Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population

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ABSTRACT: Considered one of the most endangered cetacean species, the North Atlantic right whale *Eubalaena glacialis* suffered declining abundance during the 1990s due to a high rate of anthropogenic-associated mortality and a low rate of reproduction. Previous studies have suggested that the reproductive rate is tightly coupled to the abundance of *Calanus finmarchicus* in the Gulf of Maine (GOM), which has been shown to respond to ecosystem regime shifts associated with decadal-scale climate forcing from the Arctic. Given the endangered status of the right whale population, it is vital to determine how climate-associated changes in prey availability will affect this species in the future. Here, we investigate a 3-state reproduction model that explores multiple environmental proxies as potential predictors of annual calf production during the period from 1980 to 2007. The model achieves its best fit to observations using temporally and spatially resolved *C. finmarchicus* abundance data derived from Continuous Plankton Recorder (CPR) surveys of the GOM. Building on previous research, this prey-dependent model, which uses bimonthly and geographically specific abundance anomalies of *C. finmarchicus*, significantly improves estimates of annual calf production relative to a null model. The temporal and geographic distributions of prey objectively chosen for inclusion in the new version of the model correspond well with observed right whale seasonal distribution patterns, providing further evidence that the model captures essential features of right whale reproductive ecology.

KEY WORDS: Demographic model · Reproduction · Cetacean · Right whale · Climate change

INTRODUCTION

The North Atlantic right whale population was severely impacted by persistent whaling pressure from the 11th to the 20th century (Aguilar 1986, Reeves et al. 1999), and the remaining members of the population now occupy a greatly reduced range in the Northwest Atlantic. Despite the introduction of international regulations protecting right whales from commercial whaling in 1935, the North Atlantic population has failed to recover due to a combination of variable birth rates and high mortality rates (Fujiwara & Caswell 2001, Greene & Pershing 2004). The high mortality rates are largely anthropogenic in origin, with right whales being especially vulnerable in coastal waters to ship strikes and entanglement in fishing gear (Gaskin 1987, Knowlton & Kraus 2001). With an estimate of only 522 individuals remaining in

the population (Pettis & Hamilton 2014), the North Atlantic right whale has been designated as 'endangered' under the US Endangered Species Act and by the International Union for Conservation of Nature.

Caswell et al. (1999) developed a stochastic model of North Atlantic right whale population growth from 1980 to 1996. According to their model, a declining population growth rate was attributed to a decrease in survival probability and an increase in the calving interval. Given the population growth rate estimated for the mid 1990s, Caswell et al. (1999) projected that the North Atlantic right whale was on a trajectory towards extinction in less than 200 yr. Using a full demographic population model, Fujiwara & Caswell (2001) found a significant decline in female life expectancy, likely attributed to the proximity of females to shipping lanes and fishing gear during their migration to, and time spent on, calving grounds off the coast of Florida and Georgia (Kraus et al. 1986). Additionally, a change in the calving interval, the mean interval between births for reproductive females, provided strong evidence that the conception rate was declining and the frequencies of prenatal and neonatal mortalities were increasing (Knowlton et al. 1994, Kraus et al. 2001, Browning et al. 2010).

In comparison, the southern right whale *Eubalaena australis* population off the coast of South Africa exhibits higher growth rates and shorter mean calving intervals (Knowlton et al. 1994, Best et al. 2001). Brown et al. (1994) report that only 38% of the reproductive females in the North Atlantic had calved, compared to 54% in the southern population. These differences suggest that the North Atlantic right whale may be capable of higher growth rates and reproductive output under improved environmental conditions.

Greene et al. (2003b) and Greene & Pershing (2004) hypothesized that fluctuations in prey availability associated with climate-associated changes in the ocean environment could explain the high reproductive variability observed in the population. This hypothesis is consistent with the high energetic costs associated with pregnancy and lactation in right whales (Fortune et al. 2013), and prey availability has been linked to body condition and pregnancy rate in other cetacean species (Lockyer 2007, Ward et al. 2009, Williams et al. 2013). In light of the increasing support for this prey-limitation hypothesis, a more thorough and quantitative investigation of the relationship between changes in prey availability and right whale reproduction is warranted.

Effects of prey availability on North Atlantic right whale nutrition and reproduction

North Atlantic right whales derive most of their nutrition from the older developmental stages (i.e. copepodites) of the copepod species *Calanus finmarchicus* (Mayo et al. 2001, Baumgartner et al. 2003). A conservative estimate of right whale daily energetic demand reveals that an average-sized right whale (40 000 kg) must consume approximately 100 million late-stage *C. finmarchicus* copepodites each day (Kenney et al. 1986). To meet this demand, right whales must selectively feed on high-density patches of *C. finmarchicus* to ensure net positive energy intake (Kenney et al. 1986). Consistent with this need for high prey abundance, the seasonal spatial distributions of right whales are significantly correlated with those of *C. finmarchicus* (Michaud & Taggart 2007, Pendleton et al. 2012). There are 4 recognized major feeding grounds for the North Atlantic right whale population, beginning with Cape Cod Bay and Massachusetts Bay during the spring, transitioning seasonally to the Great South Channel during the late spring and summer, and to the Bay of Fundy and Roseway Basin during the late summer and autumn (Hlista et al. 2009). However, the whales have also been observed to desert feeding grounds during periods when the abundance of this prey species becomes too low (Kenney 2001, Patrician & Kenney 2010).

Owing to the extreme energetic demands of pregnancy and nursing, female mammals generally do not reproduce unless they are physically robust, which typically coincides with favorable feeding conditions (Wade & Schneider 1992). Among right whales, reproductive females are especially vulnerable to nutritional limitations due to the foraging hiatus pregnant cows must undergo during the 3-mo period spent migrating to, and residing on, the coastal calving grounds located in Florida and Georgia (Fortune et al. 2013). Recent analyses of blubber thickness in North Atlantic and southern right whales have revealed significantly thinner blubber layers in the North Atlantic species, suggesting that this species' reproduction may be nutritionally compromised in comparison to its southern hemisphere counterpart (Miller et al. 2011). This suggestion is consistent with findings that North Atlantic right whale blubber thickness is positively correlated with *C. finmarchicus* abundance (Miller et al. 2011), and both are correlated with annual calf production (Pettis et al. 2004, Klanjscek et al. 2007, Miller et al. 2012).

Role of prey availability in mediating climate effects on North Atlantic right whale population dynamics

The abundance of *C. finmarchicus* in the Gulf of Maine (GOM) has been linked to ecosystem regime shifts associated with decadal-scale climate forcing from the Arctic (MERCINA 2012, Greene et al. 2013). During the 1980s, *C. finmarchicus* abundance was elevated due to a favorable combination of high local productivity and advective supply into the region from upstream source regions (MERCINA 2004). Towards the end of the decade, the Arctic climate system underwent a regime shift that resulted in the export of large quantities of low-salinity water from the Arctic Ocean into the North Atlantic (Greene et al. 2008). The resulting salinity anomaly progressed downstream in 2 major pulses during the 1990s, leading to a sequential reduction of salinities in Northwest Atlantic shelf ecosystems from the Labrador Sea to the Middle Atlantic Bight (Greene et al. 2008). The invasion of low-salinity water altered the timing and extent of stratification in these ecosystems, which subsequently impacted the production and seasonal cycles of phytoplankton, zooplankton and higher-trophic-level consumers (Greene & Pershing 2007, Greene et al. 2008).

