Food-limited reproduction in North Atlantic right whales: understanding interannual variability through model building

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Abstract: The right whale (*Eubalaena glacialis*) population in the North Atlantic is severely endangered. In order to understand whether this population is recovering, it is necessary to understand the factors responsible for variation in its reproductive output. To investigate possible food limitation, I developed a generic model of right whale reproduction in which females are partitioned among three states: pregnant, nursing, and recovering, and the probability of moving between the states is determined by the abundance of *Calanus finmarchicus*, an important prey species. A genetic algorithm was used to find the set of parameters giving the best agreement between the modeled number of calves and observations. Parameters were fit to *C. finmarchicus* time series representing bi-monthly or yearly average conditions in four regions in the Gulf of Maine, and the significance of models was assessed using a Monte Carlo procedure. The best model from this analysis suggests that right whale births are limited by the abundance of *C. finmarchicus*, and that years of low food can initiate a boom-bust pattern in right whale births. The boom-bust cycles are likely a common feature in other baleen whales and could have important implications for right whale behavior and the recovery of this population.

Keywords: Right whale, *Eubalaena glacialis*, *Calanus finmarchicus*, Gulf of Maine, continuous plankton recorder, genetic algorithm

Introduction

The northern right whale (*Eubalaena glacialis)* is considered to be the world's most endangered large whale species, with a population in the western North Atlantic estimated at between 300-400 individuals (International Whaling Commission 2001). Recent demographic estimates have shown that this population's growth rate has gone from gradually increasing in the 1980's to gradually declining in the 1990's (Caswell et al. 1999). These demographic models suggest that, if mortality and reproductive rates remain comparable to those observed during the 1990's, the North Atlantic right whale population is doomed to extinction in less than 200 years (Caswell et al. 1999,Fujiwara and Caswell 2001).

The demographic studies cited above focused on mortality and assumed that reproductive rates were constant. However, over the last 25 years, the number of right whale calves born per year has been anything but constant (Kraus et al. 2001,Greene et al. 2003,Greene and Pershing 2004). The pattern in right whale births has become especially troubling in recent years, with a noticeable decrease in the 1990s in the number of births and an increase in the average time between successive offspring for a given mother (Knowlton et al. 1994,Kraus et al. 2001).

In response to the decline in births during the late 1990s, Reeves et al. (2001) convened a workshop to evaluate potential causes for the low reproductive rates in North Atlantic right whales. Their workshop articulated several hypotheses that could account for reduced reproductive output in this population, including environmental toxins, disease, low genetic diversity, and poor nutrition. All of these hypotheses could effectively explain a decrease in right whale reproduction; however, the number of right whale births has apparently recovered from the low period in the late 1990s. Thus, rather than searching for a reason to explain a decline in reproductive output, we seek an explanation for reproductive variability. This study focuses on potential food limitation in right whales as it is the only mechanism that could account for both the drop in reproduction in the late 90s and the increase in subsequent years. Large mammals meet the costs of pregnancy and nursing through either high food intake or large metabolic reserves (Young 1976). For this reason, variability in the abundance or availability of prey is a likely factor influencing right whale reproduction (Kenney 2001,Greene et al. 2003,Greene and Pershing 2004). Understanding the causes of reproductive variability in the right whale population would provide an insight into this species' ecology that might help refine current management strategies.

The Gulf of Maine and Western Scotian Shelf contain all of the known right whale feeding grounds. The movements of northern right whales in this region are closely tied to the distribution of its main prey, the copepod *Calanus finmarchicus* (hereafter, *Calanus*). The whales' seasonal occupation of their main feeding grounds in Cape Cod Bay, Great South Channel, and the Bay of Fundy coincides with periods when high densities of *Calanus* exist in those areas (Murison and Gaskin 1989,Kann and Wishner 1995a, b,Woodley and Gaskin 1996). Recent time series analyses of *Calanus* abundance in the Gulf of Maine have documented interannual changes in this population of over an order of magnitude (Conversi et al. 2001,MERCINA 2001). These findings lead to the hypothesis that variability in right whale calving is driven by variability in *Calanus* abundance.

In order to test this hypothesis, I developed a simple model of how prey variability could influence right whale reproduction. Then, a set of parameters for this model yielding the best fit between modeled and observed right whale births was found using a genetic algorithm. This model was used in two earlier papers to discuss the impact of climate variability on right whale reproduction (Greene et al. 2003,Greene and Pershing 2004). The current paper describes the details of how this model was developed, evaluates its performance in recent years, and considers implications of the model for right whale ecology and behavior.

Methods

The main question addressed in this study is whether the observed variability in a time series of right whale births is related to the observed variability in a time series of *Calanus* abundance from the Gulf of Maine. However, the complexities of right whale reproductive biology mean that a simple relationship between food and calves is unlikely. In order to account for these complexities, I developed a generic model of right whale reproduction and used a genetic algorithm to discover a set of model parameters yielding the closest fit to the data. Statistically, the question becomes does the model fit the data better than one would expect due to chance alone? To answer this question, I computed a distribution of possible calving predictions from the model and then compared the predictions from the best-fit model to this distribution.

Right Whale Model

Analysis of the right whale photographic catalog maintained by the New England Aquarium suggests that right whales typically require three years between births (Knowlton et al. 1994). After a pregnancy lasting roughly a year, each mother gives birth to a single calf in the calving region off of the southeast US. The mother-calf pairs then migrate to the Gulf of Maine. After the calves are weaned, mothers typically require at least one year of recovery before they can support another pregnancy. Reduced food availability during pregnancy or nursing could reduce the probability of a calf being born or of it surviving, while low quantities of food after weaning could increase the recovery period. Thus, in order to study the impact of food variability on right whale reproduction, it is necessary to use a model that captures the essential features of this species' reproductive cycle without introducing unnecessary parameters.

The model captures the whales' reproductive cycle by partitioning females among three states: recovering, pregnant, and nursing (Figure 1a). Whales advance to the next state with a probability determined by food abundance according to the functions s_1 or s_2. If a whale does not advance, then she is moved to the recovery phase. The probability, s_j, of advancing from state j is related to normalized food concentration (C) by a simple function:

$$s_j(C) = \begin{cases} \frac{p_j}{\tau_j} C, & C < p_j \\ p_j, & C \geq p_j \end{cases}$$

described by two parameters, τ_j and p_j. For values of C below τ_j, the saturating food concentration, the probability of advancing increases linearly, from 0 to p_j. If C is above the saturating value, the probability is constant (Figure 1b).

