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation (NAO). International Council for the Exploration of the Sea Journal of Marine Science **57**: 1536-1544.

Greene, C.H., and A.J. Pershing. 2003. The flip-side of the North Atlantic Oscillation and modal shifts in slope water circulation patterns. Limnology and Oceanography **48**: 319-322.

Greene, C.H., and A.J. Pershing. submitted. Climate and the conservation biology of North Atlantic right whales: being a right whale at the wrong time? Frontiers in Ecology and the Environment.

Hillaire-Marcel, C., A. de Vernal, G. Bilodeau, and A.J. Weaver. 2001. Absence of deep-water formation in the Labrador Sea during the last interglacial period. Nature **410**: 1073-1077.

Hoerling, M.P., J.W. Hurrell, and T. Xu. 2001. Tropical origins for recent North Atlantic climate change. Science **292**: 90-92.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science **269**: 676-679.

Hurrell, J.W., Y. Kushnir, and M. Visbeck. 2001. The North Atlantic Oscillation. Science **291**: 603-605.

Hurrell, J.W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. An overview of the North Atlantic Oscillation, Pages 1-35 *in* J.W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, editors, The North Atlantic Oscillation: Climatic Significance and Environmental Impact. American Geophysical Union, Washington, D.C.

IPCC. 2001. Climate Change 2000: The Science of Climate Change, the Contribution of Working Group 1 to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jones, P.D., T.J. Osborn, and K.R. Briffa. 2001. The evolution of climate over the last millennium. Science **292**: 662-667.

Kenny, R.D., C.A. Mayo, and H.E. Winn. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. Journal of Cetacean Resource Management, Special Issue **2**: 251-260.

Knowlton, A.R., S.D. Kraus, and R.D. Kenney. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). Canadian Journal of Zoology **72**: 1297-1305.

Knowlton, A., and S. Kraus. 2001. Mortality and serious injury of northern right whales (*Eubalaena glacialis*) in the western North Atlantic Ocean. Journal of Cetacean Resource Management, Special Issue **2**: 193-207.

MERCINA. 2001. Oceanographic responses to climate in the Northwest Atlantic. Oceanography 14: 76-82.

Reeves, R.R., and E. Mitchell. 1986. The Long Island, New York, right whale fishery: 1650-1924. Reports of the International Whaling Commission, Special Issue **10**: 201-220.

Winn, H.E., C.A. Price, and P.W. Sorensen. 1986. The distributional biology of the right whale (*Eubalaenea glacialis*) in the western North Atlantic. Reports of the International Whaling Commission, Special Issue **10**: 129-138.

Wood, R.A., A.B. Keen, J.F.B. Mitchell, and J.M. Gregory. 1999. Changing spatial structure of the thermohaline circulation in response to atmospheric CO_2 forcing in a climate model. Nature **399**: 572-575.