This climate-driven ecosystem regime shift lasted throughout the 1990s in the GOM. Associated with it, the abundance of early-stage *C. finmarchicus* copepodites increased significantly, while the abundance of late-stage copepodites declined. The exact mechanism underlying this decline in abundance is uncertain; however, it has been hypothesized that changes in the ecosystem resulted in an increase in planktivorous fish, especially herring, and their size-selective predation on *C. finmarchicus* (Greene et al. 2013).

Correlated with the decline in late-stage *C. finmarchicus* abundance, right whale annual calf production also decreased significantly at the beginning of the 1990s (Greene & Pershing 2003). Annual calf production remained lower throughout the decade relative to the 1980s. In 1999 and 2000, calf production per reproductive female plummeted to an all-time low since the start of rigorous demographic observations on the species (Fig. 1B). Greene & Pershing (2003) hypothesized that the reproductive failure observed during these 2 yr was driven by a crash of the *C. finmarchicus* population in the GOM during 1998 (Fig. 1A). They associated this crash with a decrease in the advective supply of *C. finmarchicus* to the GOM after the 20th century's largest drop in the North Atlantic Oscillation (NAO) index during
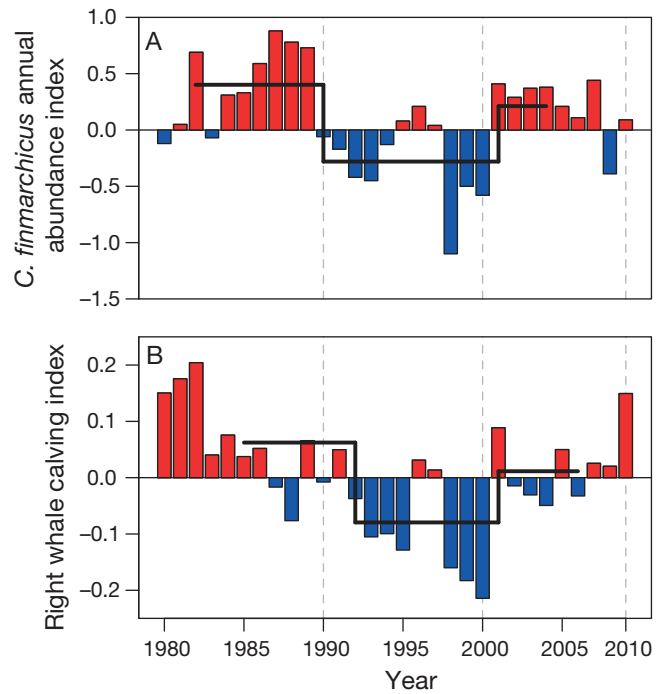

Fig. 1. (A) Late-stage *Calanus finmarchicus* annual abundance anomaly index estimated for the entire GOM CPR survey area and (B) female-specific annual right whale calf production (annual calf births/annual viable female population size). Positive values of indices above the climatological mean are shaded in red; negative values below the climatological mean are shaded in blue. A sequential *t*-test analysis of regime shifts (Rodionov 2004) was applied to each of the time series, and regime shifts that are significant at the α = 0.05 level are shown by black lines

winter 1996 altered slope and shelf water circulation patterns in the Northwest Atlantic (Greene & Pershing 2003).

At the end of the 1990s, the Arctic climate system underwent another regime shift, which persisted throughout the first decade of the 2000s (MERCINA 2012). A reduction in freshwater export from the Arctic Ocean led to elevated salinities over the Northwest Atlantic shelf. In the GOM, the plankton shifted back to resemble the assemblage characteristic of the 1980s, including a resurgence in the abundance of late-stage *C. finmarchicus* copepodites (Fig. 1A). Right whale annual calf production increased rapidly and remained at an elevated level for the remainder of the decade (Fig. 1B).

Given the North Atlantic right whale's status as an endangered species and the large reproductive variability observed from one decade to the next, it is vital to determine how changing climate and corresponding changes in prey availability affect the population dynamics of this species. This type of

long-term, multi-species research is difficult to accomplish in any ecosystem, but is especially challenging in pelagic marine systems that are relatively large and open. Fortunately, for this particular ecosystem, over 30 yr of co-occurring, but independently collected, right whale demographic data and climate-associated environmental data are available for analysis.

Here, we report results from an analysis of right whale reproduction, which uses a 3-state matrix model to explore how well a number of environmental variables, including *C. finmarchicus* abundance, perform as potential predictors of annual calf production. Within this modeling framework, we tested the predictive skill of these environmental variables against one another and against a null model that assumes a constant calving rate. In the case of *C. finmarchicus*, we compared the model's predictive skill using abundance estimates for the late-stage copepodites averaged over the entire year for the full GOM versus abundance estimates resolved into bimonthly time periods and for specific geographic subregions. Such temporal and spatial resolution may yield additional insights into what times of year and which geographic locations are most important to right whale reproduction.

MATERIALS AND METHODS

Right whale demographic monitoring data

The North Atlantic Right Whale Consortium (Right Whale Consortium 2011) identifies right whales by using unique markings, scars and callosity patterns. The corresponding database of identifications has been photographically cataloged in a consistent manner since 1980. This database provided the foundation for our studies of right whale reproduction. First, we used the database to develop a time series of annual calf production. This time series included all known calf births, regardless of whether the mother was known and whether the calf survived its first year of life. Owing to high survey effort near the calving grounds off the coasts of Florida and Georgia, mother/calf pairs have an especially high sighting probability, and we assumed that all newborn calves have

been observed (Kraus & Rolland 2007). Next, we used the database to develop a time series of reproductively viable females. A female is considered reproductively viable if she has been known to give birth or has reached 9 yr of age. A female is considered nulliparous or senescent if she has not reproduced for 9 consecutive years while in the viable pool. A female is considered missing if she has not been sighted in 5 consecutive years and is presumed dead after the 5th yr (Knowlton et al. 1994). Females that have been categorized as senescent or missing were removed from the time series of reproductively viable females.

Continuous Plankton Recorder survey data

The Continuous Plankton Recorder (CPR) is an instrument towed behind ships of opportunity to collect and preserve plankton filtered through a 270-µm mesh silk gauze for subsequent analyses in the laboratory (Warner & Hays 1994). Since 1961, the NOAA National Marine Fisheries Service has operated a CPR survey of the GOM running between Boston, Massachusetts and Cape Sable, Nova Scotia, at approximately monthly intervals (Fig. 2) (Jossi & Kane 2013). Although the CPR is not
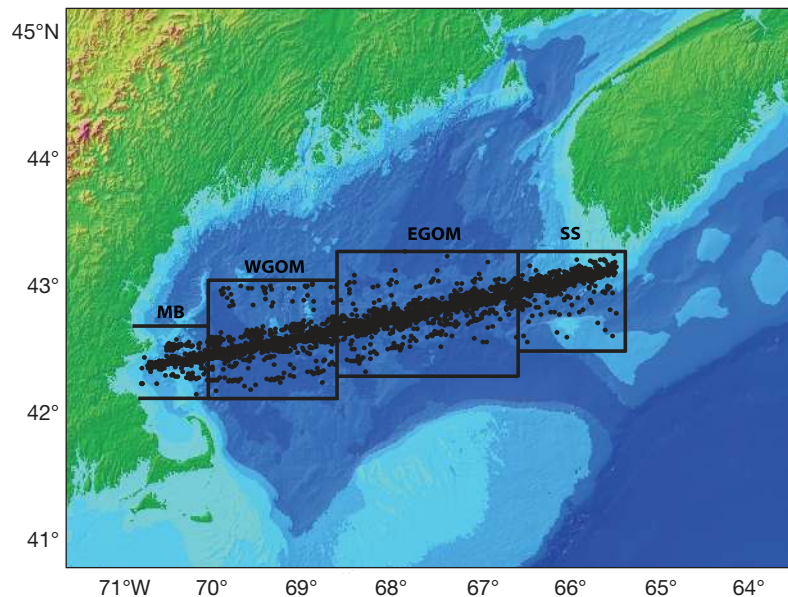