The vector $\boldsymbol{p}$ containing the four parameters: τ_1, p_1, τ_2, and p_2, completely describes a particular right whale model, denoted $M[\boldsymbol{p}]$. Starting from $\boldsymbol{w}^*$, an initial distribution of N right whale females among the three states, the operator M determines a distribution of whales according to the probabilities determined by the transition functions and the concentration of *Calanus*. This yields a stochastic recurrence equation:

$$\begin{aligned} \boldsymbol{w}_{t+1} &= M[\boldsymbol{p}](C_t, \boldsymbol{w}_t), \\ \boldsymbol{w}_0 &= \boldsymbol{w}^* \end{aligned}$$

where $\boldsymbol{w}_t$ is the distribution of females among the three states at time t.

The above model assumes a fixed population size N. Based on over 20 years of photographic records, Knowlton et al. (1994) estimated that the number of reproductively active females was 51, and this number was stable throughout the 1980's and early 1990's. A more recent analysis by (Kraus et al. 2001) refined these estimates and concluded that the number of reproductively active females increased during the 1990's from 51 in 1987 to 75 in 1997. All runs of the model reported below used the number of reproductively active females from Kraus et al. (2001) for the period 1987-1997. Prior to 1987, I assumed that the number of females was constant at 51 females, while after 1997, the last year with published numbers, I assumed the population was fixed at 70 females.

Time-varying population size adds a slight complication to the model, requiring a procedure to add and remove animals. Whales are only determined to be reproductively active if they have been observed with a calf. In terms of the model, this represents an observation of a whale in state 3. Observing a new whale in state 3 implies that this whale was in the recovery state two years earlier. Thus, if in a given year the population of females increased, the new whales were added to the population by placing them in the recovery state (state 1) two years before. This ensures that the number of whales in state

3, and therefore, the number of calves in the model, reflects the dynamics of the model. For years when the population declined, the necessary number of whales were removed at random from the population.

Calanus Time Series

Most of the studies describing long-term zooplankton variability, especially those examining the impact of climate, have used data from the Continuous Plankton Recorder (CPR) (Pershing et al. 2004). The CPR sieves plankton on to a silk gauze that is periodically advanced to expose a fresh section of gauze, providing a quantitative record of the abundance of zooplankton and large phytoplankton in discrete segments along the ship's path (Warner and Hays 1994). The main advantage of the CPR is that it can be towed from ships of opportunity—usually, commercial ships traveling along their normal routes. Furthermore, CPR surveys using a standardized methodology have been conducted since the 1940's, principally by the Sir Alistair Hardy Foundation for Ocean Science in the United Kingdom (Warner and Hays 1994).

Since 1961, NOAA Fisheries in the United States has operated a CPR survey in the Gulf of Maine, following the SAHFOS protocols (Jossi and Goulet 1993,Warner and Hays 1994,Greene et al. 2003). The CPR is towed from a commercial vessel running between Boston, MA and Cape Sable, NS, and the transect is sampled at approximately monthly intervals. After a cruise, the CPR silk is cut into sections representing 18.5 km, the silks are examined under a microscope, and zooplankton and large phytoplankton are counted. For this study, we focus exclusively on the largest stages of *Calanus* (copepodite stages 5 and 6) due to their importance in the diet of right whales (Kenney et al. 1986,Mayo and Marx 1990,Mayo et al. 2001). To account for different physical and biological conditions in the Gulf of Maine, the CPR samples were divided into four regions: Cape Cod Bay (CCB) in the west, Western Gulf of Maine (WGOM), Eastern Gulf of Maine (EGOM), and the Scotian Shelf (SS) (Figure 2). Furthermore, within each region the data were divided into time bins of 1/6 of a year, and for each period, the mean deviation from the seasonal cycle was computed (see Appendix A). The anomalies were then used to form six time series of annual values representing approximately bi-monthly periods. A yearly average time series was also produced for each region.

Right Whale Calving Data

Fitting the parameters for the model requires a time series corresponding to one or more of the model states. Among the three model states: recovering, pregnant, and nursing, only the nursing state can be directly observed. From their photographic database, the New England Aquarium produces an estimate for the total number of calves observed in each year (Kraus et al. 2001), and this time series was used to as an estimate of the nursing state. This number includes all calves, even those that died within the year. As such, it is not an indicator of recruitment but of total reproductive output.

Parameter Selection via a Genetic Algorithm

Computationally, the purpose of this study is to find the vector of parameters $\boldsymbol{p}$ minimizing the difference between the observed number of right whale calves and the numbers predicted by $M[\boldsymbol{p}]$ when forced by a particular *Calanus* series. The stochastic nature of the model makes it difficult to find $\boldsymbol{p}$ using standard optimization procedures. For this reason, I conducted the minimization using a genetic algorithm (Holland 1975,Michalewicz 1996).

A genetic algorithm (GA) seeks to optimize a function by mimicking organic evolution, and much of the terminology should be familiar to biologists. A GA has two essential components: a numerical or alphabetic encoding called a chromosome and a function that ranks chromosomes by assigning each a fitness. A chromosome can be thought of as representing a specific computer program, and in the case of our model, a chromosome is a vector of parameters $\boldsymbol{p}$. The fitness function takes a chromosome as input and returns a real number indicating the performance of the chromosome, with larger fitness values assigned to better chromosomes. For this study, the fitness function is the reciprocal sum of squared deviations between observed calves and those predicted by the model, e.g.:

$$Fitness(\boldsymbol{p}) = \frac{1}{\sum_{j=1}^{n}(model_j - observed_j)^2}$$

The GA was used to find the optimal parameters for each of the 24 bimonthly-regional *Calanus* time series as well as the yearly-average time series for each region. The GA procedure used in this study is described in more detail in Appendix B.

