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Demographic analysis of sperm whales using matrix population models

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ABSTRACT

The focus of this study is to investigate the demographic and sensitivity/elasticity analysis of the endangered sperm whale population. First, a matrix population model corresponding to a general sperm 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. Extinction time probability distribution is also studied. The results show that the sperm whale population grows slowly and is potentially very fragile. The asymptotic growth rate is most sensitive to the survivorship rates, especially to survivorship rate of mature females, and less so to maturity rates. Our results also indicate that these survivorship rates are very delicate, and a slight decrease could result in an asymptotic growth rate below one, i.e., a declining population, leading to extinction.

1. Introduction

The sperm whale, *Physeter macrocephalus*, is the largest odontocete, or toothed whale (Rice, 1989), and can be found throughout the world's oceans, gulfs, and seas (Rice, 1989; Whitehead, 2002). The studies of sperm whale populations in the literature are dominated by the studies of the geographic structure of sperm whale populations, which in recent years have mainly been through genetic techniques and assessment of regional and global population estimates of sperm whales. The genetic studies, including (Lyrholm et al., 1999; Lyrholm and Gyllensten, 1998; Richard et al., 1996) and others, have used mitochondrial DNA, which is DNA inherited from the mother, and also nuclear microsatellite. Samples for these genetic studies can come from commercial catches, bycatches, historical artifacts, and strandings, just to name a few (Whitehead, 2003). The genetic analyses of Lyrholm and Gyllensten (1998) suggest that present-day sperm whale populations have very low mitochondrial DNA diversity and show little geographical differentiation over their global range.

In the assessment of regional and global population estimations, scientist use different techniques, such as catch-per-unit-effort analyses, length-specific techniques, mark-recapture techniques, acoustic data (Ackleh et al., 2012), and ship or aerial surveys (Whitehead, 2003). These techniques were used to study populations of sperm whales in the Gulf of Mexico (Fulling et al., 2003; Waring et al., 2009a,b), in the southern Australian waters (Evans and Hindell, 2004), in the Eastern Caribbean Sea (Gero et al., 2007), in the Northeastern (Barlow and Taylor, 2005) and Southern (Whitehead and Rendell, 2004) Pacific, in the Northern Atlantic (Waring et al., 2009a,b), in the Mediterranean Sea (Gannier et al., 2002) and in other waters around the world. These techniques, along with others, were also used by Whitehead (2002) to get estimates of the global population size and historical trajectory for sperm whales.

Even with all this research dedicated to sperm whales, very little is known about the sperm whale's population dynamics. There is a definite lack of research dedicated to the study of stage-structured population models applied to sperm whales. This is probably due to the lack of reliable estimates for the vital rates of sperm whales. Evans and Hindell (2004) suggest that techniques used to study smaller cetaceans, such as the bottlenose dolphins and orcas, and large baleen whales, such as the humpback and bowhead whales, are harder to apply to sperm whales. There are very few articles in the literature in which vital parameters are given for sperm whales, much less age-specific vital parameters needed to develop stage-structured models used to study these populations.

In this paper, we develop a stage-structured matrix population model for sperm whales. The parameters for our model were obtained from the limited information in the literature or by construction using other vital rates as in Doak et al. (2006) and techniques from Caswell (2001). We present the best and worst cases for these vital rates in terms of survivorship rates, along with the values that were used in the analysis of the population dynamics. We use our model and these parameters to construct the asymptotic

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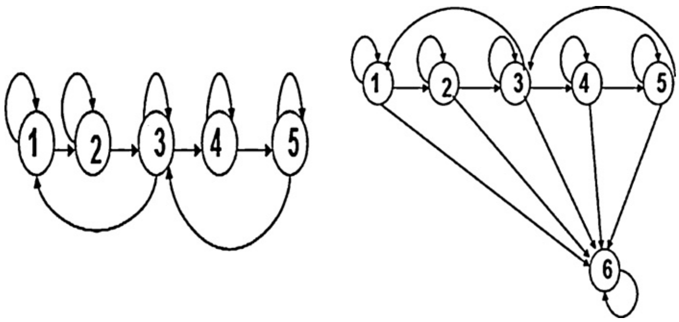

Fig. 1. Life cycle graph for female sperm whales with (right) and without (left) the consideration of death stage. Numbers represent different stages. 1: calf; 2: immature (juvenile); 3: mature; 4: mother; 5: post breeding; 6: mortality.

growth rate λ for the population. We also calculate other deterministic values for the population such as life expectancy, lifetime reproduction number, and the inherent net reproduction number R_0. We then perform sensitivity and elasticity analysis to each of the vital rates to see which ones affect these values the most. Also, we calculate the extinction time and distribution of sperm whales from the matrix population model, treating transitions and reproduction as independent events.

