

A Comparative Analysis of Cetacean Vital Rates Using Matrix Population Modeling Analysis of Cetacean Vital Rates

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Abstract

*A modeling effort has been conducted in order to determine which vital rates are most important in determining the growth and sustainability of cetacean populations. An analysis of the elasticity and sensitivity of cetacean matrix population models suggests that: 1) Most whale populations appear to be most sensitive to changes in adult female survival and least sensitive to calf survival; 2) Most whale populations appear to be secondarily sensitive to changes in juvenile survival and growth; 3) Most whale populations, with the exception of North Atlantic right whales (*Eubalaena glacialis*), appear to be insensitive to changes in fecundity at any age; and 4) Adult female whales may be particularly sensitive to changes in foraging success. A risk assessment of anthropogenic impacts on cetacean populations based on the modeling conclusions would suggest that any increase in anthropogenic impacts in the marine environment which reduces adult female survival is to be avoided.*

Key Words: Cetacean, Vital Rate, Leslie matrix, Lefkovitz matrix, matrix modeling, elasticity

1. Introduction

1.1. Goals and Objectives

In 2005 the National Academy of Sciences U.S.A. proposed a model for the “Population Consequences of Acoustic Disturbances (PCAD)” (NRC 2005). PCAD (Figure 1) is a heuristic model that was created as a first attempt to trace the impacts of acoustic disturbances through the life history of a cetacean population and then to determine the consequences to the population. The model has five levels of variables that are related by four transfer functions. The variables include sound in the marine environment, behavioral changes in response to sound, effects on life functions such as feeding, breeding, and survival, subsequent effects on vital rates, and the consequent impacts of these effects on populations of cetaceans. The second stage of the PCAD model attempts to evaluate how changes in behavior might affect life functions that are critical to population dynamics. With the exception of direct impacts on life, the exact relationship of these functions to life-history characteristics is unclear (NRC 2005). The final stages of the model relate changes in life functions to impacts at the population level. These relate changes in life functions to changes in vital rates of individuals and populations and are largely unknown (NRC 2005). In an attempt to clarify how changes in life functions and vital rates influence cetacean population dynamics, a comparative modeling study has been conducted.

Insert Figure 1 about here.

Our objective was to synthesize and summarize the results of population modeling with respect to the relative importance of different vital rates in determining cetacean population trends and stability.

Our goal was to determine which vital rates are most important to determining the growth and sustainability of cetacean populations. We also wanted to determine how much each vital parameter can change before a change in population trend would be expected, using elasticity and sensitivity analyses of cetacean population models.

1.2. Matrix Population Models

One of the most popular and effective tools for modeling population growth is the matrix population model (van Groenendael et al., 1988; Caswell, 1996a, 2001). As originally formulated, these models were based on an age-structured population with an annual time step (Lewis, 1943; Leslie, 1945). Lefkovich (1965) demonstrated that the matrix approach would work just as well with stage- or size-based models with variable time steps. All of the matrices constructed in this paper are Lefkovich matrices. Although such models can be used in many ways, e.g. incorporating harvesting (Doubleday, 1975), pertinent applications include the calculation of population growth rate and age- or stage-specific sensitivities or elasticities to indicate factors that most affect population growth and stability (Mills et al., 1999). The intrinsic rate of natural increase (r in the logistic growth equation) is equal to the natural logarithm of the dominant eigenvalue of a population projection matrix (Caswell, 2001). The sensitivity of the rate of population increase to a demographic parameter is defined as the incremental change in population growth due to an incremental change in the parameter (Link & Doherty, 2002; Caswell, 2001). The sensitivity is also proportional to the product of the reproductive value (see below) of a given stage and the abundance of the next stage in the stable age distribution (Caswell, 1978, 1996a). Another interpretation is that the population growth rate is most sensitive to life history parameters describing the production of high reproductive value individuals by members of abundant age classes (Caswell, 1978).

One of the more exciting aspects of matrix projection models is the possibility of linking sensitivities with quantitative genetic theory (van Groenendael et al., 1988). This elevates such models from being largely descriptive or forecasting tools into the more speculative realm of evolutionary theory. This link was most clearly elucidated by Lande (1982) in his version of the secondary theory of natural selection that described the rate of change in the phenotypic mean of a set of traits as being dependent upon a vector of selection gradients on the traits. This vector is precisely the eigenvalue sensitivities described above. Those sensitivities, which can be calculated directly from the population projection matrix, give the direction and intensity of selection on the life history characteristics of the organism (van Groenendael et al., 1988).

Another way to analyze population projection matrices involves the use of elasticities. The elasticity of a matrix parameter is the log proportional change in the population growth rate following a log proportional change in that parameter (Link & Doherty, 2002; Caswell, 2001; van Tienderen, 2000; Benton & Grant, 1999). Elasticity analysis has become a major avenue for the analysis of population projection matrices, and was the subject of a special series of articles in the journal *Ecology* in 2000 (Heppell et al., 2000a). Elasticities are given by the right eigenvector of the population projection matrix, and the stage-specific reproductive value (see below) is given by the left eigenvector of the population projection matrix (Caswell, 2001; Heppell et al., 1996). The elasticity values sum to one (1.0) and thus can be used to compare the relative impact of stage-specific survival, growth, and fecundity on population growth (de Kroon et al., 2000). Elasticities are a measure of how much the population growth rate changes with an infinitesimal change in a matrix element, and extrapolating from small to large changes assumes that the relationship between population growth rate and the matrix element is linear, which is unlikely for mathematical and biological reasons (Benton and Grant, 1999).

Fisher (1930) developed the concept of reproductive value in order to evaluate the relative contributions of individuals of different ages or stages to population growth, and conversely to evaluate the relative importance of fitness events at different times in the life history. Leslie (1945) developed the calculation of this quantity via operations on the population projection matrix. Reproductive value combines the two essential life history parameters, fecundity and survivorship, into a single value that takes into account an individual's proportionate contribution to the future population (Goodman, 1982).

An elasticity pattern is composed of the relative contributions of matrix entries to population growth that are grouped in biologically meaningful ways for comparative analysis (van Tienderen, 2000). For example, in cetacean populations it is often desirable to compare the relative contributions of fertility, juvenile survival, and adult survival (Heppell et al., 2000b). Both fertility and juvenile survival elasticities are strongly correlated with age at maturation, mean fertility, generation time and life expectancy. However, sensitivities and elasticities of matrix elements do not take covariation in these life cycle components into account.

A method to calculate “integrated” sensitivities and elasticities in order to measure the net effect of a matrix element was presented by van Tienderen (1995). Populations, such as those of marine mammals, with high mean adult survival rates, have low fertility elasticities and higher adult survival elasticities, with juvenile survival elasticity dependent upon the proportion of life spent as a juvenile (Heppell et al., 2000b).