Bootstrapping

The GA procedure finds a model (a vector of parameters) that yields the minimum difference between observed and predicted calving data possible for a given *Calanus* series. However, from a scientific standpoint, the goal is not necessarily to predict right whale calves but to find a model that adequately represents right whale biology and a food series that represents their feeding conditions. The trick is defining "adequately" in an objective manner. If we knew how often we could expect to encounter an arbitrary parameter vector with a particular fitness, then we could define an adequate model as one having fitness higher than 95% of all other models. While we don't know the distribution of fitness values *a priori*, it is possible compute through a Monte Carlo procedure by applying the GA to many random food series.

One feature complicating the Monte Carlo procedure is that the *Calanus* series contain some autocorrelation at a lag of 1 year. To incorporate the autocorrelation in the *Calanus* data, the original *Calanus* data were resampled in blocks of 5 years, a process known as bootstrapping (Chernick 1999). The random food series, were created from a set containing all possible five year blocks from the WGOM Year *Calanus* data, as well as each block reversed. For a time series with 18 samples, there are 2*(18-5+1)=28 such blocks. This means that this procedure can create over 98,000 unique time series with the same length as the original. This procedure was used to create 500 random food series. Applying the GA to each food series produces a set of 500 parameter vectors and their corresponding fitness values.

Results

The GA fitness values for the 24 bi-monthly *Calanus* series ranged from 0.033 to 0.067 (Figure 3). Within the four regions, fitness was generally higher during summer, with the maximum fitness always occurring between May and August. The range of fitness values among the yearly-averaged *Calanus* series was similar to that for the bi-monthly series (Figure 3 stars), with higher values in the central regions. The fitness value of 0.073 for the WGOM series was the highest fitness value found for any of the 28 *Calanus* series. The bootstrapping procedure established critical values for 95% and 99% confidence intervals of 0.063 and 0.07, respectively (see Appendix C). Comparing the results from the bi-monthly food series with these critical values identifies the May-June

WGOM and July-August EGOM bi-monthly series as significant at the 95% level (Figure 3, dashed line). From the yearly series, only the WGOM model was significant, but it was significant at the 99% level (Figure 3, solid line).

The fitness values provide a good indication of how well the models perform, while the parameter vectors provide insight into how the models achieve their level of performance. The two parameters for each function specify a point in food-probability space (the inflection point in the function), and the points from the bootstrapped models map out a probability distribution for the parameter values. For both s_1 (Figure 4a) and s_2 (Figure 4b) the points bootstrapped models are clustered near the top, center of the figures (high maximum probabilities, mid-range saturating food concentrations). However, the distribution is tighter for s_2 than s_1. For both functions, the random series with fitness in the top 10% (black dots) had parameter distributions similar to the overall distribution. This similarity suggests that the model is sensitive to the particular input series, and more importantly, that there is not a region of parameter space which always gives high-fitness, regardless of input.

The three series with significant fitness values: WGOM May-June, EGOM July-August, and WGOM Year, had very different functions s_1 controlling the transition from the recovery state to pregnancy (Figure 4a). The difference was most pronounced for the maximum probabilities (p_1), which ranged from 0.3 to 0.9. The difference between the saturating food concentrations (τ_1) was smaller, although the two parameters were linked, with high $\tau_1$implying high p_1. The second functions (s_2), the function controlling the transition between pregnancy and nursing, were essentially the same for all three series (Figure 4b). In all cases, both the maximum probabilities and saturating food concentrations were high. Comparing the two functions suggests that both WGOM models are less sensitive to food during pregnancy than during the recovery phase. Compared to the bootstrapped points, both points for the EGOM July-August series are located near the center of distribution, while the two WGOM series are found closer to the edges.

Evaluation of the WGOM Year Model

The WGOM Year model had the highest fitness of any of the models considered, implying that it captures essential features of the relationship between right whale reproduction and *Calanus* abundance in the Gulf of Maine. Until the early 1990s, *Calanus* was abundant, and both the observed and modeled number of calves exhibited little year-to-year variability (Figure 5b). After 1990, *Calanus* became less abundant and more variable, and the variability in both right whale series increased. The expected number of calves in each year from the WGOM Year model does a good job reproducing the variability in the observations (Figure 5b, thin black line), and most of the observations fall within the 95% confidence interval surrounding the predictions (Figure 5b). *Calanus* data after 1998 were deliberately excluded from the parameter fitting; thus, the model values for 2000-2005 represent an out of sample test of the model. One of the pitfalls of empirical modeling is that the models often perform poorly when confronted with novel data. With the exception of 2002, all of the observations from this period fall within the 95% confidence limits. The model explains 48% of the variance in the calving data, and the regression line (slope=0.67, intercept=1.7 calves) is close to the ideal one-to-one relationship (Figure 5c). Furthermore, the WGOM Year model suggests a return to conditions similar to those in the 1980s.

Discussion

This analysis identified *Calanus* abundance in three regions and time periods as good predictors of right whale reproduction: EGOM in July-August, WGOM in May-June, and WGOM averaged over a year. However, the question remains whether or not the models corresponding to these series represent real mechanistic relationships. One way of evaluating the models is to compare them with known patterns of right whale feeding behavior.

There are three main right whale feeding grounds in the Gulf of Maine: Cape Cod Bay, Great South Channel, and Bay of Fundy (Figure 2), and whales are most abundant in these regions during characteristic time periods. Cape Cod Bay is used during the late winter and early spring, with a peak in abundance in April (Hamilton and Mayo 1990) . Right whales are most abundant in Great South Channel during late spring and early summer and are most abundant during May (Kenney et al. 1995), while Bay of Fundy is most important during the late summer (Kraus et al. 1982: Winn, 1986 #511). The WGOM region from the CPR survey is upstream from the Great South Channel (Figure 2), and the abundance of *Calanus* in WGOM should be a good indicator of *Calanus* abundance in that region. The close correspondence in space and time between the WGOM May-June right whale feeding in Great South Channel suggests that this model represents a true trophic relationship. The Great South Channel is also the main outflow for the surface waters of the Gulf of Maine (Bigelow 1927,Brooks 1985 {Naimie, 1996 #116}); thus, it is likely that average yearly abundance of *Calanus* from the WGOM does a good job of representing the average feeding environment for right whales.

If the two models from WGOM are realistic, then two questions remain: what is the nature of the EGOM July-August model and why were significant relationships not found in the two shallow regions? Some insight into the EGOM relationship can be found by examining its parameter values relative to the random models (Figure 4). For both transition functions, the parameters from the EGOM models were found much closer to the center of the distribution from the random models than either of the WGOM models. This pattern is especially obvious for the Recovering-to-Pregnant function (Figure 4a). This suggests that the EGOM model may represent a spurious relationship and underscores the value of the bootstrapping procedure.