2. Stage-structured model and parameter estimations

In Section 2.1, we develop a stage-structured matrix model to describe the dynamics of the female sperm whale. The female population is divided into stages similar to those used by Fujiwara and Caswell (2001) for the North Atlantic right whale. In Section 2.2, we use techniques from Caswell (2001) and Doak et al. (2006) to construct vital rates for the female sperm whale. We will use these parameters in our model to study the dynamics of the population.

2.1. Stage-structured population matrix model

The life cycle of the female sperm whale is typical of most large whales. After calves are born, they are suckled by their mother for about 2 years (Best et al., 1984) and reach maturity at the age of 9 (Doak et al., 2006). The interbirth interval for sperm whales differs from 3–5 years (Boyd et al., 1999; Doak et al., 2006) to 4–6 years (Best et al., 1984; Rice, 1989; Whitehead, 2003) which includes a gestation period of 14–16 months (Evans and Hindell, 2004). Thus, we divide the female sperm whale population into five stages: calves (stage 1), juveniles/immature (stage 2), mature females (stage 3), mothers (stage 4) and post breeding females (stage 5). The life cycle for the female sperm whales is given in Fig. 1.

A mature female transits from stage 3 to stage 4 each time she produces a calf, and takes care of the calf throughout stage 4, thus the time taken for a female on stage 4 is the same as that for a calf to grow into an immature, which again is about 2 years for sperm whale (Best et al., 1984). After this 2 year period, the female sperm whale then goes into stage 5 where after the interbirth interval, the female can return to stage 3 to give birth to another calf. If the female is no longer able to reproduce due to age or other natural causes, the female will remain in stage 3. For our model and throughout the rest of the paper, we will take our time unit to be one year. Let $P_i = \sigma_i(1-\gamma_i)$ and $G_i = \sigma_i\gamma_i$, where σ_i is survivor probability of stage i and γ_i is the probability of an individual in stage i to move onto stage $i+1$ for $i = 1, \cdots, 4$. The transition probability from stage 5 to stage 3 is given by γ_5. Therefore, P_i gives the probability of surviving and staying in stage i, while G_i gives the probability of surviving and moving to stage $i+1$ for $i = 1, \cdots, 4$. G_5 gives the probability of surviving and moving to stage 3 from stage 5. From Caswell (2001) and Doak et al. (2006), we define

Table 1
Vital rates values.

Vital rates	Worst case	Estimated values	Best case
σ_1	0.8841	0.9070	0.9850
σ_2	0.8841	0.9424	0.9850
σ_3	0.9390	0.9777	0.9800
σ_4	0.9390	0.9777	0.9800
σ_5	0.9390	0.9777	0.9800
γ_1	0.4783	0.4732	0.4888
γ_2	0.1085	0.1151	0.1244
γ_3	0.2198	0.2586	0.3436
γ_4	0.4934	0.4920	0.4875
γ_5	0.4934	0.4920	0.4875

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

where T_i is the duration of stage i and λ is the population's asymptotic growth rate, i.e., the growth rate of the population at the stable stage distribution. Since γ_i is actually used in the calculation of λ, we first set λ to one. Then, as described in Caswell (2001), we use an iterative process to get better estimations of γ_i. With λ = 1, we calculate the projection matrix for our model. The eigenvalues of this projection matrix will yield a second estimation for λ, which we use to estimate γ_i again. We then repeat this process until we get a projection matrix whose entries are compatible with its own eigenvalues. This is how we obtain the estimated values for γ_i in Table 1. Now, we define the fertility number as

$$b_1 = 0.5\sigma_3\gamma_3\sqrt{\sigma_4}, \tag{2}$$

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 (Caswell, 2009). The 0.5 comes from the assumption that the sex ratio is about equal at birth (Whitehead, 2003). Thus, we obtain the following model corresponding to the life cycle shown in Fig. 1(left):

$$\mathbf{n}(t+1) = A\mathbf{n}(t), \tag{3}$$

where $\mathbf{n}(t)$ is a vector representing the population of female sperm whales at each stage. The projection matrix A is given by

$$A = \begin{pmatrix} P_1 & 0 & b_1 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & G_5 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix}. \tag{4}$$

2.2. Estimating model parameters

Despite the small number of references for vital rates of sperm whales in the literature, we estimate the birth, mortality, and transition rates for model (3) and (4). Sperm whale mortality is the least known aspect of a sperm whale's life history (Whitehead, 2003). In 1982, International Whaling Commission's Scientific Committee estimated the annual mortalities of 0.055 for female sperm whales and 0.093 for infants. However, according to the experts, these estimates, for the infants especially, were based on "extremely shaky evidence" (Whitehead, 2003). Whitehead (2001) provides an estimate of 0.021 for the annual mortality rate of female and immature sperm whales in the eastern tropical Pacific. Doak et al. (2006) give a minimum of 0.02 and a maximum of 0.061 for the annual adult