Fig. 2. The GOM, showing the CPR survey area used to characterize *Calanus finmarchicus* abundance in the region. The CPR survey area is divided into 4 geographical subregions: Massachusetts Bay (MB), Western GOM (WGOM), Eastern GOM (EGOM) and Scotian Shelf (SS). CPR survey sampling (•) in the GOM occurs at approximately monthly intervals (modified from Fig. 2b in Meyer-Gutbrod & Greene 2014)

an ideal instrument for quantitative and synoptic estimates of plankton species abundance due to the limited geographic, depth and temporal coverage of the sampling, its consistent use in long-term surveys of the region has provided an invaluable data set for studying relative abundance patterns on seasonal to decadal time scales (e.g. Greene et al. 2013). Our hypothesis that the *Calanus finmarchicus* abundance index serves as a good proxy for right whale prey availability is supported in studies by Pendleton et al. (2009) and Pershing et al. (2009), which demonstrate that regional scale, near-surface *C. finmarchicus* abundance measured with the CPR is significantly correlated with right whale sightings in the GOM. We used only the abundance of late-stage *C. finmarchicus* copepodites (stage 5 and adults) as a proxy for food availability due to the importance of these stages in the diet of right whales (Mayo et al. 2001).

For evaluating the model's predictive skill when using yearly averaged *C. finmarchicus* abundance estimates for the entire GOM, we used data from samples collected along the full CPR transect (Fig. 2). Late stage *C. finmarchicus* abundance index anomalies were calculated from the seasonal climatological cycle as described by Pershing et al. (2005).

For evaluating the model's predictive skill when using temporally and spatially resolved *C. finmarchicus* abundance estimates, data were averaged into temporal bins spanning 2 mo to yield 6 seasonal indices of plankton abundance corresponding to the averages of January and February, March and April, May and June, July and August, September and October, and November and December. Bi-monthly averages provide sufficiently fine temporal resolution to demonstrate seasonal variations in prey abundance while still averaging over sufficient time to avoid data gaps in the survey time series. The *C. finmarchicus* abundance estimates were spatially resolved by breaking the CPR transect into 4 distinct subregions: Massachusetts Bay (MB), Western GOM (WGOM), Eastern GOM (EGOM) and Scotian Shelf (SS) (Fig. 2). This geographic breakdown coincides reasonably well with some of the most common right whale feeding grounds, with MB encompassing Cape Cod Bay, WGOM lying just upstream of the Great South Channel, EGOM lying just downstream of the Bay of Fundy and SS being representative of prey conditions on the shelf and in the nearby Roseway Basin. A total of 35 seasonal and subregion-specific variables were explored ([4 subregions + 1 full transect area] × [6 seasons + 1 annual average] = 35 indices).

Other environmental variables as predictors of annual calf production

As right whale reproduction appears to be linked to *C. finmarchicus* abundance, and as interannual to interdecadal variability in this species' abundance has been linked to climate-associated ecosystem changes and regime shifts in the GOM/SS region, we also explored how well other environmental variables might be used as predictors of annual calf production. We looked at environmental variables that are associated with 2 basin- to hemispheric-scale mechanisms hypothesized to drive these regional ecosystem changes (Greene et al. 2013).

The first of these mechanisms is a basin-scale phenomenon associated with changes in the phase of the NAO. It has been hypothesized that the NAO is linked to right whale calf production through its affects on the Northwest Atlantic's coupled slope water system and the advective supply of *C. finmarchicus* into the GOM/SS region (Greene & Pershing 2003, 2004, Caswell & Fujiwara 2004, Greene et al. 2013). The Regional Slope Water Temperature (RSWT) index, which is the first derived mode of a principal component analysis of 8 slope water temperature time series anomalies for the GOM/western SS region, serves as an indicator of the state of this coupled slope water system (MERCINA 2001). Negative values of the RSWT index are associated with increased transport of the Labrador Current around the tail of the Grand Banks, contributing more of the colder, fresher Labrador Subarctic Slope Water to the region and displacing the warmer, fresher Atlantic Temperate Slope Water further off the shelf. The abundance of late-stage *C. finmarchicus* copepodites has been correlated with the RSWT index, and it has been hypothesized that this correlation is the result of slope water circulation changes potentially limiting the advective supply of *C. finmarchicus* into the region (Greene & Pershing 2000, MERCINA 2001, 2004). To explore how this NAO/coupled slope water system mechanism might be linked to right whale annual calf production, the NAO index and RSWT index were each used to drive the reproduction model, with time lags ranging from 0 to 5 yr.

The second of these mechanisms is hemispheric in scale and associated with decadal-scale changes in Arctic climate that regulate freshwater export from the Arctic Ocean into the North Atlantic and subsequently affect stratification and plankton productivity patterns throughout the shelf waters of the Northwest Atlantic (Greene et al. 2008, MERCINA 2012, Greene et al. 2013). Shifts in the atmospheric and

oceanic circulation patterns of the Arctic, as measured by the Arctic Oscillation (AO) index and Arctic Ocean Oscillation (AOO) index, respectively, have been linked to the storage and release of freshwater from the Arctic Ocean's Beaufort Gyre. When the Beaufort Gyre weakens and freshwater is released, salinity anomalies can be traced as they exit the Arctic Ocean and propagate down the Northwest Atlantic shelf (Greene et al. 2008). Once they reach the GOM/SS region, such freshwater anomalies can be quantified with the Regional Shelf Water Salinity (RSWS) index, which is the dominant mode of a principal component analysis of shelf-water salinity data from the GOM/SS/Georges Bank region (MERCINA 2012, Greene et al. 2013). The increased buoyancy of the surface waters alters the seasonal patterns of stratification and primary production, which in turn can lead to a regime shift in the plankton assemblage (Greene & Pershing 2007, MERCINA 2012, Greene et al. 2013). The seasonal changes in primary production include an increase in autumn phytoplankton abundance, which can be quantified with an autumn phytoplankton color index derived from the GOM CPR survey samples (Greene & Pershing 2007). Greene et al. (2013) hypothesize that the length and productivity of the phytoplankton growing season affect the feeding conditions and population abundances for *C. finmarchicus* and the smaller copepod species in the GOM. To explore how this stratification mechanism remotely forced from the Arctic might be linked to right whale annual calf production, the AO index, AOO index, RSWS index and autumn phytoplankton color index were each used to drive the reproduction model, with time lags ranging from 0 to 5 yr (only lags of 0, 1 and 2 yr were analyzed for CPR-derived time series due to some data gaps during the late 1970s).

To examine the likelihood of finding spurious correlations between right whale calf production and the various *C. finmarchicus* and environmental variables, a resampling technique was used to examine the distribution of model Akaike's information criterion indices (AICs) (Akaike 1974, Burnham & Anderson 2002) calculated using bootstrapped data. The moving-block bootstrap method (Wilks 1997) was employed by randomly selecting 4-yr blocks of data with replacement from a single variable to generate a new, resampled time series of the same length. As the time series considered in this study is 28 yr long (from 1980 to 2007), each bootstrapped variable was composed of 7 blocks, with each block consisting of 4 yr of sequential data. This effectively randomizes the relationship between right whale reproduction

and prey availability while preserving the short-term autocorrelation in the independent variable. The calf production and viable female time series were not randomized to preserve the demographic relationship between the number of cows and calves, as well as the long-term trend of population growth that can be expected in this system. Each new variable was drawn uniformly from 1 of the 36 genuine lagged and unlagged variables, and tested in the reproduction model. This trial was performed 10 000 times to produce a probability distribution for the AICs.