Figure Captions

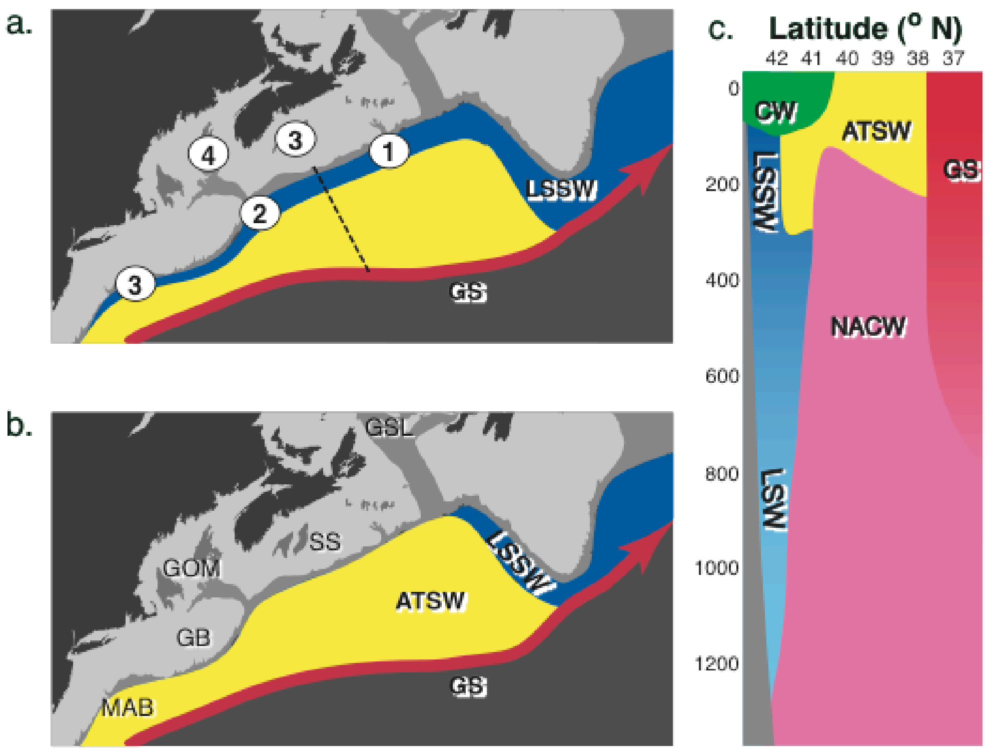
Figure 1. The Northwest Atlantic's coupled slope water system (CSWS). A. Minimum modal state of the CSWS. Circled numbers indicate 1997-98 advance of LSSW frontal boundary along continental margin: 1 – September 1997, 2 – January 1998, 3 – February 1998, 4 – August 1998. B. Maximum modal state of the CSWS. C. Hydrographic section shown in Fig. 1A as indicated by dashed line. Geographical features, water masses, and currents are labeled as follows: Georges Bank = GB, Gulf of Maine = GOM, Gulf of St. Lawrence = GSL, Middle Atlantic Bight = MAB, Scotian Shelf = SS, Atlantic Temperate Slope Water = ATSW, Coastal Water = CW, Labrador Sea Water = LSW, Labrador Subarctic Slope Water = LSSW, North Atlantic Central Water = NACW, Gulf Stream = GS.

Figure 2. 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 CSWS, with positive (negative) values corresponding to maximum (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 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. Contact authors for further details.

Figure 3. Right whale reproduction model. 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 Continuous Plankton Recorder 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. Contact authors for further details.