1.3. Modeling Overview

Lefkovitch population projection matrices for five different species of cetaceans, with both odontocete and mysticete representatives, have been developed using data from the literature. Leslie and Lefkovitch matrices are useful in predicting the efficacy of different management approaches on increasing population growth rates. Leslie and Lefkovitch matrices, which are only concerned with females of the species, model populations that are closed to migration. A population modeled by a Lefkovitch matrix is divided into stages or age-classes with each individual time step represented by a vector containing elements for each stage (Caswell, 2001). Each element in this vector indicates the number of individuals in that specific stage. The population projection matrix (PPM) is a square matrix which includes the same number of rows and columns as the population vector contains elements. A typical Leslie matrix (Table 1) commonly denoted as A , is arrayed with fecundity values (F-values) in the top row, and survival rates (S-values) in the subdiagonal. In Lefkovitch matrices, more matrix elements can be included to represent transitions between different life stages. Probabilities of remaining in the same stage- or age-class (i.e. stasis) are often represented in the matrix diagonal.

Insert Table 1 about here.

To generate subsequent population vectors for future time steps, the current population vector (P), is multiplied by the matrix, such that $P_{t+1} = A$ times P_t . Using the matrix exponential the future age structure of the population at any future time (t) can be modeled as $P_t = P_0 e^{At}$ (Caswell, 2001). Each matrix is defined by a characteristic polynomial equation of the same order as the number of columns and rows in the matrix (Caswell, 2001). The roots of this equation are known as eigenvalues, and generally only one of these roots, the dominant eigenvalue (or λ) is positive. The other remaining roots are typically negative or imaginary numbers. The dominant eigenvalue is used to describe a population’s growth rate. A dominant eigenvalue greater than one represents a growing population, while a dominant eigenvalue less than one characterizes a declining population. Additionally, the natural log of the dominant eigenvalue is r , the intrinsic rate of natural increase, an important parameter in population ecology. Each eigenvalue of a matrix is associated with an eigenvector. The right and left eigenvectors of a matrix A , w and v , respectively, represent the stable age distribution and reproductive values of the population. van Groenendael et al. (1994) developed an alternative method of examining life histories based on elasticities. This method utilizes the limit properties of population projection matrices. This process, known as ‘loop analysis’, recognizes that vital rates are part of life history pathways, which themselves form loops within a complete life cycle graph (Figure 2).

Insert Figure 2 about here.

A complete loop in this graph, for example, could be an organism in Stage 1, growing to Stage 2 and then 3, and then reproducing to contribute a calf to Stage 1. The elasticities of these loops can be derived from the elasticities calculated in population projection matrices in an explicit manner. To conduct a loop analysis, all potential life cycle loops in a population are identified. The sum of the elasticities entering a node is assumed to equal the sum of the elasticities leaving that same node, and all elasticities are presumed to sum to one (1.0) (Caswell, 2001). All unique arcs in each loop are acknowledged. Because the elasticities of the population growth rate for all arcs in a loop are presumed to be identical, all arcs in each loop therefore must have the same elasticity as that of the unique arc in each loop. This elasticity value, then, is assigned to all arcs in the loop. The elasticities for all arcs in a loop are summed to determine the overall loop elasticity (Caswell, 2001). This population demographic tool, then, can provide meaningful analysis on the importance of varying life history paths in specific populations (van Groenendael et al., 1994). The results of loop analysis help to clarify the relative contributions of alternative life history pathways to the population growth rate.

2. Materials and Methods

A series of simplified population projection matrices were developed utilizing previously published data. After parameterization of the population projection matrix, the sensitivities, elasticities, dominant eigenvalue, population growth rate, and cohort specific reproductive values and stage age distributions were calculated using the Excel add-in PopTools, developed by Greg Hood at CSIRO in Australia (<http://www.cse.csiro.au/poptools>).

2.1. Killer Whale

The first species to be modeled was the killer whale, using data from Brault & Caswell (1993). The model constructed here was identical to that of Brault & Caswell (1993); these calculations were conducted as a check to verify that our estimates yielded results identical to those published previously. Killer whale population dynamics were examined using a stage-classified model (Figure 3), which depicts killer whale population structure much more easily than does an age-based model, as most killer whale populations do not contain enough individuals to accurately estimate age-based model parameters. Males were excluded from the analysis, as they do not provide reproductive or parental benefits to population growth. Four stage classes were included in this analysis: yearlings (first-year animals), juveniles (immature individuals over one year of age), mature females, and senescent females (Table 2). To define maturity, a female must have been viewed with a calf. Similarly, if a female has not been seen with a calf in over ten years, senescence is assumed to have begun at the start of the ten-year period (Brault & Caswell, 1993).

Insert Figure 3 about here.

Insert Table 2 about here

2.2. Bottlenose Dolphin

A model was then constructed for the bottlenose dolphin using data from Stolen and Barlow (2003). Four stage classes were derived by collapsing data from their life table (Figure 3), with Stage 1 being calves, Stage 2 being juvenile females (1-9 years of age), Stage 3 being young breeding females (10-20 years of age), and Stage 4 being older breeding females (> 20 years of age). Life table data for age-specific fecundities were summed to arrive at a fecundity for a specific multi-year life stage. Life table data for age-specific survival were multiplied to yield a survival probability for a specific multi-year life stage. Mortality of the younger age groups was relatively high and then decreased until around age 15. Fecundity rates peaked during the second decade of life and declined with age after that (Table 2).

2.3. Sperm Whale

The model used to examine the population dynamics of sperm whales was similar to that used for the killer whale, i.e. yearlings, juveniles, mature females, and senescent females (Figure 3). The population projection matrix was parameterized using data from Tiedemann & Milinkovitch (1999) and Evans & Hindell (2004) (Table 2) after condensation as described above for the bottlenose dolphin.

2.4. Humpback Whale

The model used to examine the population dynamics of humpback whales (Figure 3) was similar in structure, but not in age category, to that used for the bottlenose dolphin, i.e. Stage 1 being calves, Stage 2 being juvenile females (1.5-3.5 years of age), Stage 3 being young breeding females (4.5-9.5 years of age), and Stage 4 being older breeding females (10.5-34.5 years of age). Data were taken from a life table in Barlow & Clapham (1997) and condensed as before (Table 2).

2.5. North Atlantic Right Whale

The life cycle model used to simulate the population dynamics of North Atlantic right whales was considerably different from the models used above (Figure 3). Stage 1 was calves, Stage 2 was juveniles, Stage 3 was reproductively capable females, and Stage 4 was females with calves. This model is similar to that used by Fujiwara & Caswell (2001), except that they included another stage representing death. Their data were used to parameterize the population projection matrix. Additionally, there were no fecundity terms in the top row of the population projection matrix as fecundity was represented by flows from Stages 2 and 3 to Stage 4 (Table 2).

