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A MATRIX POPULATION MODEL OF BEAKED WHALES

ROSS A. CHIQUET[1], TYLER MONTGOMERY[1], BAOLING MA[2], AZMY S. ACKLEH[1]

[1]Department of Mathematics, University of Louisiana at Lafayette
Lafayette, LA 70504-1010, USA
[2]Department of Mathematics, Millersville University of Pennsylvania
Millersville, PA 17551, USA

ABSTRACT. The focus of this study is to investigate the demographic and sensitivity/elasticity analysis of the beaked whale population. First, a matrix population model corresponding to a general beaked whale life cycle is presented. The values of the parameters in the model are then estimated. The population's asymptotic growth rate λ, life expectancy and net reproduction number are calculated. The results show that the beaked whale population grows slowly and is potentially very fragile. The asymptotic growth rate is most sensitive to the survivorship rates, especially to the survivorship rate of mature females, and less so to maturity rates. Our results also indicate that these survivorship rates are very delicate, and our interval estimates for the asymptotic growth rate and inherent net reproductive number show the possibility of values below one, i.e., a declining population leading to extinction.

AMS (MOS) Subject Classification. 39A10.

1. Introduction

Beaked whales are a species of cetaceans in the family *Ziphiidae* and are some of the deepest diving and most geographically diverse species of marine mammals [11, 15]. Despite this diversity, the family remains one of the least known families of marine mammals [17]. The ecological data and life cycle information regarding these whales is sparse and somewhat unreliable. Many of the species within this family are morphologically similar and are often misidentified with some distinct species having been historically classified as a single species until recent years [15]. Sightings and identifications of the beaked whales are also difficult due to their tendency to stay in deeper offshore environments, long dive times, and relatively inconspicuous surface profiles [10, 15, 25]. Because of this, most of what is known about beaked whales comes from the studies of stranded individuals [7, 10, 15, 16, 18]. In fact, some members of this family have never been seen alive [19]. Many of the studies in the literature on beaked whales are based on short term observations [14]. However, there have been successful long term, detailed studies of living beaked whales that have significantly contributed to our knowledge of the species [26].

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In recent years, more attention has been given to the study of beaked whale ecology and behavior due to the possible impact of military sonar and seismic surveys. Several strandings of beaked whales have coincided with naval activities using active sonar [1, 6, 12, 13, 21] (just to name a few). The first association of a mass stranding of beaked whales and naval maneuvers was noted by Simmonds and Lopez-Jurado in 1991 [6]. Since then, there have been a number of atypical strandings in Greece, the Bahamas, the Madeira Islands, the Canary islands, and the Gulf of California [6, 11] most of which have been in the vicinity of naval or seismic activities. The exact ways sound affects beaked whales is still not well understood. This is possibly due to the lack of baseline knowledge of beaked whale behavior, anatomy, physiology, distribution, ecology, etc.

In addition to the lack of this basic knowledge for beaked whales, the literature is almost devoid of any vital parameters, much less having age-specific vital parameters needed to develop stage-structured models for beaked whales. The purpose of this paper is to use available data and reasonable assumptions to develop a stage-structured matrix population model similar to those used on sperm whales [2] and right whales [3] for a general beaked whale population. We determine reasonable approximations for the asymptotic growth rate, lifetime reproduction numbers, and inherent net reproduction numbers. We then perform sensitivity and/or elasticity analysis to determine which parameters have the greatest affect on the model. Also, because of all of the uncertainties in the vital rates, we provide interval estimates for the asymptotic growth rate and inherent net reproduction numbers. Our model creates the foundation for additional significant research on beaked whales. Having reliable estimates for these parameters allows for better direction of conservation efforts and could help to determine the actual effects of major stochastic events.

2. **Parameter estimates and population model**

In this section, we establish a stage-structured matrix population model to represent the demographic characteristics and vital rates of a general population of beaked whales. After defining the necessary terms and variables, we estimate the model's parameters. As is common for population modeling, we only consider the females of the species. Therefore, any further mention of these whales is understood as referring to the females of the population.