This resampling scheme provides a conservative evaluation of the likelihood of finding spurious relationships between right whale calf production and each variable being examined. With such a short time series, only 7 blocks can be randomized while still preserving relevant temporal autocorrelation in the data. Furthermore, given the known occurrence of regime shifts, and the occasional resemblance between regimes, such as that of the 1980s and the early 2000s, the bootstrap-generated time series will resemble the genuine variables more often than with a completely random resampling process.

Reproduction model

The reproduction model we employed assigns reproductively viable females to 3 states: resting, pregnant and nursing (Fig. 3) (Greene & Pershing
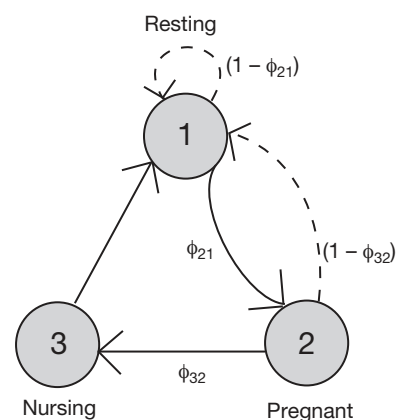

Fig. 3. Three-state reproduction model for the North Atlantic right whale. ϕ_{21} and ϕ_{32} represent the probability of a female transitioning from the resting state between pregnancies (1) to the pregnant state (2), and the probability of a female transitioning from the pregnant state (2) to the nursing state (3), respectively. Resting females can remain in that state or become pregnant. Pregnant females can give birth and enter the nursing state or experience prenatal or neonatal mortality and re-enter the resting state. After 1 yr, nursing females return to the resting state. Transitions between states can occur each year

2003, 2004). The resting state corresponds to the period of time between nursing and when the female can be impregnated. In this model, the resting state lasts for a minimum of 1 yr, and can last longer depending on the nutritional state of the female and environmental conditions. The pregnant state in the model lasts 1 yr, which corresponds to the ca. 12-mo gestation period (Best 1994). If a pregnant female experiences a spontaneous abortion or neonatal mortality occurs before the calf is sighted, then the female transitions from the pregnant state back to the resting state. Otherwise, the pregnant female enters the nursing state. The nursing state in the model lasts 1 yr, which corresponds to observations of a ca. 12-mo lactation period. After the nursing state, all females return to the resting state (Fig. 3) (Hamilton et al. 1995). In our study, we equate the model-generated time series of nursing females with annual calf production, and model parameters are optimized to fit this time series with the observed calves in the population.

This 3-state reproduction model was implemented with the following transitional probability matrix, A, (Caswell 2001):

$$A = \begin{pmatrix} 1-\phi 21 & 1-\phi 32 & 1 \\ \phi 21 & 0 & 0 \\ 0 & \phi 32 & 0 \end{pmatrix}$$

Each element in the matrix A_{ij} contains the probability of a reproductively viable female transitioning from state j to state i in a year. The projection matrix A is multiplied by the female abundance vector N_{t-1}, the number of viable females in each of the 3 reproductive states during year $t-1$, to estimate the female abundance vector N_t during the following year t:

$$N_t = (A) \times N_{t-1}$$

The 3 elements in N correspond to the number of resting females, the number of pregnant females and the number of nursing females, respectively, and the number of nursing females is equated with the model-projected number of calves produced that year. Female mortalities (subtractions from N) and new recruits into the reproductive pool (additions to N) were manually added and subtracted from the population vector at each annual time step to avoid confounding errors in mortality rates with errors in the reproductive transitional probabilities.

The transitions of viable females among the 3 reproductive states were estimated over the time period from 1980 to 2007. This range was chosen because 1980 marks the year when right whale pop-

ulation monitoring methods became standardized, and 2007 is the last year before a gap occurred in the CPR survey data set.

Initial conditions were set to reflect the likely distribution of females among the 3 states in 1980. The 16 known reproductively viable females in 1980 were assigned to the 3 reproductive states by setting the number of females in the nursing state equal to the number of calves born that year, and the number of females in the pregnant state equal to the number of calves born in the following year, 1981. The remaining reproductively viable females identified in 1980 were assigned to the resting state. While assigning initial conditions always has the potential to introduce some bias into a model, this method performed better than other methods evaluated. In addition, the amount of bias introduced by fixing these initial conditions was very limited because of the small numbers of viable females and calves observed in 1980 relative to later in the time series.

The 2 probabilities optimized in this study are ϕ_{21} and ϕ_{32}, which represent the probability of a female transitioning from the resting state (1) to the pregnant state (2), and the probability of a female transitioning from the pregnant state (2) to the nursing state (3), respectively (Fig. 3). The transitional probabilities were estimated as polychotomous logistic functions, as described in Fujiwara & Caswell (2002), to constrain the probabilities between 0 and 1 while offering flexibility in the shape of the function:

$$\phi_{21} = e^{\beta_{21} \times X}/(1 + e^{\beta_{21} \times X})$$

$$\phi_{32} = e^{\beta_{32} \times X}/(1 + e^{\beta_{32} \times X})$$

The parameter vectors β_{21} and β_{32} determine the contribution of the independent prey variable(s), X, to the transitional probabilities ϕ_{21} and ϕ_{32}. These transitional probabilities were fitted into a demographic matrix model and the parameter vectors β_{21} and β_{32} were estimated in AD Model Builder (Fournier et al. 2012). Parameters were optimized to yield a predicted annual calf production time series that most closely resembles the observed calf time series (Right Whale Consortium 2011).

In determining the best fit for including the temporally and spatially resolved *C. finmarchicus* data into the reproduction model, the 35 *C. finmarchicus* abundance indices (7 time periods × 5 region/subregions) were tested as predictive variables, both independently and in combination. Each variable was treated objectively and first tested as the sole predictor in both transitional probabilities simultaneously. The best-performing variable was then fixed as a

constant for the first transitional probability, of a female moving from resting to pregnant, while each of the 35 variables was tested for the second transitional probability, of a female moving from pregnant to nursing. Then this process was repeated by fixing the second transitional probability as a constant while all 35 variables were tested for the first transitional probability. The best of these models was selected and the addition of a second predictor, etc., was tested in the same objective manner. Model complexity was increased incrementally until each instance in a suite of models demonstrated a higher AIC than the best-fitting, more parsimonious model. In this way, the temporally and spatially resolved reproduction model was built in a stepwise fashion to objectively select the best-fitting regional and seasonal prey variables to predict calf production.

While each of the 35 regional and seasonal late-stage *C. finmarchicus* indices provides a unique signal of prey abundance in the GOM, some geographically or temporally adjacent variables are highly correlated, as expected. None of the 3 variables present in the best-fit model are strongly correlated, but caution must be applied when interpreting the relative importance of these temporal and regional signatures relative to those that are adjacent. However, some confidence in the model selection process is warranted since the best-fitting variables correspond with known right whale foraging habits.