3. Results

3.1. Killer Whale

The dominant eigenvalue of the killer whale population projection matrix represents the population growth rate, here equivalent to 1.025 (Table 3). This value is identical to that calculated by Brault & Caswell (1993). A dominant eigenvalue greater than 1 indicates that this population is growing. The log of the dominant eigenvalue represents r , the intrinsic rate of increase for the killer whale population, 0.025 in Table 3, again identical to that calculated by Brault & Caswell (1993).

Insert Table 3 about here

For the killer whale, the probability that a female remains in Stage 3 (breeding adult) had the highest sensitivity (0.579), followed by the probability that a female moves from Stage 2 to Stage 3 (i.e. matures from the juvenile stage to the adult stage; 0.567) suggesting that these vital rates are most subject to natural selection (Table 4).

Insert Table 4 about here

The probability that a female remains in Stage 3 had the highest elasticity (0.538), suggesting that this vital rate contributes most to the rate of population growth, and that a 1% change in this vital rate would increase population growth by 0.54%. The probability that an animal remains in stage 2 (juvenile in this case) had the second highest elasticity (0.336) suggesting that a 1% change in this vital rate would increase population growth by 0.34% (Table 5).

Insert Table 5 about here

The right eigenvector of the population projection matrix illustrates the stable stage structure of the killer whale population (Table 6), while the left eigenvector demonstrates reproductive values of the group (Table 7).

Insert Table 6 about here**Insert Table 7 about here****3.2. Bottlenose Dolphin**

The dominant eigenvalue of the bottlenose dolphin population projection matrix was 1.067 yielding a population growth rate of 6.4% per year (Table 3), close to that of 4.6% per year estimated by Stolen & Barlow (2003). For the bottlenose dolphin, the survivorship of older females had the highest sensitivity (0.717) and elasticity (0.671), suggesting both that this vital rate is most subject to natural selection in this population, and that a 1% increase in this parameter would result in a 0.67% increase in population growth rate (Tables 4 and 5). This stage was also predominant in the stable age distribution (71.7) (Table 6). All stages had similar reproductive values (Table 7).

3.3. Sperm Whale

The dominant eigenvalue of the sperm whale population projection matrix was 1.110 yielding a population growth rate of 10.4% per year (Table 3). The probability that a juvenile female grew into an adult female had the highest sensitivity (1.262), with the probabilities that juvenile and adult females survive within their stage having the next highest sensitivities (0.451 and 0.455 respectively). This suggests that all of these vital rates are subject to natural selection (Table 4). However, the probabilities that juvenile and adult females survive within their stage had the highest elasticities (0.316 and 0.324 respectively), suggesting that a 1% increase in either of these vital rates would cause a 0.32% increase in population growth (Table 5). Juvenile females were most abundant in the stable age distribution (62.1%) (Table 6) but adult reproductive females had the highest reproductive value (53.6) (Table 7).

3.4. Humpback Whale

The dominant eigenvalue of the humpback population projection matrix calculated here was 1.13 (Table 3), close to that of 1.065 calculated by Barlow & Clapham (1997). The population growth rate was 12.1% per year in the current analysis, as compared to 6.3% for Barlow & Clapham (1997). As above, this difference in population growth rate can likely be attributed to combining ages into discrete life stages (this model) as opposed to the strictly age-based model of Barlow & Clapham (1997). The survival of older breeding females had the highest sensitivity (0.694) and elasticity (0.615), suggesting both that this vital rate is subject to the greatest selection pressure, and that a 1% increase in this vital rate will increase population growth rate by about 0.62% (Tables 4 and 5). Older females comprised almost 2/3 of the stable age distribution (Table 6) and older breeding females had the largest reproductive value (29.2), followed closely by young breeding females (26.0) and juvenile females (25.2) (Table 7).

3.5. North Atlantic Right Whale

The dominant eigenvalue of the population projection matrix was 0.999 (Table 3), similar to the value of 1.01 determined by Fujiwara & Caswell (2001). The intrinsic rate of increase of the population was found to be -2.16×10^{-5} (Table 3), compared to 9.96×10^{-3} as determined by Fujiwara & Caswell (2001) and within their confidence interval.

The fecundity and survival of mature females had the highest sensitivity values (0.671 and 0.637 respectively), suggesting that these vital rates are under the highest degree of natural selection (Table 4), and the fecundity of mature females had the highest elasticity (0.282) suggesting that a 1% increase in this vital rate would increase population growth by about 0.3% (Table 5). These results are consistent with those of Fujiwara & Caswell (2001) who suggest that increased mortality of adult females can explain the declining population size, and that preventing the death of only two adult females per year could increase the population growth rate to replacement (sustainable) levels. A recent rise in mortality rate has increased concern for the survival of this species in the western North Atlantic and led to pleas for immediate changes in management of this species focusing on reducing human-caused mortality (Kraus et al., 2005).

4. Discussion

In four of the five species examined here (killer whale, bottlenose dolphin, sperm whale, and right whale) adult female survival had the highest elasticity. This suggests that this vital rate is most important in governing population growth or decline, and that this relationship is a linear one, such that a given increase or decrease in adult female survival will cause a corresponding increase or decrease in adult female survival. Thus, any environmental or anthropogenic impact on this vital rate will likely have a large impact on population growth in these species.

However, another perspective is that other vital rates, such as survival of younger, non-reproductive age classes and/or female fecundity, are less important in determining overall population increase and decline, and thus these vital rates are more resilient to change. Therefore, any increase in anthropogenic noise in the marine environment that reduces adult female survival, for whatever reason, is to be avoided, whereas anthropogenic noise that impacts other vital rates might be better tolerated by these species. In the case of the sperm whale, reproductive female survival had the highest elasticity, and using the same logic as above, one could conclude that any impact from anthropogenic noise on this vital rate in this species is to be avoided if possible.

With respect to reproductive value, the picture is somewhat different. Adult reproductive females had the highest reproductive value in killer whales, sperm whales, humpback whales, and right whales. It is of interest that the vital rate with the highest elasticity for sperm whales was juvenile female survival while the stage class with the highest reproductive value is adult females. This suggests the value in conducting both analyses. Interestingly for the bottlenose dolphin, there was very little difference in reproductive value among the four different life stages modeled here.

Reproductive values (RVs), the left eigenvector of the dominant eigenvalue in a PPM, are complex, taking into account timing, survival, and reproduction in a population. RVs are typically low in the first population stage, representing both the probability that a calf or yearling will not survive before reproducing, and also the delay before the calf or yearling reaches an age where reproduction is possible (Caswell, 2001). In increasing populations (which include all cetaceans examined except the right whale), delays before reproduction are important because the value of delayed offspring is reduced by the larger, and growing, population size when these organisms are produced. RVs decline with age eventually in all species, though these trends may not be identifiable if stages or ages are not examined in great detail or resolution.