2.1. **Stage-structured model.** We now develop a discrete stage-structured population model for beaked whales. The model will be divided into four stages: calves (stage 1), juveniles (stage 2), adults (stage 3), and postbreeding adults (stage 4). Individuals are calves from birth until weening at the age of one. Then, they move on to the juvenile stage until reaching sexual maturity when they are 7 to 11 years old [20]. We will use 9 years in our calculation for our projection matrix. After this, they are considered to be adults. The life span of most species of beaked whales is unavailable with some species believed to live anywhere between 21 and 60 years [19, 22]. Finally, the post breeding adult stage last approximately 2 to 3 years which includes gestation, time spent nursing their calf, and recovery time [17, 20].

We define $P_i = (\sigma_i)(1-\gamma_i)$ to be the probability of a whale in stage i surviving and remaining in their current stage and $G_i = (\sigma_i)(\gamma_i)$ to be the probability of surviving and moving on to stage $i+1$, where the value σ_i is the survival probability for stage i and γ_i is the probability of transitioning from stage i to $i+1$. Finally, we define the fertility number, used to calculate γ_3, as

$$b_1 = 0.5\sigma_3\gamma_3\sqrt{\sigma_4}, \tag{2.1}$$

which depends on the mature female survivor probability, the probability of giving birth after survival, and the survivor probability of the mother caring for the calf [2, 5]. The 0.5 in (2.1) is based on the assumption that the sex distribution is even at birth and is used to ensure that we are again only considering the females in the population. From Caswell [4] and Doak et al. [8], we find γ_i for $i = 1, 2, 4$ by using the following equation:

$$\gamma_i = \frac{(\frac{\sigma_i}{\lambda})^{T_i} - (\frac{\sigma_i}{\lambda})^{T_i - 1}}{(\frac{\sigma_i}{\lambda})^{T_i} - 1}, \tag{2.2}$$

where T_i is the duration of time spent in stage i and λ is the asymptotic growth rate. Now, since γ_i is actually used in the calculation of λ, we first set λ equal to one. Then, we use an iterative technique outlined by Caswell [4] to get better estimates for γ_i. This process is discussed in greater detail in section 2.2. With these parameter values, we create the following model corresponding to the life cycle described at the beginning of this section:

$$n(t+1) = An(t), \tag{2.3}$$

where $n(t)$ is a vector representing the population of beaked whales at each stage, and t is taken to be one year. The projection matrix A is given by

$$A = \begin{pmatrix} P_1 & 0 & b_1 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & G_4 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}. \tag{2.4}$$

2.2. **Estimating model parameters.** Using the few vital rates we could find in the literature, we estimate the survival rates, transition rates, and the birth rate for model (2.3). Because of the lack of information, we will make the following assumptions: the survival rate for the post breeding females is the same as that for the mature whales, the mortality rate for the calves is 2 times that of the adults, and the juvenile mortality rate is an average of calve and adult mortality rates [2].

From the literature, we use the mature mortality rate of 0.05, thus $\sigma_3 = 0.9500$ [22]. Now using our assumptions, $\sigma_4 = 0.9500$, $\sigma_1 = 0.9000$, and therefore $\sigma_2 = 0.9250$. We use σ_i and equation (2.2) to calculate γ_i. Note that γ_i depends on the value λ, but γ_i is also used in the calculation of λ. This λ is the asymptotic growth rate for the population and is the dominant eigenvalue of the projection matrix A given in (2.4). To deal with this interdependence, we must use the iterative technique outlined by [4]. For this process, we first assume that $\lambda = 1$ and then compute initial values for γ_i. With these values and the values of σ_i, we can calculate the entries of the projection matrix (2.4). This initial projection matrix will yield a new λ value. This process repeats until the values of λ converge to one constant. Once this happens, we use the final value of λ to calculate the values of γ_i for our matrix (2.4).