To rigorously evaluate the prey-dependent case of the reproduction model, we developed a null, prey-independent version of the model for comparison. In the null version, a similar matrix model was developed with time-invariant transitional probabilities. The reproductive transitional probabilities ϕ_{21} and ϕ_{32} were estimated independently using the same optimization method. Logistic functions were fitted as before; however, only the intercepts were estimated. This method produces a single optimal probability for each transition that does not vary through time. The prey-dependent and prey-independent reproduction models were compared using the AIC, and a difference of more than 2 AIC units was the criterion used to determine an improvement in fitness between 2 models (Akaike 1974, Burnham & Anderson 2002).

RESULTS

The growth rate of the North Atlantic right whale population exhibited considerable interdecadal variability from 1980 to 2007. We hypothesize that this observed variability largely reflects fluctuations in annual calf production brought about as right whale reproductive processes respond to ecosystem changes that affect prey availability. Our model results enable us to examine in detail how these reproductive processes are linked to specific spatial and temporal changes in the feeding environment of right whales.

Calf production null model

The calf production null model is optimized when the transitional probability between the resting and pregnant states, ϕ_{21}, is equal to 0.26, and the transitional probability between the pregnant and nursing states, ϕ_{32}, is equal to 1.0 (Table 1). This result means that only a quarter of the viable resting females conceive each year, but each successful conception leads to the production of a calf. Because the null model is prey independent, and therefore transitions are constant through time, the gradual upward trend in the predicted annual calf production time series is driven only by the steady increase in the pool of viable females through the interaction of recruitment, senescence and mortality processes (Fig. 4A). The estimated time series of calf production does not exhibit the interannual variability seen in the observed calf births. The average calving interval for the null

Table 1. The intercept and, in the case of the prey-dependent model, the coefficient(s) of prey variability estimated in the logistic equations for the probability of an adult viable female transitioning from the resting stage to the pregnant stage, ϕ_{21}, and transitioning from the pregnant stage to the nursing stage, ϕ_{32}. AIC values and weights for the time-invariant (no-prey) model and the best-fit prey-dependent model are provided. Standard errors are listed in parentheses

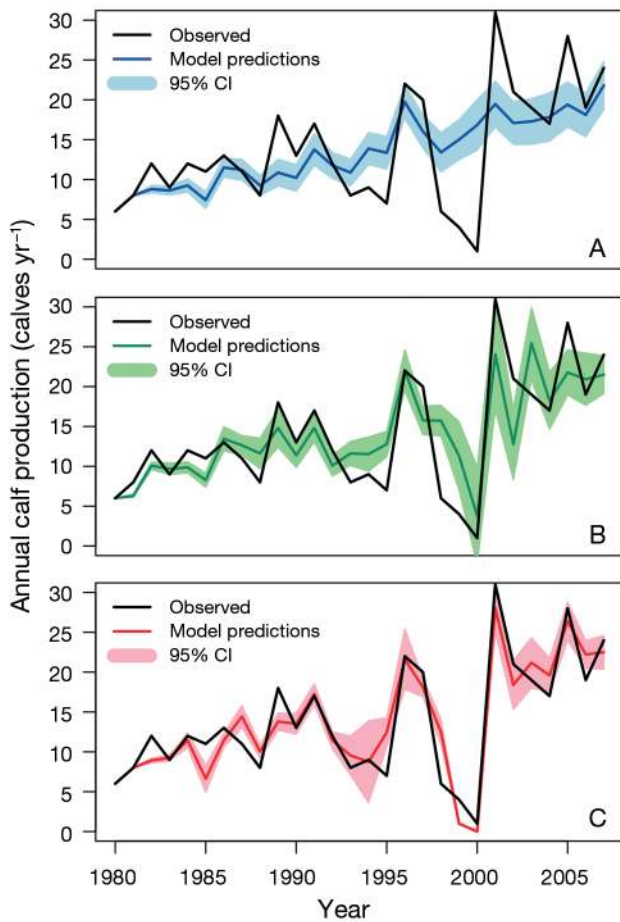| | Model | |
	No-prey	Resolved prey-dependent
AIC	99.7	64.5
AIC weight	0.0	1.0
β_{21} Intercept	−1.063 (1.78 × 10^{-1})	−0.820 (1.06 × 10^{-1})
β_{21} Coefficient: WGOM Nov to Dec		0.165 (5.61 × 10^{-2})
β_{21} Coefficient: GOM Mar to Apr		0.345 (1.37 × 10^{-1})
β_{32} Intercept	13.398 (5.93 × 10^2)	108.66 (4.00 × 10^3)
β_{32} Coefficient: EGOM Jul to Aug		145.74 (5.37 × 10^3)

Fig. 4. Annual calf production for 3 models, with observed number of calf births shown in black. (A) Null, prey-independent version of the model estimates (blue), (B) annually and spatially averaged prey-dependent version of the model estimates (green) and (C) seasonally and spatially resolved prey-dependent version of the model estimates (red). Pale bands surrounding model estimates correspond to 95% CI
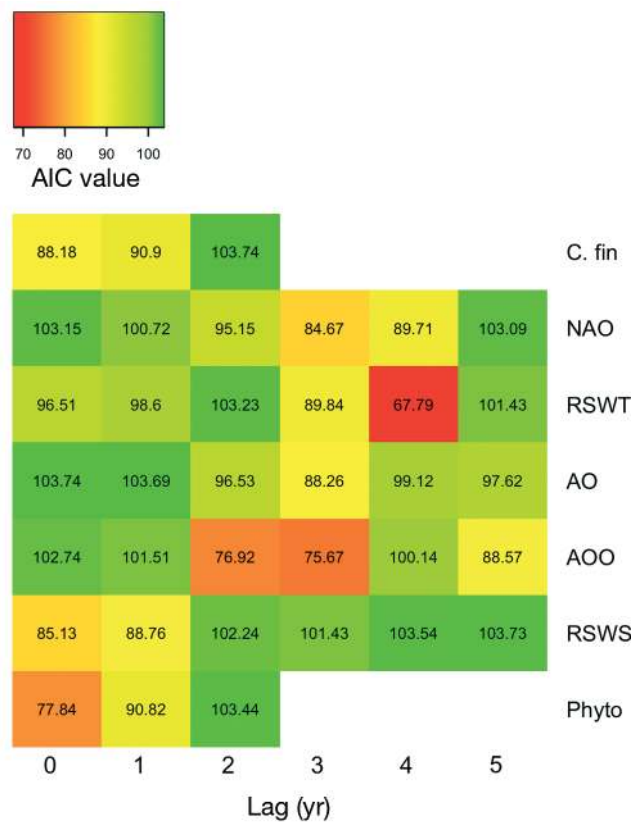

Fig. 5. AIC values of the environmentally driven versions of the model, showing the environmental variables and the time lag (yr). C. fin: CPR-derived *Calanus finmarchicus* annually averaged GOM transect-wide abundance index; NAO: North Atlantic Oscillation index; RSWT: Regional Slope Water Temperature; AO: Arctic Oscillation; AOO: Arctic Oceanic Oscillation; RSWS: Regional Shelf Water Salinity; Phyto: CPR-derived autumn phytoplankton color index. The best-performing versions of the model (lowest AICs), presented in orange/red boxes, are those that performed better than the version driven by the unlagged, annually averaged *C. finmarchicus* abundance index derived from the entire CPR transect (AIC = 88.2). The poorest-performing versions of the model (highest AICs), presented in green boxes, are those that performed worse than or similar to the null model (AIC = 99.7). Color key is shown in the upper left corner

model lasts 6 yr, with an average of 4 yr in the resting state prior to conception, and then a year each in the pregnant and nursing states. These results provide a baseline for comparisons with versions of the model that are driven by environmental variables, including prey dependence.