Loop analyses conducted for all cetacean species produced consistent results. In all species except the sperm whale, the small loop including reproductive female survival demonstrated the highest elasticity (Table 8). These findings reiterate that adult female survival is essential to cetacean population growth rates. The highest elasticity value determined in the sperm whale loop analysis was represented by the loop containing young female survival, fecundity, and calf reproduction and growth. This result implies that young reproductively active female whales are very important to the stability of sperm whale populations. This same loop had the third highest elasticity for the killer whale (0.122).

Loop analysis can clarify the relative contributions of alternative life history pathways to the population growth rate (van Groenendael et al., 1994). For example, for the bottlenose dolphin and humpback whale, the loop consisting of the entire life cycle of a female (i.e. Calf → Juvenile → Young Female → Old Female → Calf) had the second highest elasticities (0.182 and 0.317 respectively), indicating the importance of female survival, maturation, and reproduction throughout the life span of the female to population growth rate in these species.

For the North Atlantic right whale, the loop including mature female survival and reproduction (i.e. Female with calf → Mature female → Female with calf) had the second highest elasticity, emphasizing the importance of adult female survival and reproduction to population growth in this species.

For the killer whale, sperm whale, and North Atlantic right whale, the survival of younger or juvenile females had the second and/or third highest sensitivities, suggesting the importance of the survival of this cohort to population growth rate in these species.

Insert Table 8 about here

In all cetacean species examined, adult female survival demonstrated the highest elasticity. The implication is that adult female survival is the most important vital rate influencing the population growth or decline of these cetacean species. This relationship is assumed to be linear, so that a subsequent increase or decrease in adult female survival should yield a corresponding increase or decrease in the population growth rate. For cetacean management, then, any disturbance of this vital rate, anthropogenic, environmental, or otherwise, can greatly influence the health of the cetacean population. Juvenile survivability was found to be secondarily important in relation to population growth, and has been demonstrated as a critical destabilizing feature in other marine mammal populations, such as the Steller sea lion (York et al., 1994). As such, juvenile survival may be considered an important factor in all marine mammal population studies.

An important aspect of sensitivity analysis is that the sensitivities calculated from PPMs estimate the direction and intensity of selection on the life history characteristics of the organism (van Groenendael et al., 1988). For example, the probability that a female killer whale remains in Stage 3 (breeding adult) had the highest sensitivity (0.579), followed by the probability that a female moves from Stage 2 to Stage 3 (i.e. matures from the juvenile stage to the adult stage; 0.567), suggesting that these vital rates involving mature females are most subject to natural selection. The various matrix transitions representing reproduction and juvenile survival had lower sensitivity values, suggesting that these vital rates are less subject to natural selection. The pattern was similar for bottlenose dolphins where the survivorship of older females had the highest sensitivity (0.717) and reproduction by older females has the next highest sensitivity value (0.585). All other PPM transitions had much lower sensitivity values. Likewise, for the humpback whale, the survival of older breeding females had the highest sensitivity (0.694) suggesting that this vital rate is subject to the greatest selection pressure while mature female reproduction had the second highest sensitivity and is thus also under a significant level of natural selection. Mature female survival and fecundity have very similar sensitivity values for the North Atlantic right whale, emphasizing that both of these vital rates appear to be under similar levels of natural selection, while survival and maturation of juvenile females also have similar, but lower, sensitivities and thus levels of natural selection.

The situation is somewhat different for the sperm whale, where the probability that a juvenile female grew into an adult female had the highest sensitivity (1.262), with the probabilities that juvenile and adult females survive within their stage had the next highest sensitivities (0.451 and 0.455 respectively) indicating that all of these vital rates are subject to natural selection. For sperm whales, PPM transitions representing reproduction had lower sensitivities, suggesting that for this species, fecundity is under less natural selection than female survival. The various sensitivity analysis methods utilized here are analytical tools intended primarily to determine which vital rate most affects the rate of population growth, with the implication that management activities directed at the most sensitive or elastic parameter will be the most effective way to increase population growth rate (Fefferman & Reed, 2006). However, it is prudent to avoid simple interpretations of the so-called most sensitive or most elastic parameter when making management decisions. De Kroon et al. (2000) summarize some of the concerns, including: 1) the assumption that matrix values remain stable over time, 2) not all vital rates can be altered to the same extent by management, and 3) vital rates change with population size and growth rate.

Thus, the details of how sensitivity and elasticity and life-stage simulation analysis should be interpreted with respect to manipulating population growth rate are not readily transparent (Grant & Benton, 2000; Fefferman & Reed, 2006). One potential source of confusion is that some analyses determine the sensitivity or elasticity of population growth rate to alteration of the matrix elements (as was done here) rather than to the vital rates themselves. Because the top row of the population projection matrix is a composite of vital rates, it is not clear how they can be manipulated if one was to be determined to be the most sensitive. One solution to this dilemma is to calculate the sensitivity of population growth rate to vital rates, rather than matrix elements, using partial derivatives (Mills et al., 1999).

Another potential limitation to current sensitivity and elasticity analyses is that by focusing on maximizing population growth rate, the solutions are only valid for populations with stable age distributions. Although the dominant eigenvalue can be determined for any population projection matrix, when the age distribution is not stable, it no longer represents the growth rate of the population (Fefferman & Reed, 2006). If the dominant eigenvalue (or r) is a good surrogate for fitness, and small changes in a vital rate, such as survival, cause large changes in population growth, we would expect natural selection to act most strongly on that particular trait. Thus, we expect proportional sensitivities to measure selection pressure on particular traits (van Groenendael et al., 1988; Benton & Grant 1999; Doherty et al., 2004). Pfister (1998) found that the vital rates to which population growth was most sensitive were also those that were the least variable. This result was supported by Gaillard et al. (1998, 2000) who suggested that vital rates to which population growth was less sensitive were subject to greater variability and more affected by density-dependent factors or environmental stochasticity (see above).

However, these results rest upon three methodological deficiencies: 1) elasticities may not be appropriately scaled, especially in the case where parameters (such as survival) are bounded by 0 and 1 (Link & Doherty, 2002). This problem arises because the means and variances of the vital rates are not independent and log-scaling, as in the calculation of elasticity, does not eliminate the dependence (Link & Doherty, 2002); 2) estimates of matrix parameters, such as survival, often do not account for the probability of detection, leading to biased estimates. Similarly, age at maturation has been suggested to be an important vital rate (Heppell et al., 2000b); however, estimates of age-specific breeding probability corrected for survival and detection probability are lacking; and 3) the temporal variation in vital rates and their elasticities is negatively correlated, i.e. the vital rates to which population growth are most sensitive are least variable temporally (Pfister, 1998; Heppell et al., 2000b; Sæther & Bakke, 2000). Additionally, the distinction between biological process variation (the process of interest) and sample variation (due to the estimation process) is often overlooked (Doherty et al., 2004). Sensitivities and elasticities make linear approximations of the usually non-linear relationship between the matrix elements and population growth (Carslake et al., 2008). To overcome this difficulty, Caswell (1996b) and Carslake et al. (2008) recommend the use of the second derivatives of the elasticities to evaluate the relative importance of different vital rates to population growth.