Cape Cod Bay is clearly an important right whale feeding area (Hamilton and Mayo 1990) as is Roseway Basin on the Scotian Shelf (Baumgartner et al. 2003), so it is somewhat surprising that no significant models were found from these regions. Both CCB and SS are only a small fraction of the CPR trackline, and consequently, there are relatively few samples from these regions. Undersampling in this way would lead to *Calanus* series from these regions that are more variable and likely less representative of the true interannual patterns. However, if the time series are representative, this study implies that reproductively active females derive a relatively small proportion of their nutrition from these regions. Reduced nutritional quality of the prey or reduced feeding in a region would decrease its contribution to the populations overall nutrition. As the summer progresses, *Calanus* begins to prepare for its diapausing stage by accumulating lipid stores. Thus, it is likely that the *Calanus* population in GSC is a richer food resource than the population consumed by right whales in CCB earlier in the year.

Between 1993 and 1997, right whales abandoned Roseway Basin (Reeves et al. 2001), suggesting that the second hypothesis is more likely for the SS region.

Implications of the Model

The right whale calving rate has become more variable in recent years, with a series of bad years (e.g. 1998-2000) followed by a series of good years (e.g. 2001-2003). Based on our model, we interpret such cycles as an interaction between variability in *Calanus* abundance and the non-linearity inherent in the right whale's multi-year reproductive cycle. To see how this works, consider an idealized version of the model in Figure 1 with all transition functions equal to one. If this model is initialized with all of the females in the recovery state, no births would be recorded in the following year as the population moves to the pregnancy state. However, in the second year, the entire population would give birth, producing a right whale baby boom. In this idealized case, the three year boom-bust cycle is due to the initial conditions of the model. If the model were started with females partitioned evenly across the states, then there would be a steady output of calves.

According to the WGOM Year model, a year with poor *Calanus* causes pregnant females to abort and recovering females to remain in the recovery state. The net effect is that a bad *Calanus* year synchronizes the population by moving most females into the recovery state. If *Calanus* is abundant in the next two years, the population will advance together through the states, producing a boom. If feeding conditions are relatively stable, the stochasticity in the model will eventually lead to a more even partitioning of the females among the three states, and the boom-bust cycle will give way to a steady reproductive output. This behavior is evident in both the WGOM *Calanus* time series and the right whale calving series (Figure 5). During the 1980's, *Calanus* was abundant and interannual variability was low. This created stable conditions for right whale reproduction and the number of calves born per year was relatively steady. During the 1990's, *Calanus* became less abundant and more variable, leading to a boom-bust cycle.

The cycles of boom and bust that are inherent in the right whale's reproductive cycle could interact with this species' mating behavior, possibly limiting the recovery of this species. Mating in right whales is thought to occur in social aggregations called surface active groups (Kraus and Hatch 2001). These aggregations typically involve one or two females surrounded by several males. The intense competition among males implied by this behavior is thought to be a consequence of this population's average operational sex ratio of four females to one male (Kraus and Hatch 2001). The 4:1 ratio was estimated based on average time between reproduction in this population; however, the WGOM Year model suggests that this ratio is highly variable and that a value of 4:1 is only appropriate during periods of steady food. Following a bust period, the model indicates that most females should be in the recovery stage, and the sex ratio could approach 1:1. Assuming right whale mating behavior does not change, the model implies an increase in surface active groups during bust periods, possibly exposing right whales to a higher risk of ship collisions. Furthermore, by increasing female competition for mating, bust periods could limit population growth through an Allee effect (Allee 1931).

The right whale's multi-year reproductive cycle is not unique. Both fin and sei whales have reproductive cycles similar to right whales (Lockyer 1986, Lockyer 1987), and it is likely that other baleen whales share this pattern. The WGOM Year model suggests that these species could exhibit similar boom-bust cycles during periods of variable food resources.

The model also makes some explicit predictions about right whale physiology. For a given concentration of food, the probability in the WGOM Year model of moving out of the recovery phase is always lower then the probability of moving from pregnancy to nursing (Figure 4). This implies that the production of a calf is more dependent on a female's feeding prior to pregnancy. Photographic estimates of body size and condition indicate that right whales are noticeably thinner in the two years after they give birth (Pettis et al. 2004). These estimates suggest a pattern where cows build their fat reserves prior to pregnancy and then use these reserves to support the calf through pregnancy and lactation. Blubber thickness measurements using ultrasound offer additional support for this hypothesis (C. M. Angell, *pers. comm.*) and are one way of testing the implications of the model.

One drawback to the empirical approach is that the models often do poorly when they are used to extrapolate to time periods or data ranges not included in the fitting procedure. While our initial out-of-sample predictions appear to agree with observations, it would not be surprising if their accuracy begins to decline. This could arise due to changes in right whale foraging behavior or uncertainties in estimating the number of reproductively active females. Even if the model fails to give quantitative predictions, we expect it to still provide a good relative measure of right whale reproduction due to its ability to resolve the boom-bust dynamics. In this case, the model is most valuable as a formal representation of the relationship between right whale reproduction and *Calanus* dynamics as it existed in the 1980s and 1990s. Large deviations from the model's predictions would indicate a change in the relationship between right whales and the Gulf of Maine. By detecting unusual conditions that could require a change in management strategies, this model could be an important aid to the recovery of the North Atlantic right whale population.