Figure 1.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LSSW
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Latitude (° N)
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CW
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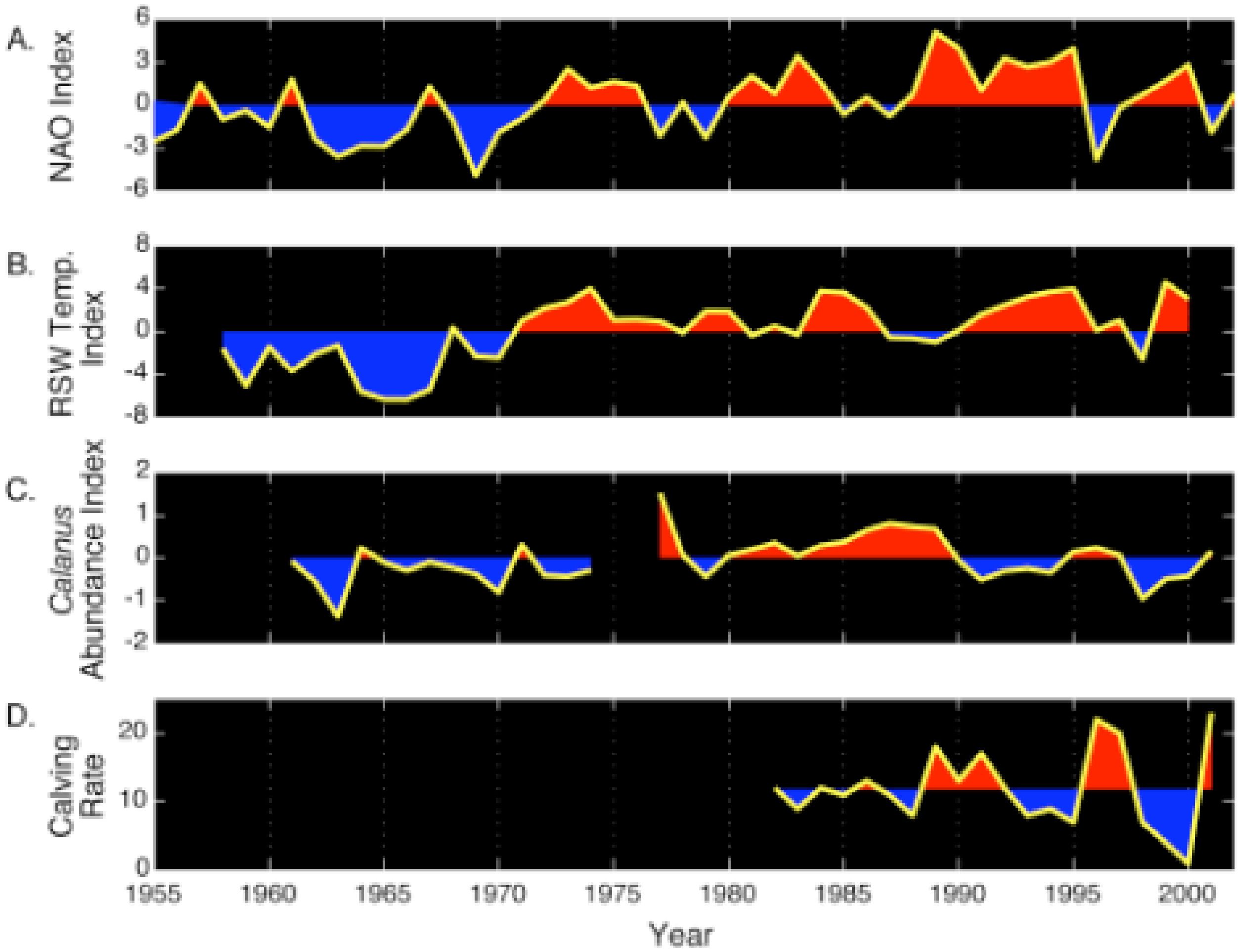
Figure 2.


A.
NAO Index
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3
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-3
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B.
RSW Temp. Index
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-8
C.
Calanus Abundance Index
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1
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-1
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D.
Calving Rate
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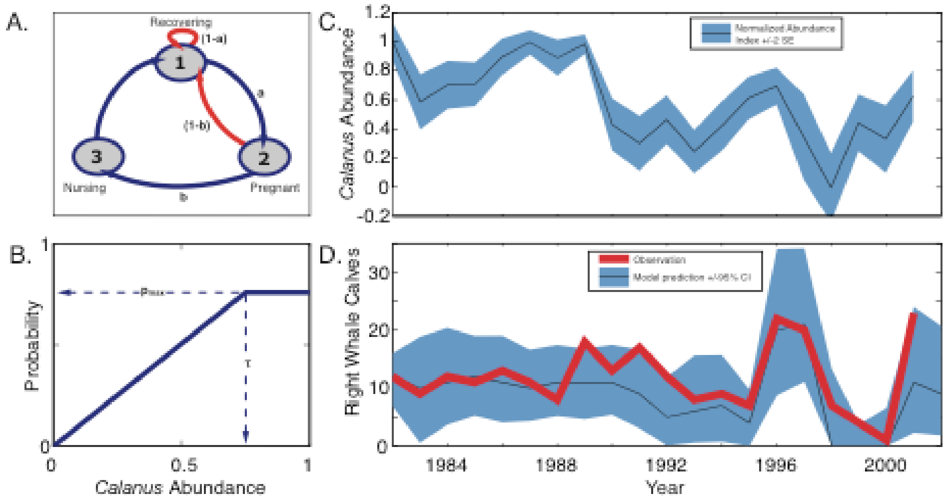
Figure 3.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Recovering
(1-a)
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a
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Nursing
b
Pregnant
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Probability
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Pmax
τ
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0.5
1
Calanus Abundance
C.
Calanus Abundance
1.2
1
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0.6
0.4
0.2
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Normalized Abundance Index +/-2 SE
D.
Right Whale Calves
30
20
10
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Observation
Model prediction +/-95% CI
1984
1988
1992
1996
2000
Year