In a study designed to overcome the limitations discussed above, Doherty et al. (2004) constructed population projection matrices for the red-tailed tropicbird (*Phaethon rubricauda*), an example of an extremely K-selected seabird. They scaled their sensitivity analysis by variance for parameters bounded by 0 and 1, and found that population growth rate was most sensitive to adult survival, followed closely by prebreeding survival, and much less sensitive to reproductive success and age-specific breeding probabilities. These results supported previous work by Pfister (1998) and Heppell et al. (2000b). Doherty et al. (2004) found equivocal support for the prediction that population growth rate is most sensitive to vital rates with small temporal variances, and suggested that previous work supporting this prediction results from high survival estimates near the upper boundary of 1 and thus should not be interpreted as a consequence of canalization by natural selection (Gaillard & Yoccoz, 2003). Doherty et al. (2004) also did not find support for the prediction that effects of environmental stochasticity (e.g. an ENSO event) would be detected in vital rates to which the population growth was least sensitive (Gaillard et al., 1998, 2000).

Additionally, matrix sensitivity analyses only reveal long-term solutions to increasing population growth rate. It would be valuable, in contrast, to have an analytical method that identifies which matrix element or vital rate should be increased in order to achieve an increase in population growth rate in the near term. One reason for this is because funding, social, or personnel constraints often limit the duration of management actions and activities. Another scenario where this might be valuable is in the management of species with small populations that are vulnerable to demographic or environmental stochasticity (Fefferman & Reed, 2006).

Fefferman & Reed (2006) present a new approach, vital rate sensitivity analysis, which is designed to identify the vital rate upon which management activities would have the greatest impact on population growth rate. Their approach is effective for both stable and non-stable age distributions, and allows for the differentiation of short-term and long-term population management activities. Wisdom et al. (2000) developed life-stage simulation analysis, a simulation method useful for analyzing the potential effects of vital rates on population growth that employs characteristics of both prospective and retrospective forms of matrix perturbation analysis.

4.1. Relevance to Risk Assessment

The work here is relevant to risk assessments designed to protect populations of marine mammals. Population modeling can obviously be used to identify life stages and vital rates that are more sensitive and have higher elasticity for different species. Clearly, mitigation of significant risks to survival of individual animals, particularly reproductive adults, would be a high priority, and survival of juveniles can have high elasticities for certain species. Specific recommendations to reduce risk include avoiding any increase in anthropogenic noise in the marine environment that reduces adult female survival, for any reason. Population modeling may not be able to reduce risk in the near term because it may be impossible to detect the impact of a change in a population vital rate on population growth due to the uncertainties inherent in the estimates, because such a change may be less than the confidence interval around the estimates of the rate of growth of most marine mammal populations.

Additionally, sensitivity and elasticity analyses of marine mammal population models predict linear changes in marine mammal population growth rates caused by linear changes in vital rates, and thus do not indicate thresholds within which vital rates can change without altering population growth rates. Since population modeling can help identify the most sensitive vital rates, the method also lends itself to identifying which transfer functions in the PCAD framework may be the highest priority to develop or design mitigation measures in managing risk with a qualitative understanding. For example, mitigation measures focused on the feeding of reproductive females may be more important than measures targeting the feeding of males. However, although population models can assist in identifying strategies to reduce risk, these strategies may not be feasible because: 1) many vital rates cannot be measured with sufficient accuracy and precision, and 2) the difficulty in partitioning the effects of anthropogenic impacts from other impacts on vital rates.

4.2. Future Research Directions

Cetaceans have many important roles in aquatic ecosystems (Bowen, 1997). They are the major consumers of production at most trophic levels, ranging from primary production all the way to top predators. Because of their large size and abundance, they are thought to have a major influence on the structure of marine ecosystems. Marine mammals rank second to fish in the total consumption of biomass in many systems, and some species of cetaceans may consume a greater quantity of prey than all human fisheries combined (Bowen, 1997). Marine mammals contribute to nutrient recycling by virtue of consuming biomass in one region and defecating in another. Even after death, whales fall to the ocean floor and thus contribute nutrients to benthic communities. Some cetaceans even modify the benthos with their feeding activities. Cetaceans also have top-down effects on the populations of their prey and upon the primary producers upon which their prey depend. Additionally, cetaceans may be the repositories of nutrients in their ecosystems by sequestering them, thus buffering short-term fluctuations in resource availability (Bowen, 1997). All of these processes and impacts of cetaceans are poorly characterized and more research is needed to elucidate these and other ecological roles of marine mammals.

With respect to the growth or decline of cetacean populations and anthropogenic impacts, this literature review and modeling effort has identified several key vital rates that deserve more investigation and focus. The first, and most important, is the survival of adult females and the factors influencing this survival, such as the relation of foraging ability and efficiency to survival. Second is the fecundity of adult females. Third is juvenile survival, except for special cases, such as the Steller sea lion, where it is likely most important. It is imperative to note that most population projection models are based on females only, and males become important only as sources of sperm to maintain fecundity. However, there may be times, such as with small, highly endangered species and populations, where males may become limited, causing a reduction in fecundity. Something similar to this may have occurred with the AT1 killer whale pod in Prince William Sound, Alaska (Matkin et al., 2008).

Clearly more focus is needed on activities that increase the quality of population and vital rate estimates, increasing their precision and accuracy, and decreasing their uncertainty. There is more today that we do not know than we know, and this lack of information limits both the ability to properly manage cetacean populations and the ability to predict the impacts of anthropogenic activities of all types. With respect to modeling, more attention is needed on life table response experiments (Caswell, 1978, 1996a). The growing appreciation that marine mammals are sentinels to ecosystem health (Bossart 2006, 2007; Moore, 2008; Moore & Huntington, 2008) suggests the need for further study of the effects of climate change, stochastic environmental effects, and anthropogenic impacts.

While some of these can have direct impacts on marine mammal mortality, they all increase the stress response experienced by cetaceans, and there is a woeful lack of information about the impact of the stress response on marine mammals (Fair & Becker, 2000). It is likely that the most important impact of low-level anthropogenic impacts on marine mammals will be in the form of increased stress, and information is needed to elucidate the relationship between an increase in stress and the vital rates governing marine mammal population stability and growth. Additional research is also needed to enhance our understanding of stress on cetaceans in order to provide a scientific basis for management decision-making. Future research should concentrate on relating marine noise, particularly from anthropogenic sources, to adult female and juvenile survival. Additionally, the precision of cetacean population and vital rate estimation needs to be increased, likely necessitating better methods of data collection. With improvements in these areas, natural resource managers have a much higher probability of restoring cetacean populations to their pre-whaling levels.