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Figure Captions

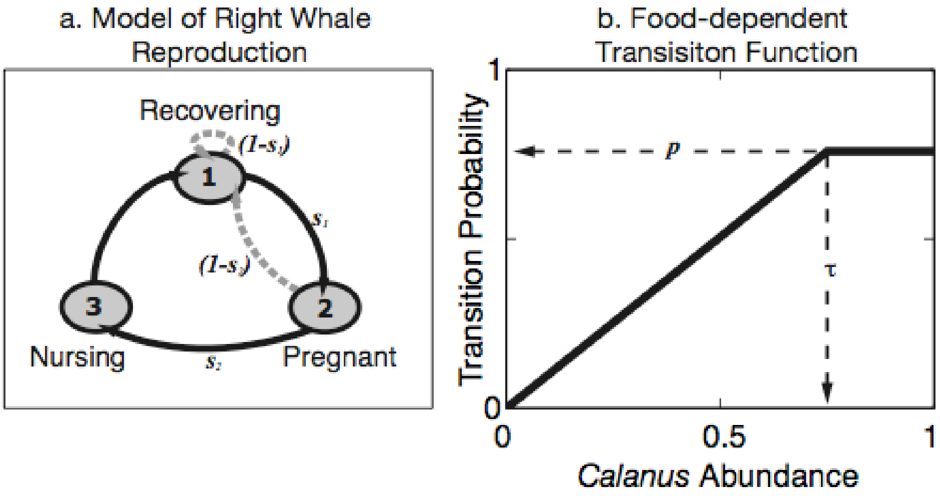
Figure 1. Generic right whale reproductive model. a. State diagram. The model consists of three states: Recovering, Pregnant, and Nursing. Females advance to the next state with probabilities determined by the functions s_1 and s_2. If a whale fails to advance, she returns to the Recovering state. b. The transition probability functions s_1 and s_2 are each controlled by two parameters: τ_j and p_j. The probability of success increases linearly with normalized *Calanus* concentration up to the saturating concentration, τ_j. If the *Calanus* concentration is greater than τ_j, then the probability is p_j .

Figure 2. Gulf of Maine regions containing zooplankton information used in this study. The CPR survey collects zooplankton samples (white circles) across the center for the Gulf of Maine at approximately monthly intervals. The samples were partitioned among four regions: Cape Cod Bay (CCB), Western Gulf of Maine (WGOM), Eastern Gulf of Maine (EGOM), and Scotian Shelf (SS). The bathymetric contours correspond to 1000m, 200m, and 80m.

Figure 3. Performance of the right whale model fit for several *Calanus* time series. The vertical bars indicate the fitness of the right whale model with parameters fit using a bi-monthly *Calanus* time series from one of the four regions. The stars indicate the fitness of the models using yearly mean data from each region. The dashed line is the 95% confidence interval based on the bootstrapped fitness distribution. The solid line is the 99% confidence interval.

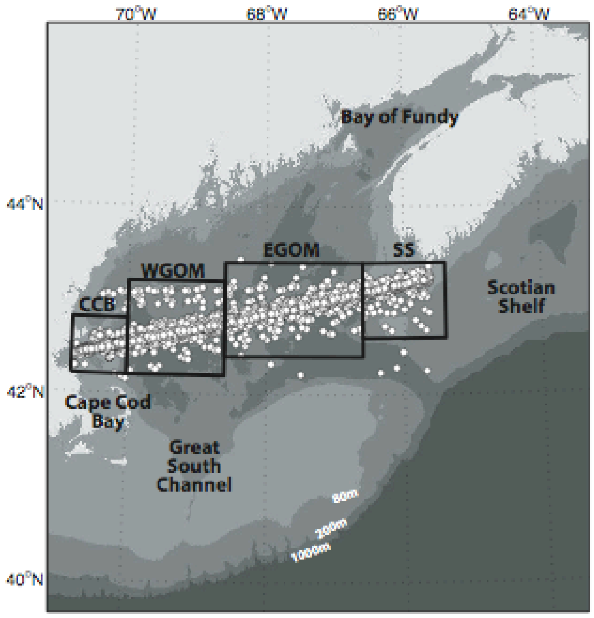
Figure 4. The transition functions from the three significant models compared with the functions from the random series.

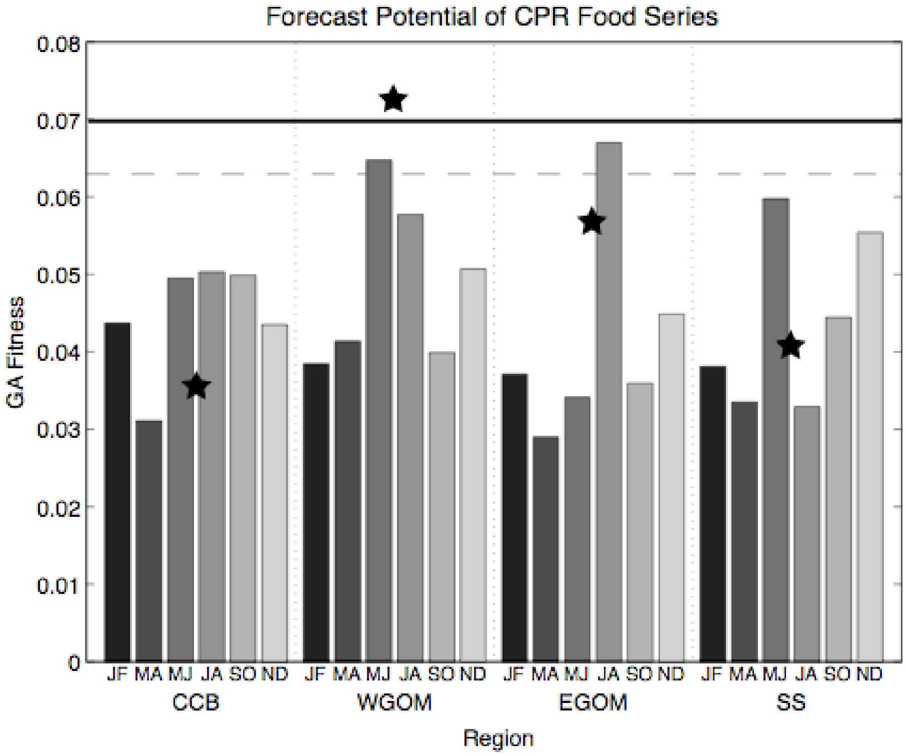
Figure 5. Performance of the WGOM Year model. a. The yearly-mean abundance index for *Calanus* in WGOM. The shaded area is +/- two standard errors around the mean. b. Predictions of right whale calves from the yearly-mean WGOM model compared with observations (black circles). The observed value for each year is the total number of calves observed in that year, including known mortalities (Kraus et al. 2001). The model values are surrounded by a 95% confidence interval (gray region) that includes uncertainties in the *Calanus* data and stochasticity in the right whale model (see Appendix D). c. Comparison between observed number of right whale calves and the number predicted from the WGOM Year model. A regression between the series is significant ($p<0.01$, $R^2=0.48$) and has little bias. Years 1982-1999 (open circles) were used in the model fitting procedure. Years 2000-2004 (closed circles) were not used to fit the model and represent out-of-sample tests of the model's validity.