Versions of the calf production model driven by annually indexed environmental variables

The results from 36 different versions of the right whale reproduction model driven by annually in-dexed environmental variables are shown in Fig. 5. Of the 36 versions tested, 18 performed better than the null model, given the criteria of a decrease of at

least 2 AIC units (null model AIC = 99.7; Table 1, Fig. 5). Models that performed comparably to or worse than the null model are colored in green (Fig. 5). The improvement in fit of many of these environmentally driven versions of the model relative to the null model supports the hypothesis that the environment plays a significant role in right whale reproduction. The unlagged, annually averaged late-stage *Calanus finmarchicus* abundance index derived from the entire CPR transect, which is the most direct measure of right whale prey avail-

ability tested, had an AIC of 88.2, more than 10 AIC units lower than the null model (Fig. 4B). Models that performed comparably to the annually and spatially averaged *C. finmarchicus* index are colored in yellow in the AIC heatmap, while those that performed significantly better are shown in orange and red (Fig. 5).

In terms of model results, the best performing of the annually indexed environmental variables is the RSWT index lagged by 4 yr, with an AIC of 67.8 (Fig. 5). This result is consistent with the hypothesis that the Northwest Atlantic's coupled slope water system regulates prey variability in the GOM by altering the advective supply of *C. finmarchicus*. Specifically, GOM *C. finmarchicus* have been known to respond to changes in the coupled slope water system after a lag of 4 yr (Greene & Pershing 2003, Greene et al. 2003a). This version of the model performs especially well because it accurately captures the unusual behaviors in right whale calving efficiency in the late 1990s.

The 2- and 3-yr lagged AOO index and the unlagged autumn phytoplankton color index also perform very well, with AICS of 76.9, 75.7 and 77.8, respectively (Fig. 5). These models support the hypothesis that the export of freshwater from the Arctic and the resulting changes in seasonal stratification within the GOM affect right whale calving rates via changes in prey availability. The hierarchy of best-fitting environmental variables associated with changes in seasonal stratification (AO, AOO, RSWS and autumn phytoplankton) exhibit a sequence of time lags consistent with the timing of events driving this phenomenon (Fig. 5) (Greene et al. 2013). Interannual to interdecadal variability in late-stage *C. finmarchicus* abundance is most likely driven by a combination of advective processes linked to the Northwest Atlantic's coupled slope water system and changes in seasonal stratification linked to freshwater export from the Arctic. However, the development of a right whale calving model that incorporates both of these mechanisms and their effects on prey availability are beyond the scope of this study.

The distribution of model AICs calculated using moving-block bootstrapped data is shown in Fig. 6. When ranked from lowest (best fit) to highest (worst fit), the AIC is 86.3 at the 5th percentile and 90.2 at the 10th percentile. Of the 36 versions of the model fit by an annually indexed environmental variable, lagged or unlagged, 6 (17%) perform better (i.e. have a lower AIC) than the 5th percentile and 12 (33%) perform better than the 10th percentile, including the model driven by the unlagged, CPR-derived late-
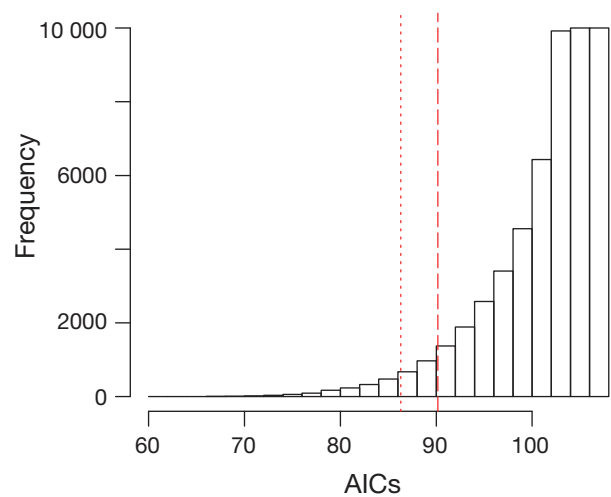

Fig. 6. The cumulative frequency plot of AIC values from the 10 000 models run in the resampling test. Each model was driven by a unique, randomized 4-yr moving-block bootstrap. The dotted vertical red line marks the value of the 500th ranked AIC (the 5th percentile; AIC = 86.3) and the dashed vertical red line marks the value of the 1000th ranked AIC (the 10th percentile; AIC = 90.2)

stage *C. finmarchicus* abundance index. The improved performance of our actual set of 36 environmental variables in comparison to the 10 000 randomly generated environmental variables provides confidence that the relationships between right whale calf production and environmentally determined prey availability are not spurious.

Temporally and spatially resolved prey-dependent calf production model

The temporally and spatially resolved prey-dependent version of the model was fitted through an iterative process to incorporate the optimal combination of *C. finmarchicus* abundance data resolved by subregion and bi-monthly time period. The predicted calf time series from this version of the model captures the largest portion of the interannual variation in calf production compared to all other versions of the model tested (AIC = 64.5; Table 1, Fig. 4C).

In this version, the transitional probability between the resting and pregnant states, ϕ_{21}, is a logistic function dependent on *C. finmarchicus* abundance in the WGOM during the November to December time period and in the whole GOM region during the March to April time period (Fig. 7B). All parameters optimized for this transition are statistically significant (Table 1). The transition between pregnant and nursing states, ϕ_{32}, is a logistic function that is exclu-
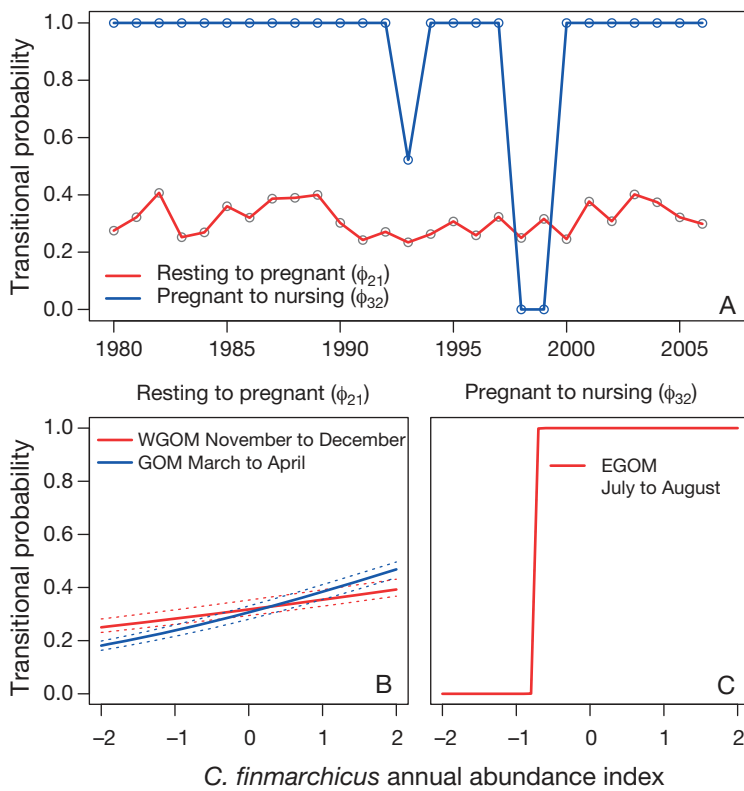
Fig. 7. (A) Transitional probabilities for the temporally and spatially resolved prey-dependent reproduction model, showing ϕ_{21} (red) and ϕ_{32} (blue). (B & C) Transitional probabilities estimated in the prey-dependent reproduction model as functions of the associated *Calanus finmarchicus* abundance indices: (B) ϕ_{21} as a function of the WGOM November to December index and the GOM March to April index and (C) ϕ_{32} as a function of the EGOM July to August index. Two functions are shown for ϕ_{21} (B): the transitional probability as a function of the WGOM November to December prey abundance index while the GOM March to April prey abundance is held at the upper quartile, median and lower quartile abundances averaged over 1980 to 2006 (upper dashed line, solid line and lower dashed line, respectively) is shown in red; the transitional probability as a function of the GOM March to April prey abundance index while the WGOM November to December prey abundance is held at the upper quartile, median and lower quartile abundances averaged over 1980 to 2006 (upper dashed line, solid line and lower dashed line, respectively) is shown in blue