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Table 1. A representative Leslie population projection matrix: To construct the matrix, populations are segregated into age-classes or life-stages for which both fecundity (F) and survival (S) are known. These are arrayed into a square matrix (A), with the fecundities in the top row of the matrix, and the survival rates occupying the subdiagonal. In Lefkovitch matrices, more matrix elements can be included to represent transitions between different life stages. Additionally, elements can be included on the diagonal to represent remaining in the same stage for the next time step in the model.

F₁	F₂	F₃	F₄	F₅	...
S₁	0	0	0	0	...
0	S₂	0	0	0	...
0	0	S₃	0	0	...
0	0	0	S₄	0	...
...

Table 2. Matrix parameterization for all species.

MATRIX CELL	TRANSITION	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
A ₁₁	Probability of remaining in the first stage.	0.000	0.000	0.000	0.000	0.000
A ₁₂	Probability of moving from the first stage to the second stage.	0.978	0.872	0.980	0.875	0.920
A ₁₃	Probability of moving from the first stage to the third stage.	0.000	0.000	0.000	0.000	0.000
A ₁₄	Probability of moving from the first stage to the fourth stage.	0.000	0.000	0.000	0.000	0.000
A ₂₁	Probability of the second stage contributing to the first stage.	0.004	0.000	0.000	0.000	0.000
A ₂₂	Probability of the second stage remaining in the second stage.	0.911	0.397	0.900	0.217	0.860
A ₂₃	Probability of the second stage contributing to the third stage.	0.074	0.603	0.075	0.885	0.080
A ₂₄	Probability of the second stage contributing to the fourth stage.	0.000	0.000	0.000	0.000	0.020
A ₃₁	Probability of the third stage contributing to the first stage.	0.113	0.148	0.600	0.179	0.000
A ₃₂	Probability of the third stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₃₃	Probability of the third stage remaining in the third stage.	0.953	0.585	0.901	0.115	0.800
A ₃₄	Probability of the third stage contributing to the fourth stage.	0.045	0.415	0.099	0.783	0.190
A ₄₁	Probability of the fourth stage contributing to the first stage.	0.000	0.083	0.600	0.192	0.335
A ₄₂	Probability of the fourth stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₄₃	Probability of the fourth stage contributing to the third stage.	0.000	0.000	0.000	0.000	0.830
A ₄₄	Probability of the fourth stage remaining in the fourth stage.	0.980	0.999	0.119	0.999	0.000

Table 3. Eigenanalysis results for all species: The killer whale, bottlenose dolphin, sperm whale, and humpback whale populations are increasing, with humpback whales achieving the most rapid growth rate. The North Atlantic right whale population, however, is declining.

Modeling Results					
SPECIES	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
DOMINANT EIGENVALUE	1.025	1.067	1.110	1.129	0.999
GROWTH RATE	0.025	0.064	0.104	0.121	0.000

Table 4. Sensitivity analysis for each matrix parameter for all species.
SENSITIVITIES

MATRIX CELL	TRANSITION	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
A ₁₁	Probability of remaining in the first stage.	0.000	0.000	0.000	0.000	0.000
A ₁₂	Probability of moving from the first stage to the second stage.	0.044	0.072	0.097	0.118	0.031
A ₁₃	Probability of moving from the first stage to the third stage.	0.000	0.000	0.000	0.000	0.000
A ₁₄	Probability of moving from the first stage to the fourth stage.	0.000	0.000	0.000	0.000	0.000
A ₂₁	Probability of the second stage contributing to the first stage.	0.361	0.000	0.000	0.000	0.000
A ₂₂	Probability of the second stage remaining in the second stage.	0.379	0.094	0.451	0.113	0.201
A ₂₃	Probability of the second stage contributing to the third stage.	0.567	0.104	1.260	0.116	0.279
A ₂₄	Probability of the second stage contributing to the fourth stage.	0.000	0.000	0.000	0.000	0.249
A ₃₁	Probability of the third stage contributing to the first stage.	0.369	0.096	0.144	0.077	0.000
A ₃₂	Probability of the third stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₃₃	Probability of the third stage remaining in the third stage.	0.579	0.131	0.456	0.102	0.637
A ₃₄	Probability of the third stage contributing to the fourth stage.	0.000	0.117	0.087	0.114	0.671
A ₄₁	Probability of the fourth stage contributing to the first stage.	0.000	0.585	0.014	0.465	0.084
A ₄₂	Probability of the fourth stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₄₃	Probability of the fourth stage contributing to the third stage.	0.000	0.000	0.000	0.000	0.127
A ₄₄	Probability of the fourth stage remaining in the fourth stage.	0.000	0.717	0.009	0.694	0.133

Table 5. Elasticity analysis for each matrix parameter for all species.
ELASTICITIES

MATRIX CELL	TRANSITION	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
A ₁₁	Probability of remaining in the first stage.	0.000	0.000	0.000	0.000	0.000
A ₁₂	Probability of moving from the first stage to the second stage.	0.042	0.059	0.119	0.091	0.028
A ₁₃	Probability of moving from the first stage to the third stage.	0.000	0.000	0.000	0.000	0.000
A ₁₄	Probability of moving from the first stage to the fourth stage.	0.000	0.000	0.000	0.000	0.000
A ₂₁	Probability of the second stage contributing to the first stage.	0.002	0.000	0.000	0.000	0.000
A ₂₂	Probability of the second stage remaining in the second stage.	0.336	0.034	0.316	0.022	0.173
A ₂₃	Probability of the second stage contributing to the third stage.	0.041	0.059	0.119	0.091	0.022
A ₂₄	Probability of the second stage contributing to the fourth stage.	0.000	0.000	0.000	0.000	0.006
A ₃₁	Probability of the third stage contributing to the first stage.	0.041	0.013	0.118	0.012	0.000
A ₃₂	Probability of the third stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₃₃	Probability of the third stage remaining in the third stage.	0.539	0.072	0.324	0.010	0.510
A ₃₄	Probability of the third stage contributing to the fourth stage.	0.000	0.046	0.002	0.079	0.127
A ₄₁	Probability of the fourth stage contributing to the first stage.	0.000	0.046	0.002	0.079	0.028
A ₄₂	Probability of the fourth stage contributing to the second stage.	0.000	0.000	0.000	0.000	0.000
A ₄₃	Probability of the fourth stage contributing to the third stage.	0.000	0.000	0.000	0.000	0.105
A ₄₄	Probability of the fourth stage remaining in the fourth stage.	0.00	0.671	0.000	0.615	0.000