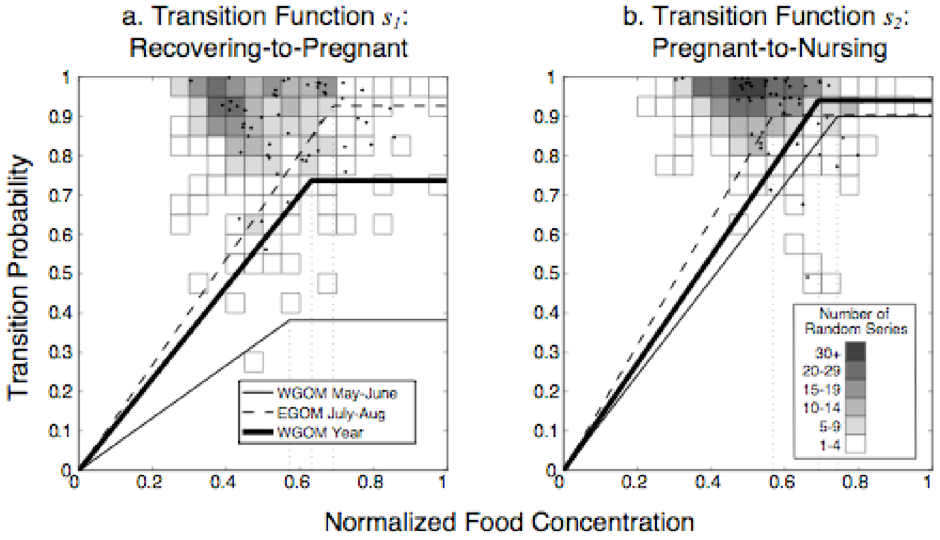
a. Model of Right Whale Reproduction

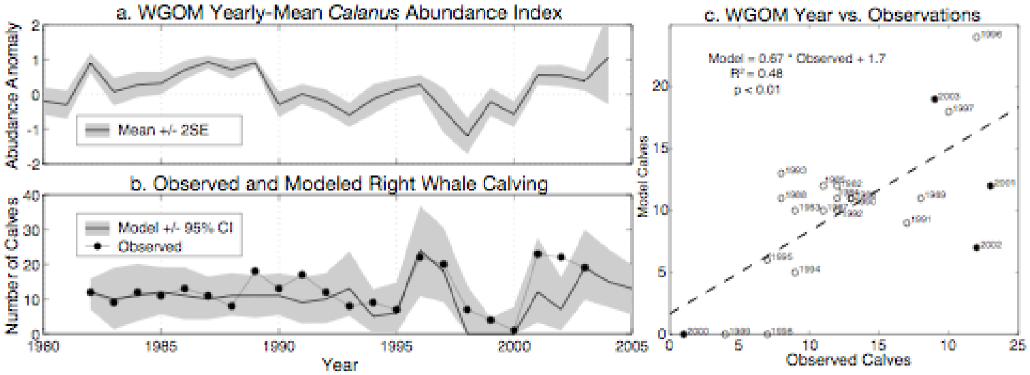
b. Food-dependent Transisiton Function


70°W
68°W
66°W
64°W
44°N
42°N
40°N
Bay of Fundy
EGOM
SS
WGOM
CCB
Scotian Shelf
Cape Cod Bay
Great South Channel
80m
200m
1000m


Forecast Potential of CPR Food Series
GA Fitness
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
JF MA MJ JA SO ND
CCB
WGOM
EGOM
SS
Region

535


a. Transition Function s_1:
Recovering-to-Pregnant
b. Transition Function s_2:
Pregnant-to-Nursing
Transition Probability
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.2
0.4
0.6
0.8
1
WGOM May-June
EGOM July-Aug
WGOM Year
Number of Random Series
30+
20-29
15-19
10-14
5-9
1-4
Normalized Food Concentration


a. WGOM Yearly-Mean *Calanus* Abundance Index
Abundance Anomaly
2
1
0
-1
-2
Mean +/- 2SE
b. Observed and Modeled Right Whale Calving
Number of Calves
40
30
20
10
0
Model +/- 95% CI
Observed
1980
1985
1990
1995
2000
2005
Year
c. WGOM Year vs. Observations
Model = 0.67 * Observed + 1.7
$R^2 = 0.48$
$p < 0.01$
Model Calves
Observed Calves
0
5
10
15
20
25
1996
2003
1997
1990
2001
1988
1989
1993
1991
2002
1995
1994
2000
1999
1998

Supplemental Material for:

Food-limited reproduction in North Atlantic right whales: understanding interannual variability through model building

Andrew J. Pershing

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Cornell University

Appendix A—Processing CPR Time Series

From the point of view of time series work, the most difficult aspect of working with the CPR data is the irregular sampling frequency. This problem is compounded by the high reproductive potential of *Calanus* that allows the population in the Gulf of Maine to increase by an order of magnitude in two months (Meise and O'Reilly 1996). To account for these issues, I have developed a standard methodology that has been used successfully in several other studies (MERCINA 2001, 2003).

This procedure begins with the computation of the average annual cycle in abundance for the species in question. First, the year is divided into 11 evenly spaced bins. Next, the mean log-transformed abundance and mean sampling date in each bin is computed forming a time series of sample dates (in julian days) and abundances. From the base time series a new series if formed by repeating the original series three times, producing a time series spanning the period –365 to 730 days. Then, a cubic spline is fit to this time series using the *csape* function in the Matlab Spline Toolbox. Repeating the time series ensures that the value of the spline function on day 365 is the same as that on day 0. For the current study, the seasonal cycle was fit to all of the *Calanus* abundance data before 2000 (Figure A1). This ensures that the resulting time series are consistent with prior studies using this data.