As in Doak et al. [8] and Chiquet et al. [2], we calculate the annual fecundity rate, b_1, by taking half of the reciprocal of the interbirth interval, where the one half is to account for only the female whales. For our model, we use the estimate from New et al. [17] of two years for the interbirth interval for most species of beaked whales. Thus, we have $b_1 = 0.25$. The values of all of the vital rates are given in Table 1. Using these values, we get the completed projection matrix

$$A = \begin{pmatrix} 0 & 0 & 0.25 & 0 \\ 0.9 & 0.8380 & 0 & 0 \\ 0 & 0.0870 & 0.5396 & 0.3657 \\ 0 & 0 & 0.4104 & 0.5843 \end{pmatrix}. \tag{2.5}$$

Note that $A_{11} = 0$ because the whales only remain calves for one year before moving on to the next stage and therefore cannot remain in stage one. We use the projection matrix (2.5) to establish different deterministic values for beaked whales.

i	1	2	3	4
σ_i	0.9000	0.9250	0.9500	0.9500
γ_i	1.000	0.0784	0.5400	0.4862
P_i	0	0.8525	0.4370	0.4881
G_i	0.9	0.0725	0.5130	0.4619

TABLE 1. Summary of vital rates.

3. **Model analysis**

In section 3, we conduct some analyses of model (2.3) in order to determine the fundamental matrix, lifetime reproduction number, lifetime expectancy, asymptotic growth rate, and inherent net reproduction number. These characteristics and their interpretation give us a better understanding of the population dynamics and help us to formulate expectations for the species' future. We also perform sensitivity and/or elasticity analysis using similar techniques in [2] and [5] to identify which of our model's parameters most influence our model.

3.1. **Fundamental matrix and lifetime reproduction number.** We now calculate the fundamental matrix for model (2.3). This matrix tells us how many times each life stage is visited, on average, by an individual. In order to do this, we must first split the projection matrix A, given by (2.5), into a transition matrix T and a fertility matrix F, such that $A = T + F$, where

$$T = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0.9 & 0.8380 & 0 & 0 \\ 0 & 0.0870 & 0.5396 & 0.3657 \\ 0 & 0 & 0.4104 & 0.5843 \end{pmatrix}, \tag{3.1}$$

and

$$F = \begin{pmatrix} 0 & 0 & 0.25 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{3.2}$$

Matrix (3.1) represents the transition probabilities for each stage, and the value in matrix (3.2) is the individual fertility number. We now define the fundamental matrix by $N = (I - T)^{-1}$, where I is the identity matrix. Therefore,

$$N = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 6.1028 & 6.7808 & 0 & 0 \\ 4.4183 & 4.9092 & 9.9895 & 9.0138 \\ 4.4276 & 4.9195 & 10.0105 & 10.9862 \end{pmatrix}, \tag{3.3}$$

where $N(i, j)$ gives the expected number of visits over a lifetime to stage i from an individual starting at stage j.

To better understand matrix (3.3), let us interpret a few specific entries. The first column represents beaked whales in the calf stage of their life cycle. The first entry of column 1 tells us that calves will spend, on average, one year as a calf, 6.1 years as a juvenile, 4.41 years as an adult, and 4.43 years as a post breeding adult. Thus, a calf can be predicted to give birth 4.43 times. This value is called the expected lifetime reproduction number for the calf stage. The third column corresponds to the adult stage, so $N(4, 3) \approx 10.01$ is the expected lifetime reproduction number for an adult. Therefore, a mature adult is expected to give birth around 10 times over the course of its lifetime. This is significantly larger than the same value for calves due to the mortality rates in transitioning from calf to adult.