Table 6. Calculated stable age distributions for all life stages and all species

Stable Age Distribution for All Life Stages and All Species					
LIFE STAGE	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
1	3.7	7.2	13.3	12.7	3.9
2	31.6	9.4	62.1	12.2	25.7
3	32.3	11.7	22.4	10.6	58.7
4	32.4	71.7	2.20	64.6	11.7

Table 7. Reproductive values for all life stages and all species

Reproductive Value for All Life Stages and All Species					
LIFE STAGE	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
1	27.6	20.8	16.9	19.6	19.3
2	29.0	25.5	19.2	25.2	21.0
3	43.4	28.3	53.6	26.0	29.1
4	0.00	25.4	10.3	29.2	30.6

Table 8. Loop analysis of life histories of all species: In all species except the sperm whale, the small loop including reproductive female survival demonstrated the highest elasticity. These findings emphasize that adult female survival is essential to cetacean population growth rates. The highest elasticity value determined in the sperm whale loop analysis was represented by the loop containing young female survival, fecundity, and calf reproduction and growth. This result implies that young reproductively active female whales are very important to the stability of sperm whale population numbers.

LOOP	KILLER WHALE	BOTTLE-NOSE DOLPHIN	SPERM WHALE	HUMP-BACK WHALE	N. ATL. RIGHT WHALE
Survival of older female	0.000	0.671	2.34E-5	0.615	1.33E-7
Survival of younger female	0.539	0.072	0.324	0.010	0.510
Survival of juvenile female	0.336	0.035	0.316	0.022	0.173
Calf → Juvenile → Calf	0.003				
Calf → Juvenile → Young Female → Calf	0.122	0.040	0.353	0.036	0.056
Calf → Juvenile → Young Female → Old Female → Calf		0.182	0.007	0.317	0.113
Female with calf → Mature female → Female with calf					0.210

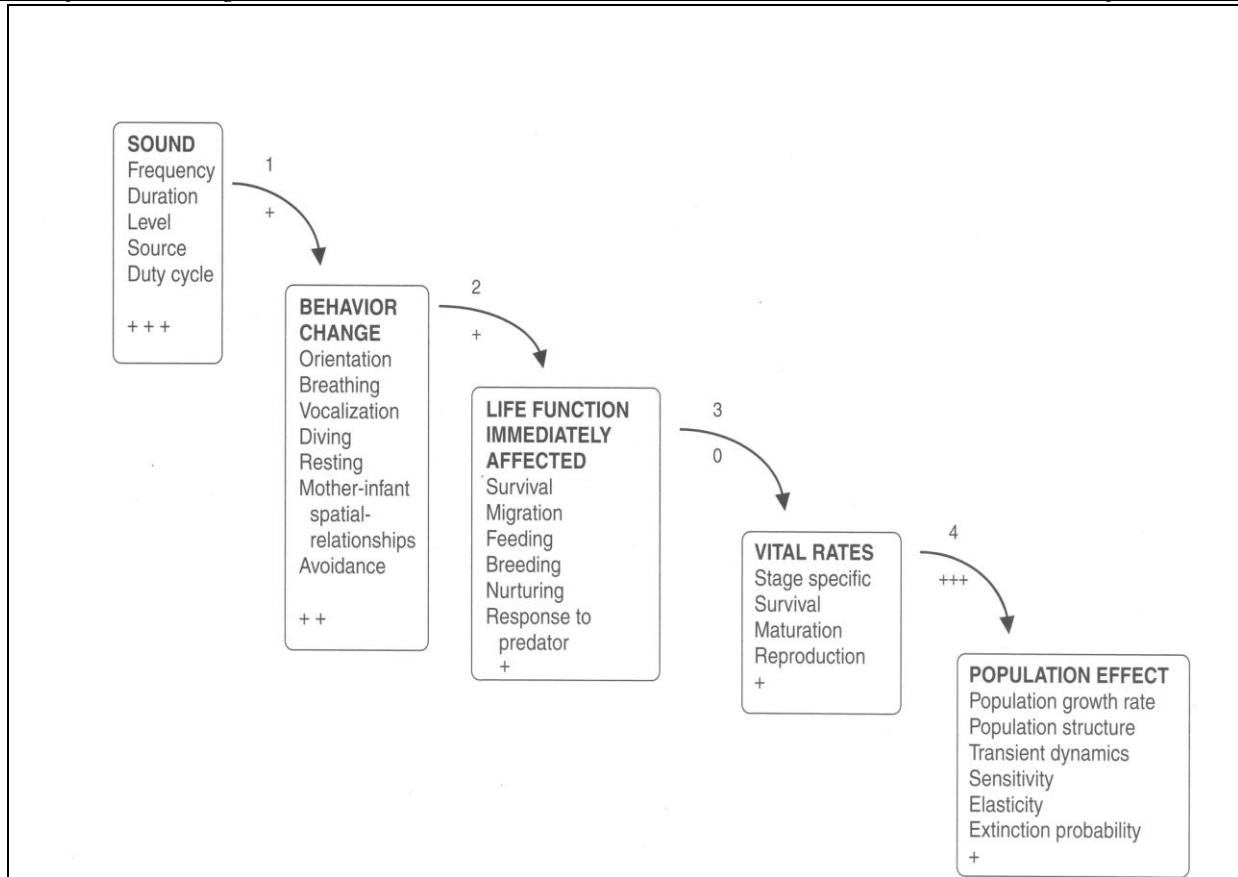


Figure 1. A model for the “Population Consequences of Acoustic Disturbances (PCAD)” (NRC 2005); PCAD is a heuristic model that was created as a first attempt to trace acoustic disturbances through the life history of a marine mammal and then to determine the consequences to the population. Our objective was to focus attention on the probable proximate impacts of anthropogenic impacts in the marine environment on marine mammal population sustainability and growth. These impacts are integrated through a suite of hierarchical variables with currently poorly understood or undefined transfer functions between the variables. We attempted to model the current state of knowledge of these transfer functions, primarily the relationship(s) between life functions such as survival, migration, feeding, breeding, etc., and vital population rates.