The spline function provides an indication of the long-term average log-abundance for any day of the year. The next step in the processing algorithm is to subtract from the observed abundances the value indicated by the seasonal cycle for the sample date. For every CPR sample, we subtracted the expected *Calanus* abundance based on the sampling date from the observed log-transformed abundance. The resulting data set consists of anomalies from the seasonal cycle and accounts for average growing conditions (Figure A2). For the present study, the anomaly data was binned into intervals of 1/6 of a year and the mean anomaly in each bin was computed. Values for bins with no data were filled in by linearly interpolating between the nearest bins with data. From the binned data, time series of the annual values for the six approximately bi-monthly periods were produced. As an example, the third bi-monthly period (approximately May-June) is highlighted in the seasonal cycle (Figure A1) and the anomaly data (Figure A2). The mean anomaly in each period forms a time series of year-to-year changes in the conditions in WGOM during this portion of the year. Yearly average values for each region were also produced by computing the mean anomaly in each year. This procedure is similar in spirit to the standard annual averaging procedure used by SAHFOS (Warner and Hays 1994), and the time series produced are nearly indistinguishable from the SAHFOS procedure (MERCINA 2003).

The right whale reproductive model requires food abundance normalized to the interval [0, 1]. Therefore, each *Calanus* time series was normalized by subtracting the minimum value between 1980 and 1999 and dividing by the difference between the maximum and minimum values during this period. Negative values were set to 0 and values greater than one were set to one.

Literature Cited

Meise, C. J., and J. E. O'Reilly. 1996. Spatial and seasonal patterns in abundance and age composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank 1977-1987. Deep Sea Research II **43**:1473-1501.

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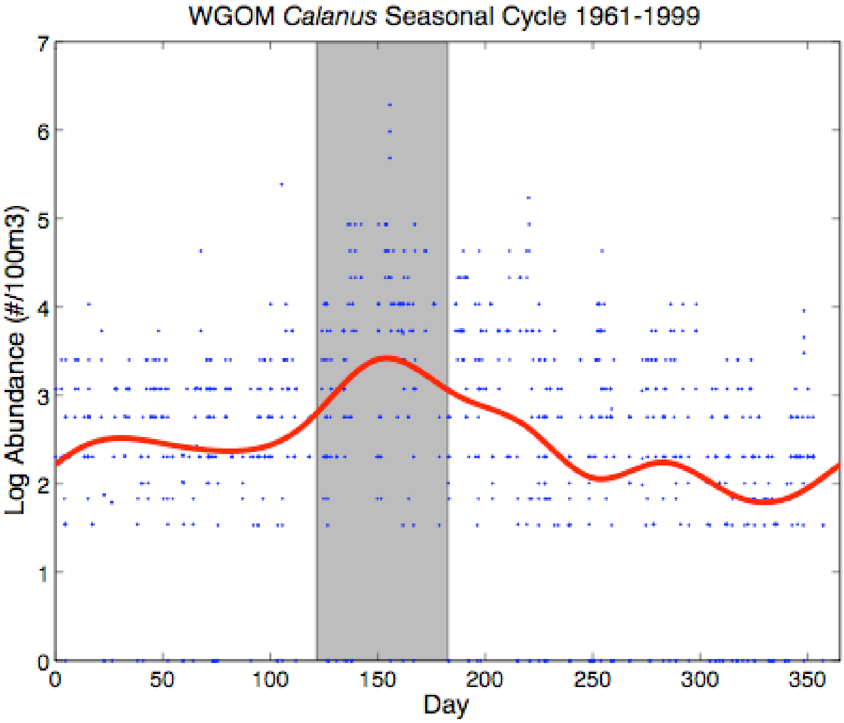
Figure Captions

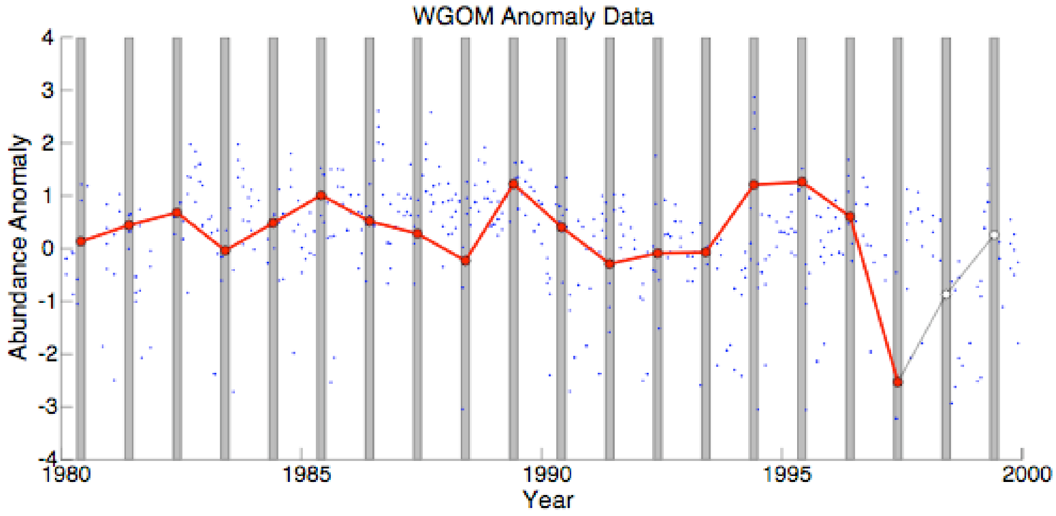
Figure A1. The annual cycle of *Calanus* abundance in the WGOM region. A periodic cubic spline (red line) was fit to all of the observations between 1961 and 1999 (blue dots). The third bi-monthly interval (approximately, May-June) is highlighted.

Figure A2. The deviations between the observed *Calanus* abundance and the seasonal cycle between 1980 and 2000. The mean anomalies in each May-June period (gray regions) form a time series of interannual changes in *Calanus* abundance during this portion of the year (red and white circles). There were no CPR samples collected during this period in both 1998 and 1999 (white circles), and these values were estimated by linearly interpolating from the adjacent time periods.