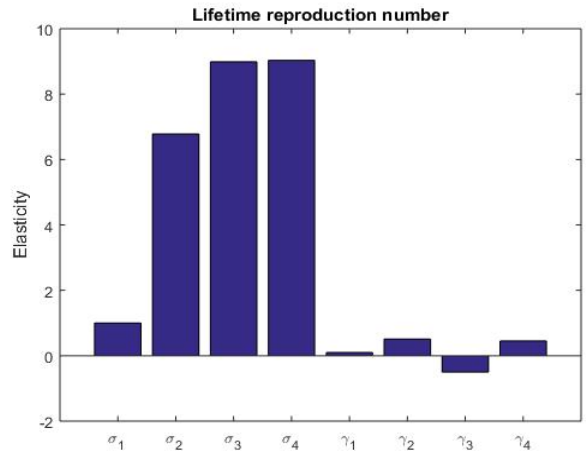

FIGURE 1. Elasticity of the lifetime reproduction number to each vital rate for the calf stage.

Figure 1 shows how the expected lifetime reproductive number for the calf stage, $N(4,1)$, is affected by each of the vital rates in our model. We see that the reproductive number for calves is most elastic to the survivorship rates, especially of the mature adults (σ_3) and the post breeding adults (σ_4), and less elastic to the transition rates. The figure shows that a 1% increase in either σ_3 or σ_4 results in an increase of approximately 9% in the reproductive number of the calves.

3.2. **Life expectancy.** Life expectancy is the average length of a whale's life and is essential to any population analysis. Each entry in the life expectancy vector E is the sum of the corresponding column in fundamental matrix (3.3). This gives us

$$E = \begin{pmatrix} 15.9487 & 16.6095 & 20 & 20 \end{pmatrix}. \tag{3.4}$$

The entries of E in (3.4) represent the life expectancies of each of the four stages of a beaked whale life cycle, starting with that stage. This means the first entry of E implies that the life expectancy for a calf is approximately 16 years. The third entry tells us that a mature adult will live, on average, an additional 20 years once an individual reaches that stage. The difference in life expectancies for calves and mature whales is a result of the higher mortality rates in calves. Since the mortality rates for adults and the post breeding adults are the same, their life expectancies are the same.

Since scientist are most interested in the life expectancy at birth [5], Figure 2 shows the elasticity of the life expectancy of a female calf. Again, we see that the life expectancy is most elastic to the survivorship rates and almost not affected by the transition probabilities.

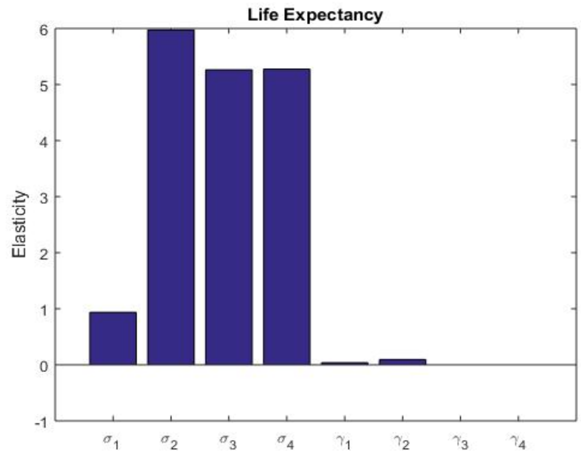

FIGURE 2. Elasticity of the life expectancy to each vital rate of a female calf.

3.3. **Asymptotic growth rate.** The asymptotic growth rate λ is one of the best indicators of the long term health of a population. Assuming the vital rates are invariant of time and environment, a population is considered growing when $\lambda > 1$ and decreasing when $\lambda < 1$. Using the vital rates in Table 1, we get that $\lambda = 1.00383$. This tells us that the beaked whale population is growing at a rate of 0.383% per year. Although the population is growing, it is at an extremely slow rate. This indicates that the population is very fragile and could be susceptible to any type of stochastic event such as an oil spill or other natural or man made disaster. Figure 3 (left) shows the sensitivity of λ to each of the vital rates. It can be seen that the asymptotic growth rate λ is most affected by the survivor probabilities of the mature adults and post breeding adults. As for the transition probabilities, λ is most affected by γ_2, which is the transition probability from the juvenile stage to the mature adult stage.