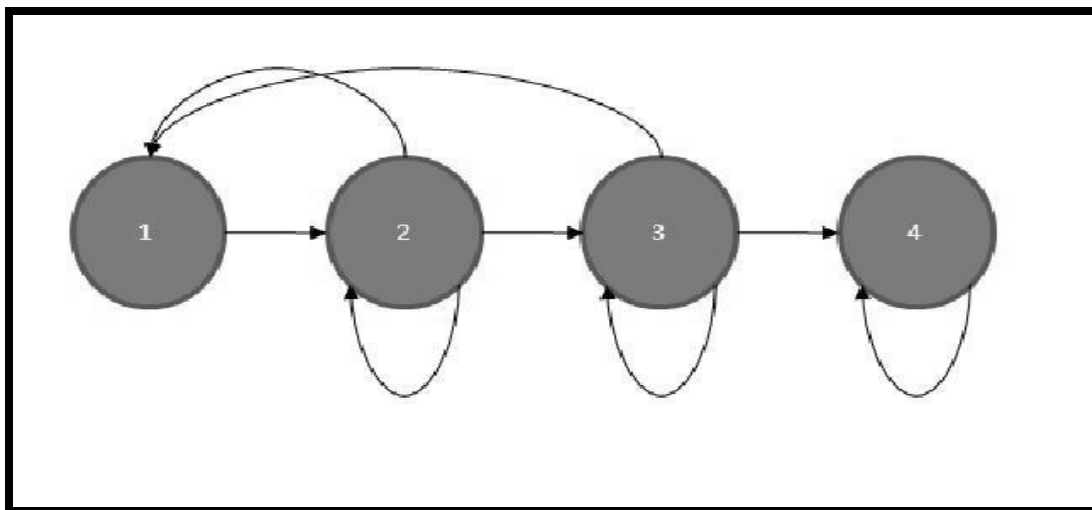


Figure 2. Generalized life history diagram; there are eight possible transitions possible in this diagram, not all of which were modeled for every species. Transitions for which no data were available were not parameterized in the individual species’ models.

- Transition 1: Probability of survival from Stage 1 to Stage 2;
- Transition 2: Probability of survival from Stage 2 to Stage 3;
- Transition 3: Probability of survival from Stage 3 to Stage 4,
- Transition 4: Probability of remaining in Stage 2;
- Transition 5: Probability of remaining in Stage 3;
- Transition 6: Probability of remaining in Stage 4;
- Transition 7: Fecundity of Stage 2 contributing young to Stage 1
- Transition 8: Fecundity of Stage 3 contributing young to Stage 1

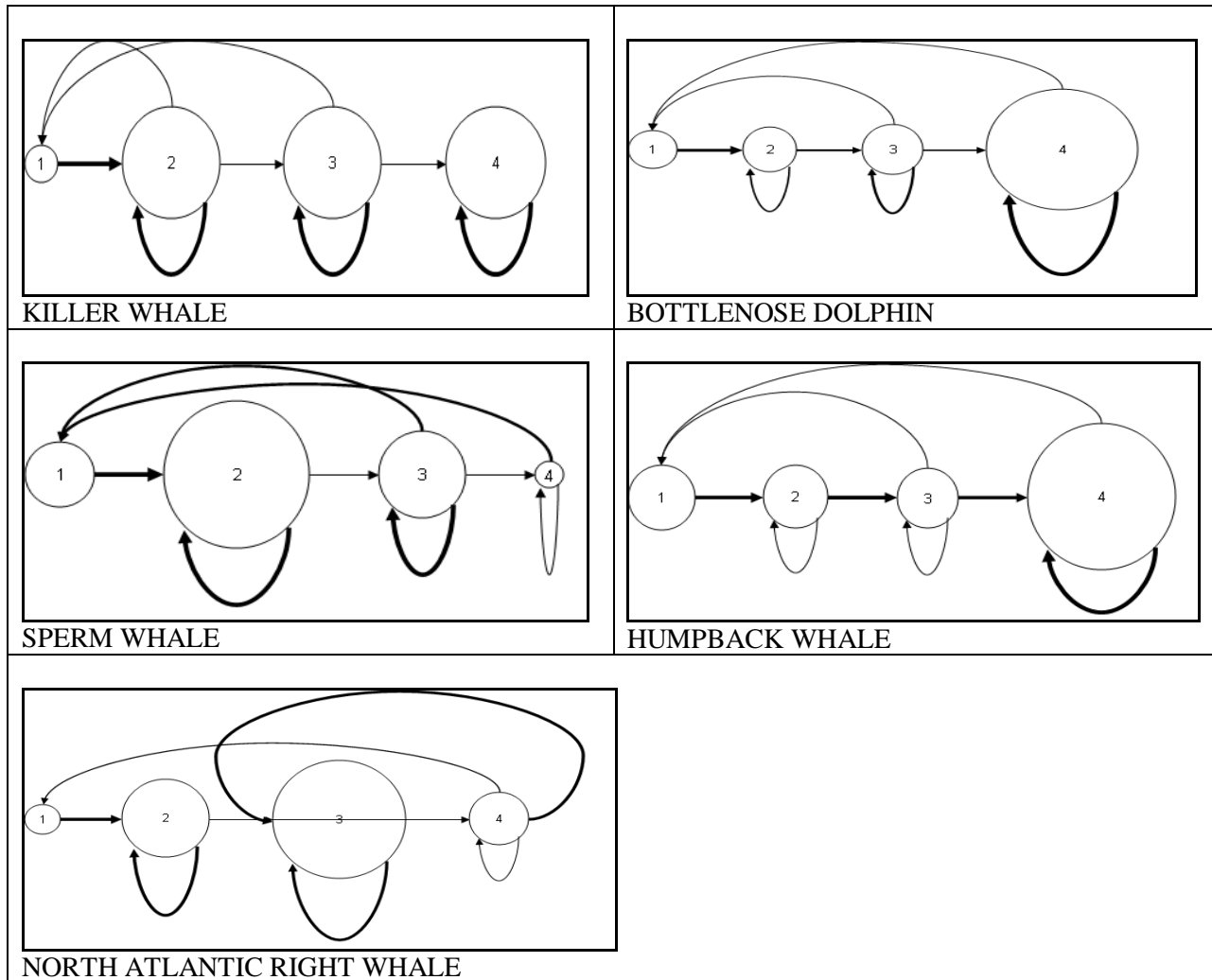


Figure 3. Life history diagrams of the five cetaceans included in this analysis. The width of the transition arrows are proportional to the probability of the particular transition in the population projection matrix, and the size of the circles is proportional to the fraction of that life history stage in the stable age distribution. For the killer whale the four stage classes were yearlings (first-year animals), juveniles (immature individuals over one year of age), mature females, and senescent females. For the bottlenose dolphin the stage classes were calves, juvenile females (1-9 years of age), young breeding females (10-20 years of age), and older breeding females (> 20 years of age). The sperm whale stages were similar to those used for the killer whale, i.e. yearlings, juveniles, mature females, and senescent females. For humpback whales the stages were similar in structure, but not in age category, to those used for the bottlenose dolphin, i.e. calves, juvenile females (1.5-3.5 years of age), young breeding females (4.5-9.5 years of age), and older breeding females (10.5-34.5 years of age). The North Atlantic right whale population model was considerably different from the others. Stage 1 was calves, Stage 2 was juveniles, Stage 3 was reproductively capable females, and Stage 4 was females with calves. This model is similar to that used by Fujiwara and Caswell (2001), except that they included another stage representing death. Fecundity was represented by flows from Stages 2 and 3 to Stage 4.