71


WGOM *Calanus* Seasonal Cycle 1961-1999
Log Abundance (#/100m3)
0
1
2
3
4
5
6
7
Day
0
50
100
150
200
250
300
350

72


WGOM Anomaly Data
Abundance Anomaly
4
3
2
1
0
-1
-2
-3
-4
1980
1985
1990
1995
2000
Year

73

Appendix B—Optimization via Genetic Algorithm

Genetic algorithms attempt to maximize a function known as the "fitness function" by a process similar to natural selection. First, a population of chromosomes—parameters for the fitness function, is created at random, and the fitness of each chromosome is evaluated. A new population of chromosomes is then created using many copies of high-fitness chromosomes and few or no copies of the low-fitness chromosomes. However, as in biology, the copying process is not perfect and can introduce slight modifications to the chromosomes. The reproductive procedure is the key to the success of the GA-approach as it provides a simple, but effective way of searching the state space. Furthermore, by keeping some low-fitness chromosomes in the population and by allowing imperfect copies, GAs avoid becoming trapped at local optima and are very good at finding the global optimum, even for complicated non-linear functions (Michalewicz 1996).

There are a wide variety of reproduction algorithms that have been employed by the GA community. These range from simple point-mutation models (where each element in the chromosome can change randomly by a small amount) to more complicated models that mimic sexual reproduction by combining features from two different chromosomes (cross-over). Dr. Stephen J. Hartley's GA package was used optimize the right whale model[1]. This package is written in Java and requires the user to write a single Java object that defines the chromosome and implements the fitness function. For this study, the probability of a point mutation was 0.001. The probability

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[1] Dr. Stephen J. Hartley, Computer Science Department, Rowan University, Glassboro, NJ 08028. Code available at http://www.mcs.drexel.edu/~shartley/ConcProgJava/GA/

of a chromosome being crossed with another was substantially higher. Chromosomes were selected with probability 0.7 from the population and placed in a pool. Pairs were selected from the pool, and with uniform probability a location in the vector $\boldsymbol{p}$ was selected. The values of parameters up to and including this location were swapped with the corresponding locations in the mated chromosome.

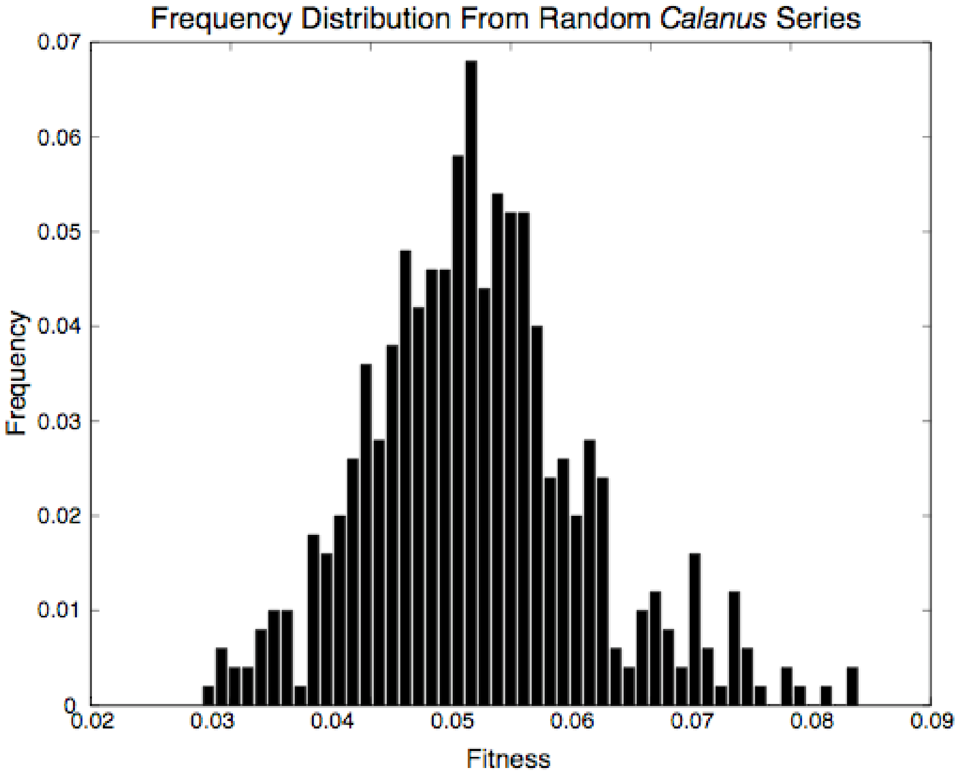
A single run of the GA for this study requires the user to provide time series of food abundance and the number of calves and reproductively active females. The program will then create a population of 100 random parameter vectors. 2,000 generations (fitness evaluation and reproduction) are performed and the parameter vector with the highest fitness (smallest deviation from the observed calves) is returned. In practice, the best-fit parameters were found after fewer than 1,000 generations.

Literature Cited

Michalewicz, Z. 1996. Genetic algorithms + data structures = evolution programs, 3rd edition edition. Springer-Verlag, Berlin.

Appendix C—Probability Density for Fitness

Figure C1. The frequency distribution of fitness from 500 random *Calanus* series is similar to a normal distribution with a mean of 0.048 and a standard deviation of 0.008. This distribution implies that fitness values of 0.063 or 0.07 are significant at the 95% or 99% levels, respectively.


Frequency Distribution From Random *Calanus* Series
Frequency
Fitness
0
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09

114

Appendix D—Confidence Intervals for WGOM Year Model

The probabilistic nature of the right whale reproduction model means that any output from the model is merely a single value selected from some distribution. To correctly estimate such a distribution, several runs of the model are required. However, the distributions from this procedure assume that all of the inputs are exact. The *Calanus* time series used in the fitting consisted of means of anomalies. In order to correctly estimate the confidence intervals surrounding the model output, a procedure is required to account for both the variance in the *Calanus* observations and the stochasticity of the model.

As with the fitness values, I employed a Monte Carlo procedure to include both sources of uncertainty. 500 *Calanus* time series were created to for the years 1981-2004. The *Calanus* values in each year were chosen from a normal distribution with a mean equal to the observed abundance anomaly and a standard deviation equal to the standard error for that year (Figure 5a). Any trophic relationship represented by this model likely reflects the total amount of food consumed by a right whale over the course of the year. Thus, the standard error, which provides an estimate of the range of likely mean values, rather than the standard deviation, which provides an estimate of likely sample values, is the appropriate variance measure for this model. For each of the 500 *Calanus* series, the WGOM Year model was run 1000 times. This procedure allows us to construct confidence intervals around the modeled calving series that incorporate both uncertainty in the *Calanus* data and stochasticity in the model.