Now, we know there are uncertainties in the calculation in the vital rates in Table 1 and hence in the calculation of λ. Therefore, interval estimates for λ can be obtained by using bootstrap resampling to estimate the mean and confidence intervals of λ using $100,000$ bootstrap samples. From the estimates of mature adult survival rates of all species of beaked whales given in [22], we assume the adult survival rate σ_3 follows a normal distribution on the interval $[0.95, 0.96]$, with $\sigma_3 = \sigma_4$. We also assume that σ_1 follows a normal distribution on the interval $[0.798, 0.95]$. This interval represents a calf survival rate of roughly 1 to 4 times the adult mortality rate, where the 0.798 is the estimate of σ_1 from [22]. Figure 3 (right) gives the histogram for the bootstrap values of λ. We see that the average asymptotic growth rate is approximately 1.0028, and using the percentile confidence interval method, we estimate the 95% confidence interval given by the $2,500$th and $97,500$th sorted bootstrap values of λ [9]. Thus, we get a confidence interval of $[0.9928, 1.0135]$. Note that for part of our confidence interval, we have $\lambda < 1$. This allows for the possibility of a declining population and gives more evidence to the fragility of the population.

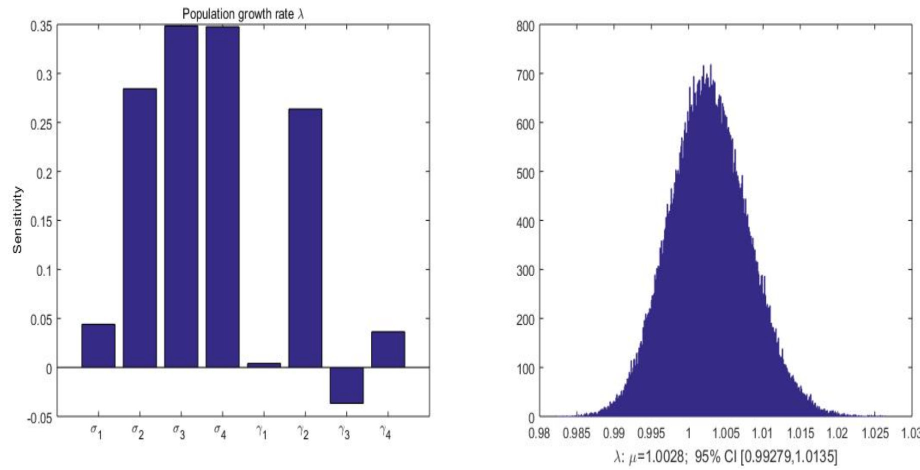

FIGURE 3. (left) Sensitivity of the asymptotic growth rate to each vital rate; (right) Histogram of the asymptotic growth rate, assuming parameters follow a normal distribution.

3.4. **Inherent net reproduction number.** Another important demographic characteristic of a population is the inherent net reproduction number R_0. This value is the expected number of offspring, per calf, over the course of its lifetime. Similar to λ, a population is considered growing when $R_0 > 1$ and decreasing when $R_0 < 1$. One way to think of this is that if $R_0 < 1$, a calf is not expected to replace itself in the population, thus leading to a declining population. In order to calculate R_0, we must first calculate the generation growth matrix. The product of the fertility matrix F given by (3.2) and the fundamental matrix N given by (3.3) gives us the generation growth matrix FN given by

$$FN = \begin{pmatrix} 1.1046 & 1.2273 & 2.4974 & 2.2535 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}. \tag{3.5}$$

The dominant eigenvalue of matrix (3.5) gives us the inherent net reproduction number R_0. Thus, we get $R_0 = 1.1046$. Calculating the elasticity and the sensitivity of R_0 to the vital rates, we see in Figure 4 that just like with λ, R_0 most affected by the survivor probabilities of the mature adults and post breeding adults.