ing this model with a similar one, in which the probability of transitioning between resting and pregnant states is prey dependent but the probability of transitioning between pregnant and nursing states is not, the results reveal that prey dependence in both transitions drastically improves the model's fit (AIC = 64.5 vs. AIC = 96.2).

The prey-dependent model's predicted probabilities of conception and successful delivery for each year in the time series are shown in Fig. 7A. These results indicate that under ideal prey conditions, a female in the resting state has a relatively low conception probability (mean probability = 0.314 over the 27-yr time period), but a relatively high probability of successfully delivering a calf once pregnant (mean probability = 0.908). For the time period considered in this study, summertime prey abundances in the EGOM fell below the threshold value of −0.75 a total of 3 times. On each of these occasions, the model predicted that a significant percentage of pregnancies would result in prenatal or neonatal mortalities (Fig. 7A).

The prey-dependent model's predicted distribution of viable females in each of the 3 reproductive states is shown in Fig. 8A. As expected, most females are found in the resting state during any given year as they recover from previous pregnancies by restoring lost blubber. The model results demonstrate that during years of higher prey availability the resting and recovery process is accelerated, leading to higher annual calf production. In contrast, during years of lower prey availability, females remain in the resting state for longer, leading to lower annual calf production.

The prey-dependent model's predicted theoretical calving interval for each year in the time series is shown in Fig. 8B. The theoretical calving interval assumes that prey availability remains constant over a complete reproductive cycle. Therefore, it does not reflect a true calving interval, since a female requires a minimum of 3 yr to complete her reproductive cycle, and prey availability does not remain constant over that length of time. Nevertheless, each predicted calving interval provides a snapshot of the effect of that year's feeding conditions on right whale reproduction. A calving interval of 3 yr is the minimum, given the model constraints, and it is achieved

sively dependent on *C. finmarchicus* abundance in the EGOM during the July to August time period (Fig. 7C). The large coefficients in this logistic function create a quasi step function, demonstrating that when the *C. finmarchicus* abundance index in the EGOM during July and August falls below a threshold value of −0.75, the probability of encountering nursing females the following year drops from 1.0 to 0.0 over a narrow range of prey abundances (Fig. 7C, Table 1). Owing to the large coefficient size of the 2 parameters calculated for this transitional probability, the associated standard errors cannot be computed precisely (Pampel 2000). However, by compar-
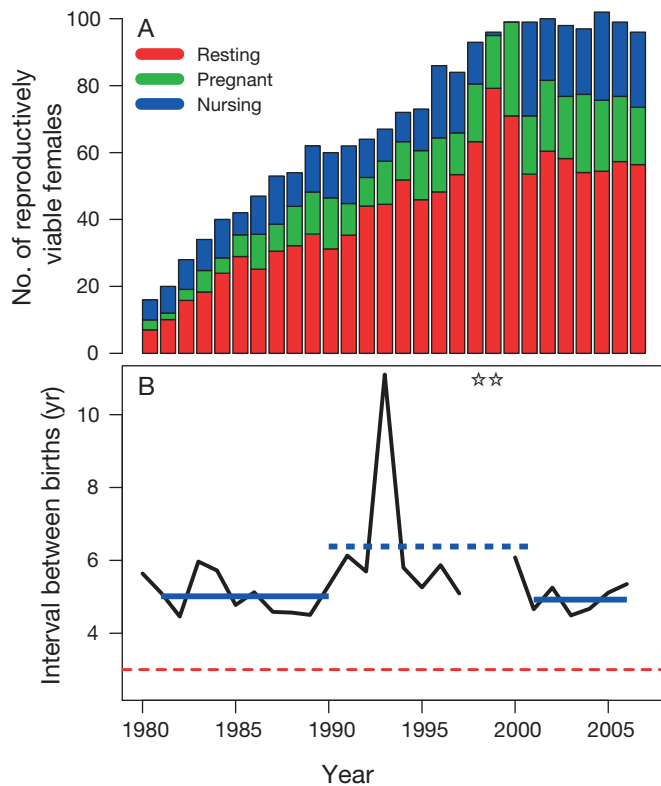
Fig. 8. (A) Model-estimated distribution of reproductive states for the population of reproductively viable right whale females. (B) Interval between births index (yr) as estimated from the temporally and spatially resolved, prey-dependent version of the model. The red dashed line shows a 3-yr calving interval, the minimum interval length constrained by the model, which corresponds to females spending only 1 yr in each of the 3 reproductive states. Blue lines show decadal averages of female-specific annual calf production and average interval between births. The average interval between births exceeded the lifespan of right whale females in 1998 and 1999 (☆☆), when prey abundances were unusually low. These values were not included in calculating the decadal average, therefore the blue dashed line is a significant underestimate of the 1990s average model-predicted interval between births

when all viable females are reproducing as fast as physiologically possible, spending only 1 yr in each of the 3 reproductive states. While this minimum value is rarely approached over an extended time period, strong deviations from it are indicative of a bottleneck in right whale population growth. Calving intervals during the good feeding conditions of the 1980s varied between 4 and 6 yr, with a decadal average of 5.0 yr. In contrast, calving intervals during the relatively poor feeding conditions of the 1990s were much more variable. For most of the decade, they varied between 5 and 7 yr, but low *C. finmarchicus* abundance drove the calving interval up to exceed the lifespan of the species during 1998 and

1999. Replacing the 1998 and 1999 calving interval with 61 yr as an estimation of the reproductive life span (70 yr lifespan minus 9 yr, or the age of reproductive maturity) yields a decadal average calving interval of 17.3 yr in the 1990s. When good feeding conditions returned during the 2000s, calving intervals dropped back to varying between 4 and 6 yr, with a decadal average of 4.9 yr.

DISCUSSION

We compared the fit of multiple versions of a right whale reproduction model using direct measures of prey abundance (late-stage *Calanus finmarchicus* abundance anomaly indices derived by the CPR) as well as a number of environmental variables that have been linked to regime shifts and changes in plankton abundance in the GOM ecosystem. The unlagged direct measures of prey abundance tested in this study, both the annually averaged, full GOM *C. finmarchicus* abundance anomaly index and the temporally and spatially resolved abundance anomaly indices tested in combination, provide a very simple mechanistic method of predicting interannual variability in right whale reproduction efficiency.

While the models driven by the lagged environmental variables do not share the same level of mechanistic parsimony as the models driven by prey abundance, they do offer some advantages. The environmental variables chosen for inclusion in this study have links to large ecosystem changes and regime shifts in the GOM and other shelf regions in the Northwest Atlantic that are well supported in the literature. For that reason, these variables may contain more synoptic, broad-scale information on the right whale feeding environment than data from the CPR transect. There is also some uncertainty about the reliability of funding for future collection and analysis of CPR data in this region. Therefore, these environmental variables may provide the only option for future analyses.