We can obtain interval estimates for R_0 using the same bootstrap resampling method used for λ. Using the same intervals for the vital rates following a normal distribution, Figure 5 gives the histogram for the bootstrap values of R_0. We see that the average inherent net reproductive number is approximately 1.0899, with a 95%

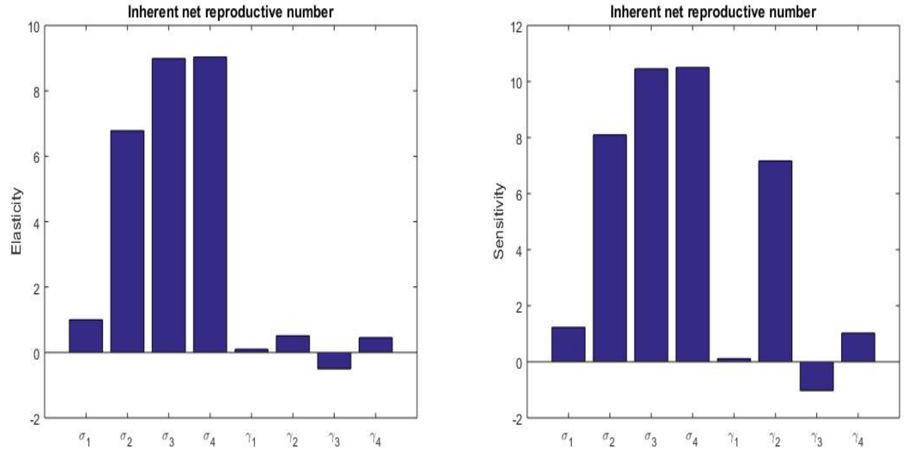

FIGURE 4. (left) Elasticity and (right) sensitivity of the inherent net reproductive number.

confidence interval of $[0.8085, 1.4365]$. Again, we see from the values in our confidence interval that there is a possibility for R_0 to be less than one and the population to be declining.

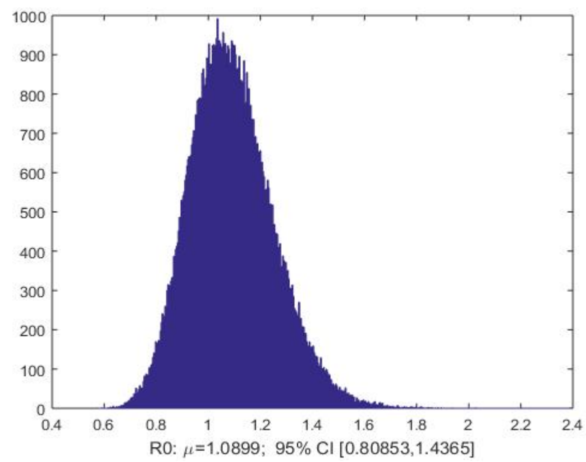

FIGURE 5. Histogram of the inherent net reproductive number, assuming parameters follow a normal distribution.

4. **Discussion**

Using what little information we can find in the literature and various techniques, we get reasonable estimates for vital rates and deterministic values for model (2.3). Using these estimates we were able to calculate several important demographic characteristics of model (2.3) such as the life expectancy, the asymptotic growth rate (λ), and the inherent net reproductive number R_0. We then perform sensitivity and/or elasticity analysis of the model parameters. We can see from Section 3 that the survival rates have the most influence on these values, with the model being most sensitive to the survival rate of the adults and post breeding adults and less sensitive to the transition rates. This tells us that an increase in the mortality rates of the adult females could have a negative affect on the population as a whole.

The value of the asymptotic growth rate, $\lambda = 1.0038$, along with $R_0 = 1.0899$, tells us that our population is growing slowly and could potentially be very fragile. Even with the uncertainty in the estimation of the parameters, we were able to get interval estimates for λ and R_0 which show the possibility that the population of beaked whales could possibly be in decline. Therefore, any large stochastic events or smaller but more frequent events like seismic surveying and anthropogenic noise from military sonar could potentially decrease the population and drive it to extinction. This is of particular concern with the increased number of research articles, like the ones listed in the introduction, noting the possible link of the mass strandings of beaked whales to such events.