The results from our modeling study provide evidence that not only is the annual calf production of the North Atlantic right whale population dependent on prey availability, this dependence is especially important in specific foraging areas and at specific times. The results provide additional insights into how various reproductive processes may be linked to specific spatially and temporally dependant features in the feeding ecology of right whales.

Of all reproduction models explored, the model driven by temporally and spatially resolved *C. fin-*

marchicus performed the best (AIC = 64.5). In this model, the *C. finmarchicus* abundance index for the WGOM during November and December is the dominant variable driving the transition of reproductively viable females from the resting state to the pregnant state. This finding is consistent both spatially and temporally with field observations. Although the habits of right whales during late autumn and winter are not well known due to poor weather conditions and visibility, sightings and acoustic monitoring of reproductive females in this region between November and January suggest that the western and central GOM are likely mating grounds (Mussoline et al. 2012, Cole et al. 2013, Bort et al. 2015) during a time period when they are thought to be sexually active (Kraus & Rolland 2007, Cole et al. 2013). We hypothesize that *C. finmarchicus* abundance in this region and during this time period affects the foraging behavior of right whales and their probabilities of conception. For example, during years of low prey availability, the right whale population may disperse in search of better feeding grounds, thereby limiting mating opportunities. Conversely, during years of high prey availability, the population may converge over favorable feeding grounds, thereby fostering improved mating conditions.

The model results also indicate that the transition from resting state to pregnant state is secondarily driven by the *C. finmarchicus* abundance index for the entire GOM during March and April. This time frame corresponds to a period when high right whale abundance is observed in Cape Cod Bay (Winn et al. 1986, Mayo & Marx 1990, Pendleton et al. 2009), Massachusetts Bay (Schevill et al. 1986) and the Great South Channel (Kenney et al. 1995), as well as on Stellwagon Bank (Mussoline et al. 2012). Prey availability in the months before conception has been linked to calving rates in other baleen whales (Lockyer 2007), including the southern right whale (Leaper et al. 2006), a closely related congener of the North Atlantic right whale. In light of these observations, we hypothesize that prey availability throughout much of the GOM during spring likely determines the nutritional condition of reproductively viable females and influences their conception probabilities during the following winter.

The best-fit transitional probability from the pregnant state to the nursing state, ϕ_{32}, is driven by *C. finmarchicus* abundance in the EGOM during July and August. This transitional probability behaves like a quasi step function, indicating that right whale pregnancies tend to be viable except in years when prey abundance falls below a certain threshold (Fig. 7C).

As right whales are typically observed nearby in the lower Bay of Fundy during late summer (Kraus et al. 1982, Gaskin 1987, Mate et al. 1997), this relationship suggests that the EGOM subregion and the downstream Bay of Fundy may be significant feeding grounds for pregnant females, and *C. finmarchicus* abundance in these areas during summer may play a critical role in determining a female's ability to sustain a pregnancy or nurse a calf.

While each of the 35 regional and seasonal late-stage *C. finmarchicus* abundance indices tested in the temporally and spatially resolved versions of the model provides a unique measure of prey abundance in the GOM, some geographically and/or temporally adjacent indices are highly correlated (for example, EGOM July and August, and WGOM July and August), as might be expected. Non-adjacent variables in the suite of regional and seasonal prey abundance indices are not strongly correlated, including the 3 variables chosen in the best-fit model. As there is some collinearity among the predictors, one might not expect such predictors to be jointly included in any particular model, as including them together would inflate the variance and result in poorer model performance as measured by standard criteria. While the stepwise regression has resulted in predictors that correspond well with known right whale foraging habits and result in good predictions of annual calf production, there may be other combinations of predictors that result in a comparable level of predictability.

CONCLUSIONS

Strong interannual fluctuations in calf production rate inevitably have a significant influence on the interdecadal variability observed in right whale population growth rate (Meyer-Gutbrod & Greene 2014). Therefore, the ability of our prey-dependent version of the reproduction model to capture a large proportion of the observed variance in annual calf production has important implications for the management of this highly endangered species.

During the 1990s, low prey availability significantly reduced calf production and, in combination with a high mortality rate, the right whale population experienced periods of negative growth. The impact of fewer calf births over the 1990s can be seen in the leveling off in recruitment of viable females in the 2000s (Fig. 8A). Persistence of the extremely poor feeding conditions observed during the final years of the 1990s would have resulted in a much more rapid

collapse of the population than that projected by Fujiwara & Caswell (2001) due to the near cessation of reproduction, regardless of any changes in anthropogenic sources of mortality. Fortunately, the feeding conditions of the 1990s did not persist, as an ecosystem regime shift led to a resurgence of the *C. finmarchicus* in the region during the subsequent decade (Greene et al. 2013). In response, the right whale population underwent a notable recovery during the 2000s. This remarkable swing, from heading towards extinction during the late 1990s to being on the path towards a relatively rapid recovery during the 2000s, demonstrates the population's high level of demographic volatility. In retrospect, it is now apparent that much of the decadal variability in the population's recovery rate is driven by changes in prey availability linked to climate-associated ecosystem regime shifts (Meyer-Gutbrod & Greene 2014). Any attempt to characterize the future fate of the right whale population must take these ecosystem regime shifts into account.

The predictability of climate-driven ecosystem regime shifts in the Northwest Atlantic is an active area of research (Greene et al. 2013). Predicting their ecological impacts is much further along than predicting exactly when they will occur. These ecosystem regime shifts have been associated with various natural modes of climate variability; however, additional regime shifts and species range shifts will undoubtedly be modified and/or triggered in the future by anthropogenic climate change. In the context of right whale conservation and management, the recent prediction by Reygondeau & Beaugrand (2011) of a northward range shift of *C. finmarchicus* in response to a warming ocean should raise serious concerns. Such a range shift could greatly limit the availability of prey to right whales in the GOM and surrounding waters over the coming decades. In response, right whales may have to change their behavior to habituate to new foraging grounds, increase the extent of their migration route, or change the location of their calving grounds. Without such behavioral changes, this population may risk a significant decrease in its viability.

As the impacts of climate on right whale demography are mediated by prey availability, specifically the distribution and abundance of *C. finmarchicus*, understanding the responses of this species to such regime shifts will be critical to developing an ecosystem-based management perspective for the North Atlantic right whale population. The shift to such an ecosystem-based management perspective does not alter the importance of implementing policies and regulations that achieve the traditional conservation goals of reducing anthropogenic sources of mortality. After all, reducing the mortalities associated with ship strikes and entanglement in fishing gear will always enhance the population's recovery rate. However, there are at least 2 additional benefits that an ecosystem-based management perspective introduces to developing conservation plans for the right whale population. First, it recognizes that the conservation goals set for management must be regime-dependent. The population's recovery rate is constrained by environmental conditions, therefore measures of success for achieving conservation goals should be expected to vary from one ecosystem regime to another, even if comparable reductions in anthropogenic sources of mortality are achieved. Second, the uncertainty introduced by our limited understanding, as well as the stochastic nature of climate variability and change, will set limits on our ability to predict the recovery of the right whale population. Therefore, rather than relying on a single demographic projection based only on recently observed environmental conditions, an ensemble of projections based on a range of climate and anthropogenic mortality scenarios should be explored. Only then will we have the means to assess the likely fate of this species in the future.

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