To quantify this fragility, we calculate how much reduction in the survival rate of the mature female, σ_3, it takes to drop the inherent net reproductive number R_0 below one, i.e. make the population start to decline. From model (2.3) and matrix (2.5), we can rewrite the model as

$$n(t+1) = A(\epsilon)n(t), \tag{4.1}$$

where ϵ is the rate of reduction and

$$A(\epsilon) = \begin{pmatrix} 0 & 0 & 0.25 & 0 \\ 0.9 & 0.8380 & 0 & 0 \\ 0 & 0.0870 & 0.5396(1-\epsilon) & 0.3657 \\ 0 & 0 & 0.4104(1-\epsilon) & 0.5843 \end{pmatrix}. \tag{4.2}$$

From the new model (4.1), we can calculate $R_0(\epsilon)$, which is the inherent net reproductive number with respect to ϵ. Using the same technique as in section 3.4 and matrix (4.2), we get

$$R_0(\epsilon) \approx \frac{0.008353}{0.007560 + 0.06795\epsilon}.$$

Figure 6 shows that if σ_3 is reduced by as little as 1.2%, R_0 would go below one and the population would start to decline. A reduction in σ_4, the survival rate of the post breeding adults, of roughly this same percent would also result in a declining population. If both σ_3 and σ_4 were reduced, it would only take about half of the previous reduction to drop R_0 below one.

In light of the Deepwater Horizon oilspill in 2010 and with the increased search for new petroleum deposits, the beaked whales of the Northern Gulf of Mexico are a particular population that could be affected by noise and chemical pollution. The Northern Gulf beaked whales are found living in close proximity to offshore oil and gas

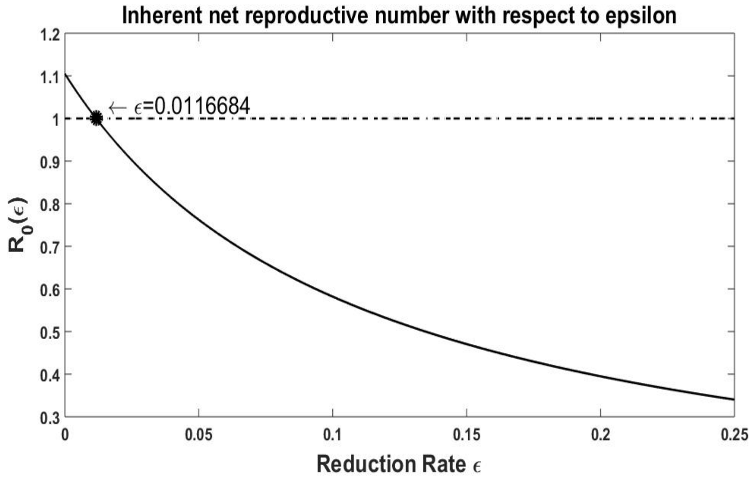

FIGURE 6. The graph shows at any reduction greater than 1.1668% in σ_3 will cause R_0 to be less than one.

exploration and in areas of current and future oil related activity. Also, the number of beaked whales in the Northern Gulf of Mexico is much smaller than the number of beaked whales found in other areas such as the Atlantic Ocean. For some species like the Cuvier's beaked whale, it is approximated that there are less than 100 of these types of whales in the Northern Gulf, where the number in the Atlantic is closer to 5000 [24]. Another indication of the fragility of this population is the potential biological removal, (PBR), which is the maximum number of animals, not including natural moralities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population. The PBR for the Cuvier's beaked whales in the Northern Gulf of Mexico is estimated to be 0.2, compared to a PBR of 50 for the Northern Atlantic Ocean Cuvier's beaked whales [23].

Hopefully, this paper will help guide and quantify future research into the current state of the beaked whale population and will help shed light on the urgency to develop more reliable vital rates for the population. This way, we can better determine the effects of human interference on beaked whales.

Acknowledgments

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